

# Establishment of a new genus for *Parastenocaris itica* (Copepoda, Harpacticoida) from El Salvador, Central America, with discussion of the *Parastenocaris fontinalis* and *P. proserpina* groups

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**ABSTRACT.** A new genus of Parastenocarididae is described from the Neotropical region. *Iticocaris* gen. nov. is established to include *Parastenocaris itica* Noodt, 1962. *Iticocaris* gen. nov. is defined by the following characters: 1) male leg 3 with 2-segmented exopod; 2) first exopodal segment short and rectangular; 3) thumb hypertrophic, longer than the second exopodal segment and inserted on the distal edge of exopod segment 1, occupying the whole distal margin; 4) exopod 2 or apophysis strongly sclerotized, articulated with the exopod segment 1 on its inner margin and curved against the thumb, forming a strong forceps; 5) leg 4 endopod without dimorphism in shape and size vs. minor dimorphism in ornamentation; 6) leg 5 with three setae and 7) lack of the anterolateral furcal seta II. The new genus is monotypic, represented by *Iticocaris itica* (Noodt, 1962) comb. nov., from El Salvador, Central America. A close relationship is hypothesized between *I. itica* and the genus *Brasilibathynelloccaris* Jakobi, 1972, the males of which both share the forceps-like elongated apophysis.

**KEYWORDS.** Freshwater, Neotropics, Parastenocarididae, Taxonomy.

**RESUMO.** Proposta de um novo gênero para *Parastenocaris itica* (Copepoda, Harpacticoida) de El Salvador, América Central e discussão dos grupos *Parastenocaris fontinalis* e *P. proserpina*. Um novo gênero de Parastenocarididae é proposto para a Região Neotropical para incluir *Parastenocaris itica* Noodt, 1962. *Iticocaris* gen. nov. é diagnosticado pela presença dos seguintes caracteres: 1) toracópodo 3 do macho com exópodo bissegmentado; 2) primeiro segmento exopodal curto e retangular; 3) “thumb” hipertrófico, mais longo que o segundo segmento do exópodo e inserido na margem distal do exópodo 1, ocupando toda a margem distal do segmento; 4) exópodo 2 ou apófise fortemente esclerotizado, articulado com o exópodo 1 em sua margem interna e curvado contra o “thumb”, formando um forte fórceps; 5) endópodo do toracópodo 4 sem dimorfismo sexual quanto à forma e tamanho vs. discreto dimorfismo quanto à ornamentação; 6) toracópodo 5 com três cerdas e 7) furca sem a cerda anterolateral II. O novo gênero é monotípico, sendo representado por *Iticocaris itica* (Noodt, 1962) comb. nov., proveniente de El Salvador na América Central. É hipotetizado que *I. itica* e o gênero *Brasilibathynelloccaris* Jakobi, 1972 sejam próximos filogeneticamente, possuindo os machos de ambos os gêneros uma apófise alongada e “thumb” formando uma estrutura similar a um fórceps.

**PALAVRAS-CHAVE.** Água doce, Neotropical, Parastenocarididae, Taxonomia.

The family Parastenocarididae (Copepoda, Harpacticoida) is a diverse group of freshwater interstitial microcrustaceans, with approximately 250 described species worldwide (SCHMINKE, 2010). Until recently, this family was represented by only a few accepted genera: *Parastenocaris* Kessler, 1913; *Forficatocaris* Jakobi, 1969; *Paraforficatocaris* Jakobi, 1972; *Potamocaris* Dussart, 1979; *Murunducaris* Reid, 1994, and *Simpliacaris* Galassi & De Laurentiis, 2004. This view has gradually changed, with new genera being established or revalidated in the recent literature (CORGOSINHO & MARTÍNEZ ARBIZU, 2005; CORGOSINHO *et al.*, 2010; COTTARELLI *et al.*, 2010; GALASSI & DE LAURENTIIS, 2004; SCHMINKE, 2008, 2009; KARANOVIC & COOPER, 2011).

It is therefore, undeniable that the most diverse genus *Parastenocaris* is a “taxonomic repository” being composed by species belonging to different phylogenetic lineages, not closely related to each other. Therefore this genus as a whole is in urgent need of profound revision. The taxonomic confusion around the type-genus of the family is further complicated by the subsequent synonymies established, as for example for the genus *Biwaecaris* Jakobi, 1972 which has been synonymized

with *Parastenocaris* by REID (1995). Moreover, according to SCHMINKE (2010), it is not unlikely that members of *Brinckicaris* Jakobi, 1972, *Enckellicaris* Jakobi, 1972, and *Oshimaensicaris* Jakobi, 1972 should be moved to the genus *Parastenocaris*, entering the *Parastenocaris brevipes* group, as defined by REID (1995), and subsequently supported by GALASSI & DE LAURENTIIS (2004) and KARANOVIC (2005, 2006). For a discussion of the taxonomy within the genus *Parastenocaris* see REID (1995), GALASSI & DE LAURENTIIS (2004) and KARANOVIC & LEE (2012).

In the last few years, Parastenocarididae has undergone significant systematic and taxonomic modifications. Three new genera, *Monodicaris* Schminke, 2009, *Asiacaris* Cottarelli, Bruno & Berera, 2010, *Dussartstenocaris* Karanovic & Cooper, 2011 and two new subfamilies have been recently established (SCHMINKE, 2010). Furthermore, CORGOSINHO & MARTÍNEZ ARBIZU (2005) and CORGOSINHO *et al.* (2007) proposed the adoption of all the genera described by JAKOBI (1972a,b) which are available according to the ICZN (1999) (articles 11.5, 13, 67.8 and 68), pending a deep revision for assessing the monophyly of these genera. Towards a better understanding of the systematics of the family as

a whole, *Remaneicaris* Jakobi, 1972 was redefined by CORGOSINHO & MARTÍNEZ ARBIZU (2005), *Siolicaris* Jakobi, 1972 was redefined by CORGOSINHO *et al.* (2012), while SCHMINKE (2008) synonymized *Cafferocaris* Jakobi, 1972 with *Kinneicaris* Jakobi, 1972, arguing in favor of the monophyly of *Kinneicaris*. Recently, *Paraforficatocaris* and *Pararemaneicaris* Jakobi, 1972 were relegated to junior synonyms of *Brasilibathynellocaris* Jakobi, 1972 when their type species were transferred to this genus (CORGOSINHO *et al.*, 2010). The former *Pararemaneicaris santaremensis* (Noodt, 1963) is temporarily accommodated into *Parastenocaris sensu lato* as *Parastenocaris santaremensis* Noodt, 1963. Neotropical parastenocaridids are highly diversified and split into several monophyletic endemic groups, *viz.*, *Potamocaris*, *Forficatocaris*, *Murunducaris*, *Brasilibathynellocaris*, *Remaneicaris*, and the *Parastenocaris columbiensis* group proposed by NOODT (1972). Although 77 species are described from the neotropics, the taxonomic diversification in this area is likely higher than presently known. For example, samples taken with different methods have provided several new species for a single sampling site (see REID, 1993a,b; CORGOSINHO & MARTÍNEZ ARBIZU, 2005; CORGOSINHO *et al.*, 2007). It is not uncommon to find 3 - 4 new species belonging to different parastenocaridid genera in samples taken by the Karaman-Chappuis method (CHAPPUIS, 1942), or other sampling devices, such as corers and kick nets.

Considering the biogeographical history of the Neotropical region and the high diversity of other taxa in this area, the fauna of parastenocaridids is potentially richer in the Central America, probably including representatives coming also from both the Holarctic region and from South America.

As a step towards a revision of Neotropical parastenocaridids, a new genus is proposed herein for *Parastenocaris itica* from Central America, and its phylogenetic position within the family is briefly discussed.

## MATERIALS AND METHODS

Specimens have been analyzed from the Noodt's collection deposited at the Senckenberg am Meer, Dept. DZMB (Deutsches Zentrum für Marine Biodiversitätsforschung; "German Centre for Study of Marine Biodiversity"). For the description of *P. itica*, NOODT (1962) did not fix the holotype, only mentioned which samples came from the type-locality and postulated other locations, where *P. itica* was plausibly present. He mentioned 5 females and 8 males from the type-locality. However, our inspection of his collection revealed only 6 male and 3 females in the slides from the type-locality. Only a single slide containing 2 females and 2 males (some of them dissected) was properly labeled as *Parastenocaris itica* Noodt, 1962 (Box 7, slide 10, S332 taken from Rio Acehuafa, El Salvador).

In the past, it was a common practice, adopted also by Noodt and other researchers, to mount several

specimens on a single slide, sometimes of different sexes, and with more than one specimen dissected and mounted together. Following the ICZN (1999) recommendation 73F, it is possible that the nominal species-group taxon was based on more than one specimen from the sample S64. In order to avoid designation of syntypes for *P. itica*, a dissected male from a multi-specimen preparation has been selected as lectotype (box 6, slide 5, S64). The illustration of the habitus is based on an undissected male from the sample S332. The identification of all other specimens was confirmed by direct comparison with the lectotype (for males) and with the original illustrations (for females and males) as given by NOODT (1962).

Drawings were made under a microscope, fitted with Nomarski interference contrast optics and a drawing tube, at 400x and 1000x magnification.

The terms furca and telson are used according to SCHMINKE (1976). The term thumb refers to the outer spine of the male swimming leg 3. This structure is homologous to the outer spine of the first segment of leg 3 exopod of the male copepodite V and females. The term apophysis refers to the second segment of swimming leg 3 exopod, which appears to be fused to the first exopodal segment in most species of Parastenocarididae. For details of the development of swimming leg 3 in males and the homologization of structures, see GLATZEL (1991). The terms seta, setules, spines and spinules are used according to HUYS & BOXSHALL (1991). Terminology and homologies of maxillary and maxillipedal structures follow FERRARI & IVANENKO (2008). The term "groundpattern" is used in the acceptance of the German term "Grundmuster" (Ax, 1984).

When necessary, Noodt's collection was examined to compare seemingly similar features in *P. itica*, *Brasilibathynellocaris* species and other Parastenocarididae.

Abbreviations used: A1, antennule; A2, antenna; Ae, aesthetasc; ap, apomorphy; Cph, cephalothorax (includes cephalon and thoracic somites 1 and 2); enp, endopod; enp-1-3, endopodal segment 1-3; exp, exopod; exp-1-3, exopodal segments 1-3; Md, mandible; Mx1, Maxillule; Mx2, Maxilla; Mxp, maxilliped; P1-P6, swimming legs 1-6; pl, plesiomorphy.

## SYSTEMATICS

### Parastenocarididae, Fontinalicariidinae *Itiocaris* gen. nov.

Type species: *Itiocaris itica* (Noodt, 1962), by monotypy.

Synonyms: *Parastenocaris itica* Noodt, 1962; *Remaneicaris itica* Jakobi (1972).

Diagnosis. 8-segmented A1 in male (pl) and 7-segmented A1 in female (pl). Male A1 haplocer (pl).

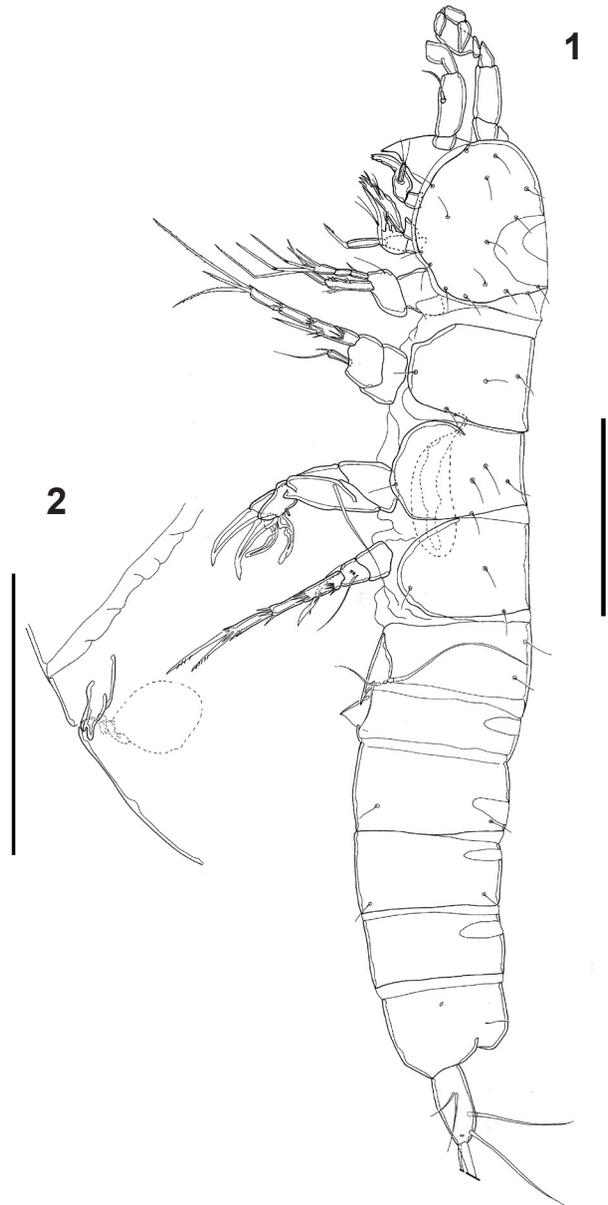
Basis of Mx2 with 2 endites, proximal endite with 1 seta (pl), distal endite with 3 elements (pl), one of them transformed into a serrated spine (pl); proximal endopodal segment drawn out into a claw, distal endopodal segment with 2 setae. Basis of P1 without sexual dimorphism (pl); enp not sexually dimorphic (pl). P2 enp without marked sexual dimorphism (pl). Male P3 with 2-segmented exp (ap). Exp-1 short, rectangular (ap), with a large tube pore on the inner margin (ap). Thumb hypertrophic longer than exp-2 (ap) and inserted on the distal edge of exp-1 (ap), occupying the whole distal margin (ap). Exp-2 or apophysis strongly chitinized (ap), articulating with exp-1 on its inner margin (ap) due to the hypertrophy of the thumb and its distal insertion; strongly curved against the thumb (ap) to form a strong forceps-like structure (ap); smooth on the inner margin and with a pronounced invagination in its proximal third (ap), on the outer concave margin. Presence of an uncinuate process of unclear nature (rudimentary endopod?) on the inner margin of basis (ap). P4 enp not sexually dimorphic in shape (ap) but dimorphic in minor ornamentation. P5 triangular, with an outer basal seta and 2 setae located close to the inner spiniform process (pl?). Caudal rami with anterolateral setae (setae I, III) located close to the dorsal seta (seta VII, pl); seta II absent (pl). P6 represented by a naked opercular plate covering the genital opening (pl).

Type material. Lectotype, Wilhelmshaven, box 6 (slide 5, S64; dissected male) (examined). Paralectotypes, box 6 (slide 5, S64; 1 undissected male), box 6 (slide 6, S64; 2 dissected males and 2 undissected males), box 6 (slide 7, S64; 1 dissected female and 1 undissected female) (examined). Additional non-type material from box 7 (slide 10, S332; 2 females and 2 males).

Type locality. Large “Barranco” Tovar, near the Instituto Tropical in San Salvador, El Salvador. Groundwater samples were taken in a coarse sand ground, at a depth of 20 cm.

Etymology. The generic name combines the specific epithet “*itica*” of the type species and the ancient Greek substantive for shrimp, *καρίς* (caris).

Description. Male, length 440  $\mu\text{m}$  (measured by Noodt). Rostrum not fused to cephalothorax, with wide base and two sensilla on tip. Cephalothorax and Urs-2-4 with dorsal integumental windows (Fig. 1). Patterns of sensilla as in Fig. 1. Telson smooth, anal operculum smooth and convex (Fig. 1), as in female. Furca (Figs 1, 21) with distal pore and 6 setae; setae I and III located proximal to the seta VII; seta II absent. A1 8-segmented and prehensile (Fig. 3); armature, beginning by the proximal segment: 0/6/4/1/5+ae/3/2/9+ae. A2 as in female (Figs 16, 17), with allobasis; 1-segmented exp, with 1 seta, and 1-segmented enp bearing 7 setae. Labrum (Fig. 4) triangular, with a distal serrated zone. Md coxal gnathobasis (Fig. 5) with tooth-like attenuations and 1 seta, mandibular palp 1-segmented with 2 distal setae. Mx1 praecoxal arthrite (Fig. 6) with 5 elements (1

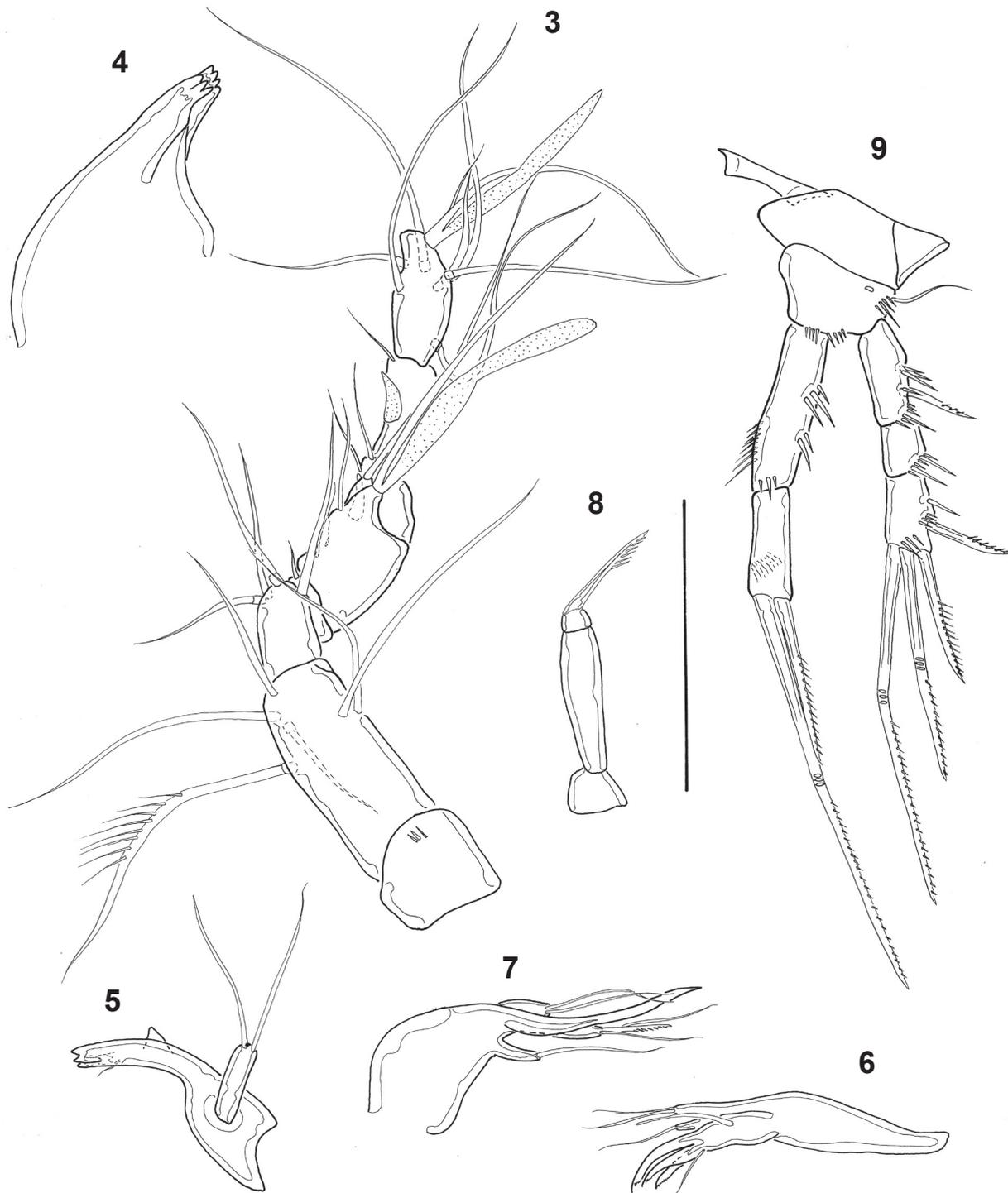


Figs 1, 2. *Iticocaris itica* (Noodt, 1962): 1, male, lateral habitus (Noodt collection, Box 7, slide 10; S332); 2, female, genital field, (Noodt collection, Box 6, slide 7; S64). Scale bar: Fig. 1, 100  $\mu\text{m}$ ; Fig. 2, 40  $\mu\text{m}$ .

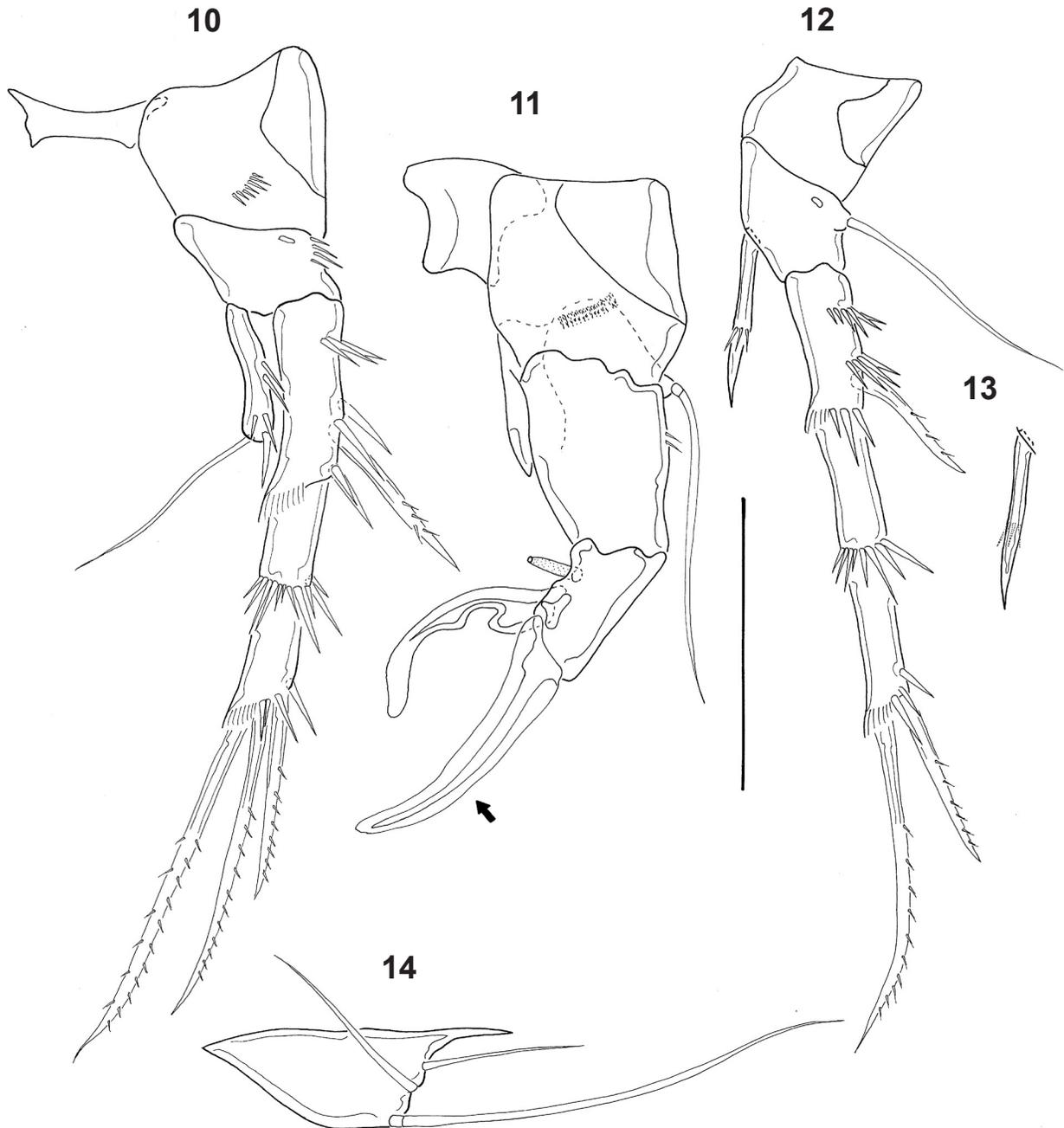
seta on dorsal surface, 3 claw-like pinnate spines and 1 slender seta), coxa with 1 seta, basis with 2 endites with 1 and 2 setae respectively. Mx2 basis (Fig. 7) with 2 endites, proximal endite with 1 seta, distal endite with three elements, one of them transformed into a serrated spine; proximal endopodal segment drawn out into a claw, distal endopodal segment with 2 setae. Mxp (Fig. 8) subchelate, composed of syncoxa, basis, 1-segmented endopod, and 1 claw-like apical seta. P1 (Fig. 9) coxa unarmed; basis with 1 outer seta, outer row of spinules, and distal row of small spinules; enp-1 of the same size as the first 2 exopodal segments; exp 3-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with 2 outer spines and 2 geniculate setae; enp 2-segmented, enp-1 with 2 rows of large spinules on outer margin and an

inner row of small spinules distally, enp-2 with 1 outer spine, 1 geniculate seta, and a posterior hyaline frill. P2 (Fig. 10) coxa unarmed, with posterior row of spinules; basis lacking outer seta but ornamented with 1 row of spinules on outer margin; exp 3-segmented, exp-1 with long outer spine and with hyaline frill on inner margin; exp-2 lacking armature and with row of spinules of unequal size; exp-3 with 3 setae, a distal hyaline frill on the inner corner, and a row of long spinules on the outer

margin; enp 1-segmented, with distal seta, distal spinule, 2 subdistal spinules, and 2 outer spinules in its medial portion. P3 (Fig. 11) coxa unarmed, with posterior row of spinules; basis large, with an inner uncinuate process of unclear nature (enp remnant?); exp 2-segmented, exp-1 short, rectangular, and with a large tube pore on inner margin, thumb hypertrophied (arrowed), longer than exp-2 and inserting on the distal edge of exp-1, occupying the whole distal surface; exp-2 or apophysis strongly



Figs 3-9. *Iticocaris itica* (Noodt, 1962), lectotype, Noodt collection, Box 6, slide 6; S64: 3, male A1; 4, labrum; 5, mandible; 6, maxillule; 7, maxilla; 8, maxilliped; 9, P1. Scale bar: 30  $\mu$ m.

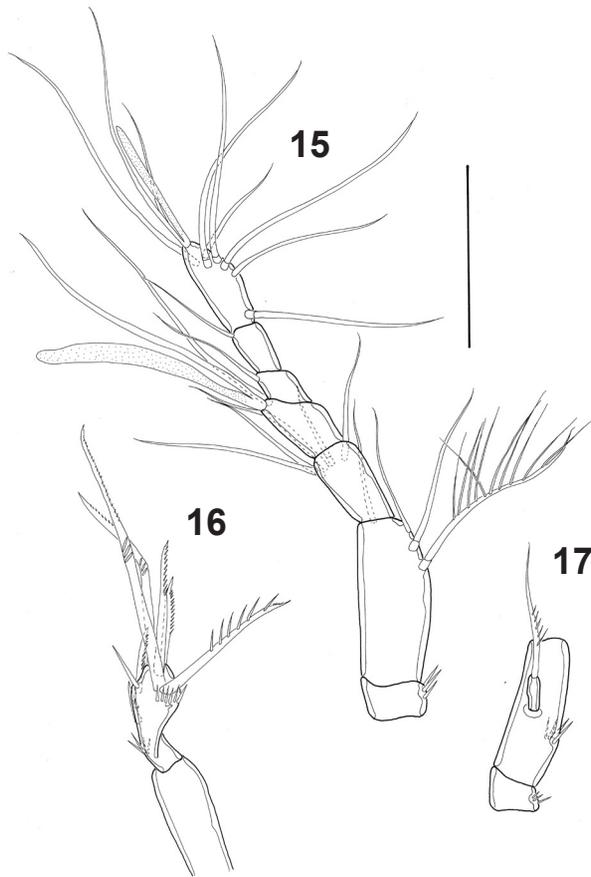


Figs 10-14. *Iticocaris itica* (Noodt, 1962), lectotype, Noodt collection, Box 6, slide 6: 10, male P2; 11, P3; 12, P4; 13, P5. Arrow indicates thumb. Scale bar = 30  $\mu$ m.

sclerotized and curved towards thumb, to form a kind of strong, cheliform forceps; additionally, exp-2 smooth on the inner margin and with a pronounced invagination at proximal third of outer concave margin, articulating with the exp-1 on its inner margin of latter due to the hypertrophy of the thumb. P4 (Fig. 12) coxa unarmed; basis with outer seta and outer pore; exp 3-segmented, exp-1 with outer spine, exp-2 lacking armature and with row of distal spinules (smaller on inner margin), exp-3 with 2 setae and row of distal spinules on outer margin; enp spiniform (Figs 12, 13), straight and with a transverse row of spinules in its distal third (probably representing the border between the enp and fused distal

seta); no sexual dimorphism in shape and only minor dimorphism in ornamentation. P5 triangular (Fig. 14), with an outer basal seta and 2 other setae between it and an inner spiniform process.

Female, length 443  $\mu$ m (measured by Noodt). Sexually dimorphic in A1, P2, P3 and genital double-somite. Cephalothorax and Urs-2-4 with dorsal integumental windows. Telson smooth, anal operculum smooth and convex (Fig. 21). A1 7-segmented (Fig. 15); armature, beginning with proximal segment: 0/4/5/2+ae/1/1/9+ae. A2 (Figs 16, 17) with allobasis, 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. P2 (Fig. 18) exp not sexually dimorphic;



Figs. 15-17. *Iticocaris itica* (Noodt, 1962): 14, female A1 (paralectotype, Noodt collection, Box 6, slide 7); 15, 16: male A2 (syntype, Noodt collection, Box 6, slide 6). Scale bar: 30  $\mu$ m.

enp with slight sexual dimorphism (slender and less ornamented in female). P3 (Fig. 19) coxa unarmed; basis with a long outer seta and an outer pore; enp represented by a short segment with 2 distal spinules; exp 2-segmented; exp-1 with an outer spine and an inner row of spinules distally; exp-2 with 2 setae, an inner hyaline frill, and an outer row of spinules. P4 (Fig. 20) showing no sexual dimorphism in shape, but less ornamented than in the male. P6 (Fig. 2) consisting of paired unarmed genital flaps; U-shaped genital field.

## DISCUSSION

*Parastenocaris itica* cannot be satisfactorily accommodated into any known LANG'S (1948) groups of Parastenocarididae, or any other genus proposed in the family. *Iticocaris* gen nov. is herein established to accommodate this species and a detailed discussion supporting the establishment of a new taxonomic rank for this species is offered.

The phylogenetic position of *P. itica* instigated several discussions. According to NOODT (1962), the description of this species fitted the diagnosis given by LANG (1948) for the group of *Parastenocaris fontinalis* Schnitter & Chappuis, 1915. However, comparison with the other species from this group revealed no particular

similarity to any of them. Rejecting an assignment to this species group, NOODT (1962) instead hypothesized a possible close affinity with the group of *Parastenocaris panamericana* Noodt, 1962 (now *Brasilbathynellocaris*: see CORGOSINHO *et al.*, 2010) due to similarities in P2, enp of female P3, female P4, P5, furca, and perhaps male P3; however, NOODT (1962) also remarked upon the lack in *P. itica* of the special characters observed in the P4 of males in this group (NOODT, 1962).

JAKOBI (1972a) included *P. itica* in *Remaneicaris*, which he defined by the presence of a male P3 exp long, thin, inwardly bent at a right angle or less, and frequently possessing an S-shaped thumb. These feature are, however, widespread in the family. Even within the genus *Remaneicaris* they appear independently in different monophyletic groups (P. H. C. Corgosinho, unpubl. data) and thus do not constitute part of the ground pattern of *Remaneicaris*. Rather, as was already noted by CORGOSINHO & MARTÍNEZ ARBIZU (2005), *P. itica* could not be included in *Remaneicaris* due to its lack of the following autapomorphies of that genus: outer distal seta of P4 exp-3 located subdistally, intercoxal sclerite of P5 absent, and a medially inserted outer spinule present on exp-2 and exp-3 of legs 2 and 4.

Recently WELLS (2007) listed *P. itica* as *Remaneicaris itica* but with no supporting for this classification.

**The inclusion of *Iticocaris* within Fontinalicaridinae.** SCHMINKE (2010) formally established Parastenocaridinae Chappuis, 1940 and Fontinalicaridinae Schminke, 2010 within Parastenocarididae. In accordance with 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.

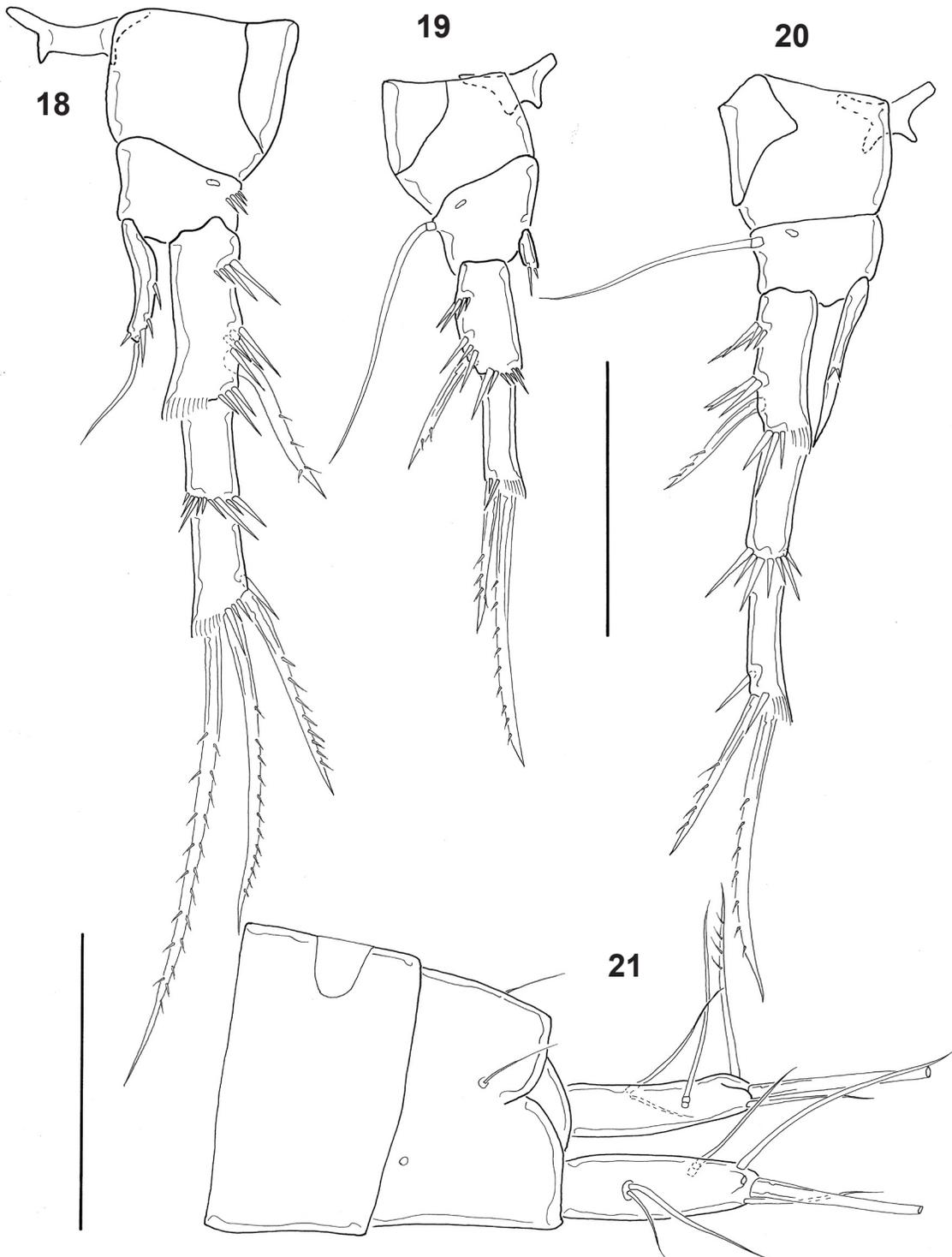
However, the Fontinalicaridinae is considered a monophyletic taxon as demonstrated by the two following autapomorphies: enp of female P3 lacking a terminal seta (appearing as a relatively short element with a rounded apex), and the shape of the female genital field (a roundish structure as broad as high). An additional diagnostic but plesiomorphic character is the clasping mechanism of the A1 of the male, in which segment 7 is not sickle-shaped and the mechanism involves the last three segments forming a coil with terminal segment 8 pointing laterally (SCHMINKE 2010; *ipsis litteris*). Such a coiled male A1 is a condition found only in *Remaneicaris*, and in the species assigned to the Fontinalicaridinae.

According to SCHMINKE (2010), the Parastenocaridinae may also be a monophyletic group as suggested by the spinule row located medially at the basis of male P4 enp and by the arrangement of the furcal setae (no gap between the outer setae I, II, III, and the dorsal seta VII). An additional apomorphic diagnostic character is the presence of a unique male A1 geniculation. While

clasping the female, segments 5 and segment 7 of the male A1 form a functional unit. "Segment 5 is dilated and has an inner conical protrusion proximally, segment 7 is sickle-shaped (the distal inner corner being extended into an apophysis) and can, like the blade of a pocket-knife, be folded back onto the fifth segment. In this position terminal segment 8 points medially" (SCHMINKE, 2010:345).

SCHMINKE (2010) considered *Remaneicaris* as belonging to the Parastenocaridinae. However, we hypothesize that *Remaneicaris* is the basalmost group within the entire family, as evidenced by the presence of many plesiomorphies (CORGOSINHO *et al.*, 2007).

*Iticocaris* gen. nov. does not possess all the diagnostic characters shared by members of the presently known Fontinalicaridinae, but it can be easily



Figs 18-21. *Iticocaris itica* (Noodt, 1962), paralectotype, Noodt collection, Box 6, slide 7: 17, female P2; 18, P3; 19, P4; 20, telson with furca and preceding urosomite. Scale bars: Figs 18-20, 30  $\mu$ m; Fig. 21, 75  $\mu$ m.

accommodated within this subfamily due to the presence of the same coiled type male A1, the reduced P3 enp of the female accompanied by the loss of its distal seta, and the roundish female genital field.

**A critical analysis of Parastenocarididae groups of LANG (1948).** A superficial comparison of LANG'S (1948) system with SCHMINKE'S (2010) proposed subfamilial division quickly shows that LANG'S (1948) species groups of Parastenocarididae are supported by weak diagnostic characters, some based on observational errors or symplesiomorphies. The likely outcome of this is the establishment non-monophyletic groups.

A comparison of the *Parastenocaris fontinalis* group, as it was proposed by LANG (1948), with the list of species included in each subfamily by SCHMINKE (2010:350-352, Table 1) shows that not all species included by LANG (1948) within the *Parastenocaris fontinalis* group are closely related to each other. In fact, only *Fontinalicaris fontinalis* (Schnitter & Chappuis, 1915) and *Parastenocaris aquaeductus* Chappuis, 1925 are clearly attributable to the subfamily Fontinalicaridinae. The remaining species, *viz.*, *Entzicaris entzi* (Török, 1935), *Pannonicaris aedes* (Hertzog, 1938), and *Parastenocaris similis* Török, 1935 are typical Parastenocaridinae.

The problem in LANG'S (1948) system of distantly related species composing artificial groups can also be observed in the group of *Parastenocaris proserpina* Chappuis, 1938, among the species of which *Proserpinicaris nollii* (Kiefer, 1938) and *Lacustricaris budapestiensis* (Török, 1935) belong to the Parastenocaridinae whereas *Proserpinicaris cantabrica* (Chappuis, 1937), *Proserpinicaris proserpina* and *Proserpinicaris phyllura* (Kiefer, 1938) belong to the Fontinalicaridinae. Within the group of *Parastenocaris minuta* Chappuis, 1925, *Pannonicaris pannonicus* is the sole representative of the Fontinalicaridinae.

A strict application of the system proposed by LANG (1948) to some genera, such as *Simplicaris*, *Monodicaris*, *Kinnecaris*, *Asiacaris* and *Dussartstenocaris* Karanovic & Cooper, 2012 reveals that each genus can be accommodated within the Langian system. *Simplicaris* could be easily integrated within the *Parastenocaris minuta* group, *Monodicaris* within the *P. brevipes* group, *Kinnecaris* within *P. muscicola* group, *Asiacaris* could tentatively be included within the *P. nana* group and *Dussartstenocaris* within the *P. fontinalis* group instead of *P. minuta* group as proposed by KARANOVIC & COOPER (2011)

Although it is possible that some of these genera will eventually prove to be junior synonyms of some JAKOBI'S (1972) genera after a phylogenetic analysis at the generic level [classification of JAKOBI (1972) is based on an orbital system which similar complex structures are not considered *a priori* homologous to each other, but rather the result of convergence or parallelism within evolutionary trends (CORGOSINHO &

MARTÍNEZ ARBIZU, 2005)], we regard it as an advance that authors have recently rejected Lang's system in favor of establishing a more stable one supported by clear diagnostic characters.

**Rejection of *Parastenocaris fontinalis* group of LANG (1948).** *Iticocaris itica* can be well accommodated within LANG'S (1948) *Parastenocaris fontinalis* group on the basis of the 1-segmented P2 enp and the lack of sexual dimorphism of the P4. However, MARTÍNEZ ARBIZU (1997) regarded as useless these two diagnostic characters for the *Parastenocaris fontinalis* group. Within this group, even in *Fontinalicaris fontinalis* the P4 enp is sexually dimorphic. In fact, a sexually dimorphic enp in P4 enp is considered an autapomorphy of the Parastenocarididae, having being lost independently more than once within this family (MARTÍNEZ ARBIZU & MOURA, 1994). A 1-segmented P2 enp is a symplesiomorphy for all parastenocaridids (MARTÍNEZ ARBIZU & MOURA, 1994; MARTÍNEZ ARBIZU, 1997) and cannot be used to endorse the inclusion of any species within the *Parastenocaris fontinalis* group. The presence of a 2-segmented P2 enp in the group of *Parastenocaris staheli* Menzel, 1916 is doubtful (LANG, 1948).

Because of these difficulties, MARTÍNEZ ARBIZU (1997) revised Lang's *Parastenocaris fontinalis* group, removing from it the parastenocaridines *Entzicaris entzi*, *Parastenocaris similis*, and *Pannonicaris aedes*, with the remainder, namely *Fontinalicaris fontinalis*, *F. meridionalis* (Rouch, 1990) (previously *F. fontinalis meridionalis*), *F. psammica* (Songeur, 1961), and *F. hispanica* (Martínez Arbizu, 1997), comprising a new *Parastenocaris fontinalis* group, *i.e.* a new conception of *Fontinalicaris*. These species share the same construction of the male P4 enp, and their monophyly is also supported by the following autapomorphies (plesiomorphies in parenthesis): fused seta of male P4 enp with subordinate spinules only on outer margin (*vs.* *P. aquaeductus* Chappuis, 1925 and other species around *P. kabiloides* Enckell, 1969 have such ornamentation on both sides of the P4 enp); male P3 basis without row of spinules (*vs.* with spinules, where the presence of such ornamentation is a symplesiomorphy of the family); male P3 exp portion of segment 1 without spinules on inner margin (*vs.* two spinules are present in *P. aquaeductus* and in the copepodite V of *P. hispanica*); male P4 exp 1 with row of spinules on inner margin subterminally inserted (*vs.* inserted distally in *P. aquaeductus* and in the copepodite V of *P. hispanica*); male P3 exp "apophysis" twice longer than wide (*vs.* as long as wide in *P. aquaeductus* and in the copepodite V of *P. hispanica*); female P4 basis without spinules between exp and enp (*vs.* *P. aquaeductus* with row of spinules in this position).

The position of MARTÍNEZ ARBIZU (1997) has been strongly criticized by KARANOVIC (2005), who argued in favor of the Lang's system and KARANOVIC & LEE (2012), who considers the *Fontinalicaris* species *F.*

*hispanica* and *F. meridionalis* as belonging to their newly revised *Proserpinicaris* (JAKOBI, 1972a), on the basis of phylogenetic analysis where some clear plesiomorphic characters are scored as apomorphies. According to KARANOVIC (2005) and KARANOVIC *et al.* (2012), MARTÍNEZ ARBIZU (1997) narrowed the *Parastenocaris fontinalis* group concept too much. However, MARTÍNEZ ARBIZU (1997) merely restricted it to the monophyletic group of species closely related to *F. fontinalis*. This author did not exclude the possibility that other monophyletic groups and, therefore, new genera, could be closely related to his concept of *Fontinalicaris*, and that these altogether could constitute a larger monophyletic unit within the Fontinalicaridinae. In other words, what SCHMINKE (2010) now defines as Fontinalicaridinae (a monophyletic subfamily) is a potential source of new genera that are closely related to the *Parastenocaris fontinalis* group (*Fontinalicaris*) defined by MARTÍNEZ ARBIZU (1997), but not directly related to any species currently comprising *Fontinalicaris*.

As the most recent word on the subject, SCHMINKE (2010) does not accept the genus *Fontinalicaris* as defined by MARTÍNEZ ARBIZU (1997), restricting it to the type species with its two subspecies *Fontinalicaris fontinalis fontinalis* (Schnitter & Chappuis, 1915), and *Fontinalicaris fontinalis borea* (Kiefer, 1960). Here we accept the concept of MARTÍNEZ ARBIZU (1997) instead.

On the basis of the above discussion on the *Fontinalicaris* “unit”, it remains to be checked whether *Iticocaris itica* can be accommodated into the genus *Fontinalicaris* as defined by MARTÍNEZ ARBIZU (1997). *Iticocaris itica* does not share any synapomorphy with *Fontinalicaris fontinalis* nor with *Fontinalicaris sensu* MARTÍNEZ ARBIZU (1997).

**Rejection of the *Parastenocaris proserpina* group of LANG (1948).** According to KARANOVIC (2005), *Fontinalicaris hispanica* is a typical member of the *Parastenocaris proserpina* group. By rejecting a close relationship of this species with *F. fontinalis*, KARANOVIC (2005) also rejected MARTÍNEZ ARBIZU’S hypothesis (1997) in favor of Lang’s system. Recently, KARANOVIC & LEE (2012) redefined the genus *Proserpinicaris*. However, their genus is basically supported by a plesiomorphy and is considered paraphyletic. Therefore, we reject this genus as it is currently defined.

The *Parastenocaris proserpina* group is another clear case of how the strict adoption of the Langian system can induce bias in the systematics of the Parastenocarididae, giving support to polyphyletic groups. We have argued above that the *P. proserpina* group is not monophyletic (with members belonging to both Fontinalicaridinae and Parastenocaridinae). Here we discuss the diagnostic characters proposed by LANG (1948), and in so doing, give support to MARTÍNEZ ARBIZU’S (1997) system. This in turn provides an endorsement of our decision not to include *Iticocaris itica* in the *Parastenocaris fontinalis* group of LANG (1948).

Accordance to LANG (1948:1219) the *P. proserpina* group can be defined by the presence of two P4 “appendages” (“Anhangen”) at the inner margin of basis in males, the outer of which is probably the enp. There are at least two problems with the LANG’S (1948) diagnosis. The first is that there is a dubious condition to define the *P. proserpina* group since it is not absolutely clear which “appendage” represents the enp. The second problem is that the enp is the outer element in the fontinalicaridids *Proserpinicaris proserpina*, *P. cantabrica* and *P. phyllura*. The inner element in these species is a hyaline spinule on the basis between the enp and exp. This spinule is present in *Fontinalicaris* and at least other 25 species of the Fontinalicaridinae (SCHMINKE, 2010), including *Fontinalicaris hispanica*. In contrast, the enp is the inner element in the remaining representatives of the *P. proserpina* group, namely the parastenocaridids *Lacustricaris budapestiensis* and *Proserpinicaris nollii*. Presence of the hyaline spinule located between the enp and exp of *Fontinalicaris hispanica* is a synapomorphy of the Fontinalicaridinae. Within this subfamily, it becomes a shared plesiomorphic character (symplesiomorphy) and cannot be used to support any close relationship of *Fontinalicaris hispanica* and the species closely related to *Proserpinicaris proserpina*.

On the basis of these arguments, *I. itica* cannot be placed in the polyphyletic *P. proserpina* group.

**Lack of dimorphism on P4 endopod.** Within the Fontinalicaridinae, it seems that only a few species do not have a sexually dimorphic P4 enp [*viz.* *Lacustricaris lacustris* (Chappuis, 1957) from North America and *P. matopoica* Wells, 1964 from Rhodesia]. In the Neotropical region, no other known species is so modified. While the male P4 enp of *Parastenocaris staheli* seems already to represent a derived condition of the ground pattern observed for the females, the P3 morphology of this species precludes any close relationship with *Iticocaris itica*. In the absence of other potential synapomorphies with either of the species mentioned above, the absence of sexual dimorphism of the P4 enp is considered an autapomorphy for *Iticocaris*, as a result of heterochrony. With the exception of the species mentioned above and *Dussartstenocaris idioxenos* Karanovic & Cooper, 2011, all the remaining Parastenocarididae that lack or show only weak dimorphism of the P4 enp belong to the Parastenocaridinae.

**Relationships between *Iticocaris* gen. nov. and *Brasilibathynellocaris*.** The inclusion of *Iticocaris itica* in the genus *Brasilibathynellocaris* might be supported by the shared presence of a very long apophysis on the male P3, strongly curved downwards and forming a cheliform forceps against the thumb. This feature might place *I. itica* as the first offshoot of *Brasilibathynellocaris*, while the absence of the following synapomorphies (CORGOSINHO *et al.*, 2010) would preclude its inclusion any higher in that genus: exp-1 of male P4 short, with an invagination on the proximal inner margin; presence of 2 strong spinules present on the anterior margin of

the coxa of P4 in males; a hyaline cushion present on the inner margin of male P3 exp-1, and a hyaline margin present on the apophysis.

The male P3 morphology described above is uncommon in the Parastenocarididae; besides *I. itica*, a similar condition is found only in *Brasilibathynellocaris* species. However, in *I. itica* the P3 in adult males is 2-segmented, a character observed only in some adult males of *Forficatocaris* (A. Ahnert, unpubl. data), in a neotenic specimen of *B. salvadorensis* Noodt, 1962 and also in the copepodid V of this species (CORGOSINHO *et al.*, 2010). This reduced segmentation is plausibly the result of post-displacement, with the concomitant retention of a neotenic structure in the adult. If so, it probably appeared independently in the evolutionary history of the Parastenocarididae, occurring in *Brasilibathynellocaris* (only in the copepodid V), *Forficatocaris* and *Iticocaris* gen. nov. It also appears in some Parastenocaridinae species, such as *Parastenocaris savita* Ranga Reddy, 2001 and *P. mahanadi* Ranga Reddy & Defaye, 2007. However, a more parsimonious assumption is to consider a 2-segmented P3 exp as having appeared independently several times in the Parastenocarididae and thus constituting a homoplastic autapomorphy for *I. itica*.

The long, downward curved apophysis of *I. itica* must not be confused with the distal spine present on the apophysis of several parastenocaridids. The articulation present between the first enp and the apophysis in *I. itica* shows that these structures are not homologous. On the other hand, it strengthens the suggestion of a homology between the condition observed in *I. itica* and the sister-genus *Brasilibathynellocaris*, since a similar condition can be observed at least during the ontogenetic development of *B. salvadorensis* (CORGOSINHO *et al.*, 2010).

*Iticocaris itica* could be hypothetically considered as the most derived species of *Brasilibathynellocaris*. However, the lack of shared apomorphies between *I. itica* and members of *Brasilibathynellocaris* (*viz.* *B. paranaensis* group and *B. salvadorensis* group, CORGOSINHO *et al.*, 2010) does not give arguments for such a position into *Brasilibathynellocaris*.

#### The phylogenetic position of *Iticocaris itica*.

The phylogenetic position of the South American fontinalicariidids is still unclear. However, it is very interesting that a group of species in South America, such as the species composing *Brasilibathynellocaris* and *Siolicaris* Jakobi, 1972, has lost the most proximal seta of the P5 of males and reduced or lost the seta II of the furca. We are not sure whether these transformations are synapomorphies for a South American group, for a larger group within the family or if they are the result of multiple origin. However, both losses are evident in *Iticocaris* gen. nov., as well. In order to arrive at a comprehensive hypothesis of the evolution of the South American parastenocaridids, we recommend focussing on the relationships between *Iticocaris* gen. nov. and the genera *Brasilibathynellocaris* and *Siolicaris*.

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#### REFERENCES

- AX, P. 1984. **Das Phylogenetische System: Systematisierung der lebenden Natur aufgrund ihrer Phylogenese.** Stuttgart, Gustav Fischer Verlag. 349p.
- CHAPPUIS, P. A. 1942. Eine neue Methode zur Untersuchung der Grundwasser-fauna. *Acta Scientiarum Mathematicarum et Naturalium* 6:1-7.
- CORGOSINHO, P. H. C. & MARTÍNEZ ARBIZU, P. 2005. Two new interstitial species of *Remaneicaris* Jakobi 1972 from Ribeirão do Ouro River, Minas Gerais, Brazil, with a redefinition of the genus (Crustacea, Copepoda, Harpacticoida, Parastenocarididae). *Senckenbergiana Biologica* 85(2):147-162.
- CORGOSINHO, P. H. C.; MARTÍNEZ ARBIZU, P. & SANTOS-SILVA, E. N. 2007. Three new species of *Remaneicaris* Jakobi, 1972 (Copepoda, Harpacticoida, Parastenocarididae) from the Ribeirão do Ouro River, Minas Gerais, Brazil, with some remarks on the groundpattern of the Parastenocarididae. *Zootaxa* 1437:1-28.
- \_\_\_\_\_. 2010. Revision of *Brasilibathynellocaris* Jakobi, 1972 (Copepoda: Harpacticoida: Parastenocarididae) with redefinition of the genus. *Zoological Journal of the Linnean Society* 159:527-566.
- CORGOSINHO, P. H. C.; RANGA REDDY, Y. & MARTÍNEZ ARBIZU, P. 2012. Revision of the genus *Siolicaris* JAKOBI, with redescription of *S. sioli* (Noodt, 1963) and *S. Jakobi* (Noodt, 1963) from South America, and *S. sandhya* (Rango-Reddy, 2001) comb. nov. from India (Copepoda, Harpacticoida, Parastenocarididae). *Zootaxa* 3493:49-71.
- COTTARELLI, V.; BRUNO, M. C. & BERERA, R. 2010. First record of Parastenocarididae from Thailand and description of a new genus (Copepoda: Harpacticoida). *Journal of Crustacean Biology* 30(3):478-494.
- FERRARI, F. D. & IVANENKO, V. N. 2008. The identity of protopodal segments and the ramus of maxilla 2 of copepods (Copepoda). *Crustaceana* 81:823-835.
- GALASSI, D. M. P. & DE LAURENTIIS, P. 2004. Towards a revision of the genus *Parastenocaris* Kessler, 1913: establishment of *Simplicaris* gen. nov. from groundwaters in central Italy and review of the *P. brevipes*-group (Copepoda, Harpacticoida, Parastenocarididae). *Zoological Journal of the Linnean Society* 140:417-436.
- GLATZEL, T. 1991. Neue morphologische Aspekte und die Copepodid-Stadien von *Parastenocaris phyllura* Kiefer (Copepoda, Harpacticoida). *Zoologica Scripta* 20(4):375-393.
- HUYS, R. & BOXSHALL, G. A. 1991. **Copepod evolution.** London, The Ray Society. 468p.
- ICZN. 1999. **International Code of Zoological Nomenclature.** 4ed. London, International Trust for Zoological Nomenclature. 306p.
- JAKOBI, H. 1972a. Trends (Enp. P4 Männchen) innerhalb der Parastenocarididen (Copepoda Harpacticoida). *Crustaceana* 22:127-146.
- \_\_\_\_\_. 1972b. Zur Kenntnis der Forficatocaris-Zoenose des Nhandiaquara (Paraná – Brasilien). *Studies on Neotropical Fauna* 7:239-251.
- KARANOVIC, T. 2005. Two new subterranean Parastenocarididae (Crustacea, Copepoda, Harpacticoida) from Western Australia. *Records of the Western Australian Museum* 22:353-374.
- \_\_\_\_\_. 2006. Subterranean copepods (Crustacea, Copepoda) from the Pilbara region in Western Australia. *Records of the Western Australian Museum* 70:1-239.
- KARANOVIC, T. & COOPER, S. J. B. 2011. Third genus of parastenocaridid copepods from Australia supported by molecular evidence (Copepoda, Harpacticoida). *Studies on Freshwater Copepoda: a Volume in Honour of Bernard Dussart*: 293-338.

- KARANOVIC, T. & LEE, W. 2012. A new species of *Parastenocaris* from Korea, with a redescription of the closely related *P. biwae* from Japan (Copepoda: Harpacticoida: Parastenocarididae). **Journal of Species Research** **1**(1):4-34.
- KARANOVIC, T.; CHO, J.-L. & LEE, W. 2012. Redefinition of the parastenocaridid genus *Proserpinicaris* (Copepoda: Harpacticoida), with description of three new species from Korea. **Journal of Natural History** **46**:1573-1613.
- LANG, K. 1948. **Monographie der Harpacticiden. Vol I and II.** Lund, Hakan Ohlssons Boktryckeri, 1. 683p.
- MARTÍNEZ ARBIZU, P. 1997. *Parastenocaris hispanica* n. sp. (Copepoda: Harpacticoida: Parastenocarididae) from hyporheic groundwaters in Spain and its phylogenetic position within the *fontinalis*-group of species. **Contributions to Zoology** **66**:215-226.
- MARTÍNEZ ARBIZU, P. & MOURA, G. 1994. The phylogenetic position of the *Cylindropsyllinae* Sars (Copepoda, Harpacticoida) and the systematic status of the *Leptopontiinae* Lang. **Zoologische Beiträge** **35**(1):55-77.
- NOODT, W. 1962. Limnisch subterrane Copepoden der Gattung *Parastenocaris* Kessler aus Mittelamerika. **Beiträge zur Neotropischen Fauna** **2**(3):223-248.
- \_\_\_\_\_. 1972. Drei neue *Parastenocaris* aus Kolumbien (Crustacea Copepoda). 1. Mitteilung über kolumbianische Grundwasser-Crustaceen. **Studies on Neotropical Fauna** **7**:101-112.
- REID, J. W. 1993a. The harpacticoid and cyclopoid copepod fauna in the cerrado region of central Brazil. 1. Species composition, habitats, and zoogeography. **Acta Limnologica Brasiliensia** **6**:56-68.
- \_\_\_\_\_. 1993b. The harpacticoid and cyclopoid copepod fauna in the cerrado region of central Brazil. 2. Community structures. **Acta Limnologica Brasiliensia** **6**:69-81.
- \_\_\_\_\_. 1995. Redescription of *Parastenocaris brevipes* Kessler and description of a new species of *Parastenocaris* (Copepoda: Harpacticoida: Parastenocarididae) from the U.S.A. **Canadian Journal of Zoology** **73**:173-187.
- SCHMINKE, H. K. 1976. The ubiquitous telson and the deceptive furca. **Crustaceana** **30**:292-300.
- \_\_\_\_\_. 2008. First report of groundwater fauna from Papua New Guinea: *Kinnecaris* Jakobi, 1972 redefined (Copepoda, Harpacticoida, Parastenocarididae), and description of a new species. **Crustaceana** **81**(10):1241-1253.
- \_\_\_\_\_. 2009. *Monodicaris* gen. n. (Copepoda, Harpacticoida, Parastenocarididae) from west Africa. **Crustaceana** **82**(3):367-378.
- \_\_\_\_\_. 2010. High-level phylogenetic relationships within Parastenocarididae (Copepoda, Harpacticoida). **Crustaceana** **83**(3):343-367.
- WELLS, J. B. J. 2007. An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). **Zootaxa** **1568**:1-872.