Revision of the genus *Siolicaris* Jakobi, 1972, with redescriptions of *S. sioli* (Noodt, 1963) and *S. jakobi* (Noodt, 1963) from South America, and *S. sandhya* (Ranga Reddy, 2001) comb. nov. from India (Copepoda, Harpacticoida, Parastenocarididae)

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Abstract

Recent revision of the family Parastenocarididae has revealed the existence of different monophyletic groups within the repository genus *Parastenocaris* Kessler, 1913 *sensu lato*. Here, we redefine the genus *Siolicaris* Jakobi, 1972, arguing for its monophyly. All the hitherto known Neotropical species of *Siolicaris* and also the Indian *Siolicaris sandhya* (Ranga Reddy, 2001) **comb. nov**., which are redescribed herein**,** share what we consider to be a unique constellation of synapomorphies: in the female, thoracopod 3 enp is absent; in the male, thoracopod 4 enp is reduced; thoracopod 3 exp is robust, strongly incurved and with a very strong thumb, longer than apophysis; and in both sexes, thoracopod 5 is trapezoidal, with all the setigerous elements inserted on the very distal margin. In addition, the proximal position of furcal setae I–III together with the extreme reduction of seta II and the reduction or complete absence of the proximal-most seta on thoracopod 5 exp are other good indications, justifying the inclusion of *Siolicaris* within a broader group of Neotropical Parastenocarididae.

The genus is probably of Gondwanan origin, with its known members distributed in the northern South America (Amazonian region) and southeastern India. *Parastenocaris digitata* Noodt, 1963a is treated here as a synonym of *Siolicaris jakobi* (Noodt, 1963a). *Parastenocaris chelifer* Delachaux, 1924 and *Parastenocaris xyrophora* Noodt & Galhano, 1969 are considered *species inquirendae* of the genus *Siolicaris*, pending their detailed redescription.

Key words: *Parastenocaris sioli*-group, *P. chelifer*, *P. xyrophora*, monophyletism, taxonomic revision, biogeography, Gondwana

Introduction

Taxonomic and phylogenetic quandary abounds the literature on Parastenocarididae Chappuis, 1940, owing, *inter alia*, to incomplete treatment of species, antiquated phylogenetic considerations (*cf.* Lang 1948), non-availability of type material, and minute size of the animals and their sparseness in regular samples. The family has thus long remained a complex taxon or a phylogenetic nightmare. Consequently, most works during the recent decades focused on alpha taxonomy, but only a few (e.g. Galassi & De Laurentiis 2004; Karanovic et al. 2012; Martínez Arbizu 1997; Reid 1994; Reid 1995) attempted to shed some light on the phylogeny and generic composition within the family.

Up till now, the family encompasses 290 described species and subspecies in 35 nominal genera, of which 28 genera are nomenclaturally available and valid (Walter & Boxshall 2012). For the Neotropical region, some hitherto unconsidered genera, such as *Remaneicaris* Jakobi, 1972 and *Brasilibathynellocaris* Jakobi, 1972 have been redefined by Corgosinho & Martínez Arbizu (2005) and Corgosinho *et al.* (2010), respectively, whereas the so-far accepted genera such as *Paraforficatocaris* Jakobi, 1972 and *Pararemaneicaris* Jakobi, 1972 were synonymized with *Brasilibathynellocaris* by Corgosinho *et al.* (2010). For the Paleotropical region (Afrotropical, Oriental and Australotropical regions, *sensu* Morrone 2002), Schminke (2008) recognized the genus *Kinnecaris*Jakobi, 1972 as monophyletic and treated the genus *Cafferocaris* Jakobi, 1972 as its junior synonym. Karanovic *et al.* (2012) redefined the Palaearctic genus *Proserpinicaris* Jakobi, 1972 and provided a key to its species. Similarly, Karanovic & Lee (2012) redefined *Parastenocaris s. str*., i. e. the *brevipes* group, along with a cladistic analysis and a key to its species, Schminke (2009) established a new genus, *Monodicaris* Schminke, 2009, for certain West African taxa. The Asian genus *Asiacaris* Cottarelli, Bruno & Berera, 2010 was erected for a single Thai species. The latest addition is the Australian genus *Dussartstenocaris* Karanovic & Cooper, 2011, which is based on both morphological and molecular data (Karanovic & Cooper 2011).

Of the 28 valid genera mentioned above, only *Brasilibathynellocaris, Forficatocaris* Jakobi, 1969*, Kinnecaris, Monodicaris, Murunducaris* Reid, 1994, *Parastenocaris sensu stricto* (viz. *P. brevipes* Kessler, 1913 group in Reid 1995), *Potamocaris* Dussart, 1979 and *Remaneicaris* Jakobi, 1972, *Simplicaris* Galassi & De Laurentiis, 2004, *Asiacaris* and *Dussartstenocaris,* are supposedly monophyletic genera.

Much like *Remaneicaris*, *Brasilibathynellocaris* and *Kinnecaris*, the genus *Siolicaris* Jakobi, 1972 has long remained unrecognized by other authors, its species thus getting lumped in *Parastenocaris sensu lato.* However, while proposing this genus, Jakobi (1972) fulfilled all the ICZN (1999) requirements (see Articles 11.5, 13, 67.8 and 68), offering a diagnosis and designating a valid type species. Therefore, the name *Siolicaris* is nomenclaturally available and can be used as valid.

The present study of the Neotropical species that compose this genus (see Noodt 1963a and Jakobi 1972), plus the Indian *Siolicaris sandhya* (Ranga Reddy, 2001) **comb. nov.**, all of which are now redescribed**,** reveal certain morphological synapomorphies, which support our hypothesis of monophyly for *Siolicaris.* So, we redefine this genus and tentatively discuss its presumed affinities within the family. As for *P. chelifer* Delachaux, 1924 and *P. xyrophora* Noodt & Galhano, 1969, despite their original accounts being incomplete, do show distinct *Siolicaris*affinities. Hence they are considered *Siolicaris species inquirendae*, pending their detailed redescription. *Parastenocaris digitata* Noodt, 1963a is proposed as a junior synonym of *Siolicaris jakobi* (Noodt, 1963a). A note on the biogeography of the species is also added.

Material and methods

For the redescription of the type material of *Parastenocaris sioli* Noodt, 1963a, *P. digitata* Noodt, 1963a and *P. jakobi* Noodt, 1963a, we studied the original Noodt's collection housed at the Senckenberg Research Institute, Dept. DZMB (Wilhelmshaven, Germany). It must be pointed out that Noodt did not always designate any single specimen as the holotype for the species studied by him. So, it is not uncommon to witness a syntype condition or even several specimens mounted together that do not always belong to one and the same species. Often it is not possible to identify which limbs had been drawn by Noodt. Due to the poor condition of his original preparations, the present redescriptions have perforce based on a reexamination of his specimens found on different slides.

Noodt's material that we studied for this work was found labeled on the slides as follows: *Parastenocaris sioli*1♂ präp, paratype, P275 Santarém (Case 2, slide 15); *Parastenocaris jakobi* typus! 1 ♂ präp, P275 Santarém (Case 2, slide 16); *Parastenocaris sioli* typus! 2 ♂♂ präp, P275 Santarém (Case 2, slide 17); *Parastenocaris digitata*, 2 ♂♂ präp (typus + paratypus), P275 Santarém + 1 ♀ *P. clandestina* (Case 2, slide 19); *Parastenocaris* ♀♀ *digitata* + *jakobi*, 2 ♀♀ präp, P275 (Case 4, slide 14).

One partly damaged specimen of *P. jakobi* was sorted from Noodt's material preserved in formalin in a vial labeled as *P. santaremensis*, and used for the present purpose. We dissected this specimen in glycerin and mounted it on a single slide. The habitus of *P. sioli*, *P. jakobi* and *P. digitata* could not be illustrated for want of suitable specimens. The thoracopod 1 of *P. sioli* could not be found in any preparation and its illustration. As given now, it follows our interpretation of the original depiction by Noodt (1963a: 132, Fig. 66).

Formalin-preserved topotypes of *S. sandhya* were studied. One male and one female were completely dissected in lactic acid and mounted on seven slides each in glycerin. One male was partially dissected in lactic acid and also mounted on slides in glycerin.

Drawings were made with a Leica DMR microscope equipped with Nomarsky interference contrast, using a drawing tube and 400x and 1000x magnifications.

Noodt (1963a) illustrated no female of his *Parastenocaris sioli*-group, but tersely referred to them only in the genus diagnosis. Here we offer a complete description of the female limbs, based on the observation of two specimens, which had been dissected and mounted on the same slide and identified by Noodt as *P. digitata* + *P. jakobi* (from sample P275, case 4, slide 14). Since it is impossible to identify as to which species these females belong (see Noodt 1963a), here we simply refer to them as *Siolicaris* sp. South American female.

The type material of *P. chelifer* was untraceable in different museums where Delachaux worked and so considered probably lost, whereas that of *P. xyrophora* was quite damaged so we could not study it properly.

Here we adopt the original species names, i. e. *Parastenocaris sioli* and *P. jakobi* instead of their subsequent incorrect spellings, i.e. *P. siolii* and *P. jakobii*. The same applies to the new combinations proposed in this work.And this is in full compliance with the ICZN (1999), article 33.4, which establishes that the "use of the genitive ending *-i* in a subsequent spelling of a species-group name that is a genitive based upon a personal name in which the correct original spelling ends with *-ii*, or vice versa, is deemed to be an incorrect subsequent spelling, even if the change in spelling is deliberate".

Terminology and homologisation of maxillary and maxillipedal structures follow Ferrari & Ivanenko (2008). The terms setae, setules, spines and spinules are used according to Huys & Boxshall (1991) whereas furca and telson are as in Schminke (1976). The term "thumb" refers to the outer spine of the male thoracopod 3, homologous to the outer spine of the first exopodite of the thoracopod 3. For details about the development of the male thoracopod 3 and homologization of structures, see Glatzel (1991).

Abbreviations used are: A1 = antennule, A2 = antenna, Ae = aesthetasc, ap = apomorphy, enp = endopodite, exp = exopodite, Md = mandible, Mx1 = maxillule, Mx2 = maxilla, Mxp = maxilliped, P1–P5 = thoracopods 1 to 5.

Systematics

Subphylum Crustacea Brünnich, 1772

Class Maxillopoda Dahl, 1956
Subclass Copepoda H. Milne Edwards, 1840
Order Harpacticoida G. O. Sars, 1903
Family Parastenocarididae Chappuis, 1940
Subfamily Fontinalicaridinae Schminke, 2010

Genus *Siolicaris* Jakobi, 1972

Synonym. *Parastenocaris* Kessler, 1913 *partim*

Emended diagnosis. Furca with 7 setae; setae I–III originating proximally from almost same region and anterior to seta VII; seta II reduced in size, sometimes indiscernible. A1 8-segmented in male, haplocer, penultimate segment without apophysis at distal inner corner, 7-segmented in female. Maxilla with 2 endites, proximal endite with 1 seta, distal one with 1 spiniform and 2 slender setae. Male P3 basis with a strong row of spinules on the outer margin; apophysis short, robust, 1- or 2- segmented, with or without distal spine, strongly bent inwards while in resting position; thumb strong, longer than apophysis, with or without distal hyaline membrane, enp reduced to slender seta. Female P3 enp reduced to a spinule or absent. Basis of male P4 with or without strong spinules on the inner margin, enp reduced in size or absent; female enp spiniform, longer than exp-1 in the South American species. P5 in both sexes similar, trapezoidal, with 3–4 elements (when 4 elements, the proximalmost exp element extremely reduced), all distally inserted; both limbs close to each other, connected by a small triangular intercoxal plate. Male P6 as irregular plate with lateral triangular projections. Female genital field roundish as in Fontinalicaridinae.

Type species. *Parastenocaris sioli* (Noodt, 1963a).

Other species. *Parastenocaris jakobi* (Noodt, 1963a) [=*Parastenocaris digitata* (Noodt, 1963a)]; *Parastenocaris sandhya* (Ranga Reddy, 2001) **comb. nov.**

Species inquirendae. *Parastenocaris chelifer* Delachaux, 1924; *Parastenocaris xyrophora* Noodt & Galhano, 1969.

Siolicaris sioli (Noodt, 1963a)

(Figs. 1–2)

Synonymy. *Parastenocaris sioli* Noodt—Noodt (1963a), Rouch (1986), Ranga Reddy (2001).
Parastenocaris siolii Noodt; incorrect spelling—Jakobi (1972), Löffler (1981), Dussart (1984), Rouch (1986), Dussart & Defaye (1990), Reid (1998).
Siolicaris siolii (Noodt), incorrect spelling—Corgosinho *et al.* (2008).
Siolicaris sioli (Noodt)—Corgosinho *et al.* (2010).

Material examined. Noodt's collection: *Parastenocaris sioli,* syntype (Case 2, slide 17), 2 ♂♂ dissected and mounted on a single slide; *Parastenocaris sioli,* paratype (Case 2, slide 15), 1 ♂ dissected and mounted on a single slide.

Type locality. Coastal groundwater of the Amazon River at Santarém-PA (Brazil).

Description. Male. Body size of 330 μm (after Noodt 1963a). Telson smooth, anal operculum smooth and slightly concave; anal sinus bordered by fine spinules (Fig. 1A and Noodt 1963a, p. 132, fig. 64). Furca (Figs. 1A) with 7 setae; setae I–III proximally inserted, anterior to seta VII; seta II reduced; seta IV subdistal, inserting dorsally, on outer margin of furca; seta V inserting on the distal margin of furca; seta VI shorter than seta V, inserting beneath it; seta VII approximately of the same size as seta VI, socketed at basis and inserted dorsally, close to inner margin of furca.

A1 (Fig. 1B–F) haplocer, 8-segmented and prehensile, 7th segment without a distal inner apophysis; armature beginning with proximal segment: 0/6/4/1/5+Ae/2 [1 hyaline spine (dotted structure) and 1 setae]/2 [1 hyaline spine (dotted structure) and 1 distal seta]/9+Ae; distal segment with distal hyaline margin.

A2 (Fig. 2A) with allobasis; abexopodal margin ornamented with 2 spinules; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae.

Md (Fig. 1G) coxal gnathobasis bearing 1 seta and 1-segmented palp with 2 setae.

Mx1 (Fig. 1H) praecoxal arthrite with 5 elements (1 dorsal surface seta, 3 claw-like pinnate spines and 1 slender seta), coxa and basis not observed.

Mx2 (Fig. 1I) basis with 2 endites, proximal endite with 1 seta, distal endite with 2 slender setae and 1 pinnate spine, proximal endopodal segment drawn into a claw, distal endopodal segment with 2 setae.

Mxp (Fig. 1I–J) subchelate, composed of syncoxa, basis, 1-segmented endopod fused to the claw-like apical seta.

P1 (Fig. 2G) coxa bare; basis with small outer seta. Exp 3-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with 2 outer spines and 2 geniculate setae of different lengths; enp 2-segmented, slightly longer than exp, enp-1 as long as the combined length of first 2 exopod segments, enp-2 with 1 apical outer spine and 1 apical geniculate seta.

P2 (Fig. 2B) coxa bare; basis without outer seta, with outer pore and row of spinules on the outer margin; exp 3-segmented, exp-1 with long outer spine and hyaline frill on distal inner corner; exp-2 without armature and with distal row of long spinules; exp-3 with 3 setae, hyaline frill on distal inner corner and row of long spinules on outer distal corner; enp 1-segmented, cylindrical, shorter than exp-1, with 2 spinules on outer margin and distal seta.

P3 (Fig. 2C–D) coxa bare; basis rectangular, longer than broad, with row of strong spinules on outer margin, below the insertion of outer seta, and pore; exp with 3 outer spinules, apophysis short, robust, 1-segmented, with rounded tip and strongly bent inwards while in rest position; thumb strong, much longer than apophysis, with pointed tip and roundish distal hyaline membrane, enp reduced to tiny seta.

P4 (Fig. 2E) coxa with 2 long and strong spinules on anterior margin; basis trapezoidal, with an outer seta and pore; exp 3-segmented, exp-1 with outer spine and hyaline frill on distal inner corner; exp-2 unarmed and with distal row of long spinules; exp-3 with 2 setae and hyaline frill on distal inner corner; enp completely absent.

P5 (Fig. 2F) trapezoidal, without inner process, with inner row of small spinules and 3 setae, all distally inserted; both limbs close to each other, connected by short, triangular intercoxal sclerite.

P6 as an irregular plate with lateral triangular projections.

Female. Unknown.

FIGURE 1. *Siolicaris sioli* (Noodt, 1963), male (syntype, Noodt's collection case 2, slide 17, Figs A, C, E, F, I, J; paratype, Noodt's collection case 2, slide 15, Figs B, D, G, H). A, telson and furca; B, A1, clasping position, armature omitted (Noodt collection, Box 6, slide 7; S64); C, A1 segments 2–8; D, male A1 segments 1–2; E, A1 segment 6; F, A1 segments 7–8; G, Md; H, praecoxa of Mx1; I, Mx2 and Mxp; J, Mxp. Scale bar 1, Figures B –J = 20 µm; scale bar 2, Figure A = 50 µm.

FIGURE 2. *Siolicaris sioli* (Noodt, 1963), male (syntype, Noodt's collection case 2, slide 17, Figs A, B, C, E, F; paratype case 2, slide 15, Fig. D). A, A2; B, P2; C–D, P3; E, P4; F, P5; G, P1 (adapted from Noodt). Scale bar 1, Figures A–F = 20 µm; scale bar 2, Figure G = 30 µm.

Siolicaris jakobi (Noodt, 1963a)

(Figs. 3–4)

Synonymy. *Parastenocaris jakobi* Noodt—Noodt (1963a), Dussart (1984), Dussart & Defaye (1990), Rouch (1986, 1988), Reid (1998), Ranga Reddy (2001).

Parastenocaris jakobii Noodt (incorrect spelling)—Jakobi (1972), Corgosinho *et al.* (2008).

Siolicaris jakobii (Noodt) (incorrect spelling)—Corgosinho *et al.* (2008).

Siolicaris jakobi (Noodt)—Corgosinho *et al.* (2010).

Parastenocaris digitata Noodt, **syn. nov**.—Noodt (1963a), Jakobi (1972), Löffler (1981), Dussart (1984), Rouch (1986, 1988),

Dussart & Defaye (1990), Reid (1998), Ranga Reddy (2001).

Siolicaris digitata (Noodt), **syn. nov**.—Jakobi (1972).

Material examined. *Parastenocaris jakobi*, type (Case 2, slide 16), 1 ♂ dissected and mounted on a single slide; *Parastenocaris digitata*, syntype (Case 2, slide 19), 2 ♂♂ dissected and mounted on a single slide (plus an undissected female of *Remaneicaris clandestina* and a dissected male of *P. jakobi*); *Parastenocaris jakobi*, 1 damaged ♂ sorted from Noodt's material stored in formalin, dissected and mounted on a single slides with glycerin (added to Noodt's collection).

Type locality. Coastal groundwater of the Amazon River at Santarém-PA (Brazil).

Description. Male. Body size of 350 µm (after Noodt 1963a). Telson smooth, anal operculum smooth and slightly concave (Fig. 3A and Noodt 1963a: 133, fig. 71). Furca (Figs. 3A) with 7 setae; setae I–III proximally inserted, anterior to seta VII; seta II reduced; seta IV subdistal, inserting dorsally, on outer margin of furca; seta V inserted on the distal margin of furca; seta VI shorter than seta V, inserting beneath it; seta VII approximately of the same size as seta VI, socketed at basis and inserted dorsally, on inner margin of furca.

A1 (Fig. 3B–F) haplocer, 8-segmented and prehensile, 7th segment without a distal inner apophysis; armature beginning with proximal segment: 0/6/4/1(short spine)/5+Ae/2? [1 hyaline spine (dotted structure) and 1 setae?]/2 [1 hyaline spine (dotted structure) and 1 distal seta]/9+Ae; distal segment with distal hyaline margin.

A2 (Fig. 3G) with allobasis; abexopodal margin with 2 rows of spinules; 1-segmented exp with 1 apical seta, and 1-segmented enp bearing 7 setae.

Md (Fig. 3H) with a coxal gnathobasis (gnathobasal seta not obeserved) and 1-segmented palp with 2 setae.

Mx1 (Fig. 3H) praecoxal arthrite with 5 elements (1 dorsal surface seta, 3 claw-like pinnate spines (small ventral seta not observed), coxa with 1 seta, basis with 3 setae.

Mx2 (Fig. 3I) basis with 2 endites, proximal endite with 1 seta, distal endite with 2 slender setae and a 1 pinnate spine, proximal endopodal segment drawn into claw, distal endopodal segment with 2 setae.

Mxp (Fig. 3J) subchelate, composed of syncoxa, basis, 1-segmented endopod and 1 claw-like apical seta.

P1 (Fig. 3K) coxa bare; basis with outer seta and outer row of spinules, 1 inner row of long spinules and 1 row of spinules near the insertion of enp. Exp 3-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with 1 outer spine, 1 spine on anterodistal corner, and 2 geniculate apical setae of different lengths; enp 2-segmented, slightly longer than exp, enp-1 as long as the combined length of first 2 exopodal segments, with 2 long spinules inserted at inner distal third, enp-2 with 1 apical outer spine and 1 apical geniculate seta.

P2 (Fig. 3L) coxa ornamented with row of tiny spinules near distal inner corner; basis without outer seta, with outer pore and row of spinules on outer margin; exp 3-segmented, exp-1 with long outer spine and hyaline frill on distal inner corner; exp-2 without armature and with distal row of long spinules; exp-3 with 3 setae, hyaline frill on distal inner corner and row of long spinules on outer distal corner; enp 1-segmented, somewhat cylindrical, distinctly shorter than exp-1, with 2 spinules distally, 1 outer spinule and 1 distal seta.

P3 (Fig. 4A, C–F, I) coxa bare; basis rectangular, with a row of strong spinules on outer margin, above the insertion of outer seta and pore; exp complexly built, 2-segmented, represented by exp-1 and apophysis (exp-2, broken in *P. digitata*); exp-1 robust, with 2 processes with blunt tip at the distal margin, apophysis strong, drawn out into a claw curved to the outside; thumb strong, longer than apophysis, with distal hyaline membrane and a proximal spur, enp reduced to tiny seta.

P4 (Fig. 4G–H, J–K) coxa with 3 long spinules on anterior margin; basis trapezoidal, with outer seta and 3 spinules near its insertion; exp 3-segmented, exp-1 with outer spine and spinules on distal inner corner; exp-2 without armature and with distal row of long spinules; exp-3 somewhat bent inwards, with 2 setae and hyaline frill on the distal inner corner; enp greatly reduced, somewhat variable: bud-like with blunt tip and 3 tiny apical spinules (Fig. 4H, K) or digitiform with distal inner corner produced into setiform structure (Fig. 4B, G).

FIGURE 3. *Siolicaris jakobi* (Noodt, 1963), male (unspecified type, Noodt's collection case 2, slides 16). A, last abdominal segment, telson and furca; B, A1, clasping position; C, A1 segment III and IV; D, A1 segment IV; E, A1 segment VII; F, A1 segment VIII; G, A2; H, Md and Mx1; I, Mx2; J, Mxp; K, P1; L, P2; M, P5. Scale bar = 20 µm.

FIGURE 4. *Siolicaris jakobi* (Noodt, 1963), male [(type Noodt's collection case 2, slide 16; figs. C–H, K), (Additional dissected material from a damaged male stored in formalin, Figs. A, B), (*Siolicaris digitata* (Noodt, 1963) **syn. nov.**, syntype Noodt collection case 2, slide 19; Figures I, J, L)]. A, P3; B, P4; C, P3; D, exp-1 P3; E, exp-2 or apophysis P3; F, thumb; G, P4; H, enp P4; I, P3 with broken apophysis; J–K, P4; L, spermatophore. Scale bar = 20 µm.

P5 (Fig. 3M) trapezoidal, without inner process, with an inner row of small spinules and 3 setae, all distally inserted; both limbs close to each other. Intercoxal sclerite not observed.

P6 as irregular plate with lateral triangular projections.

Female. Unknown.

FIGURE 5. *Siolicaris sp.* South American female (Noodt's collection case 4, slide 14). A, A1; B, P1; C, P2 (exp incompletely drawn); D, P4; E, P4 (exp incompletely drawn); F, P3. Scale bar = 20 µm.

Siolicaris sp. South American female

(Fig. 5)

Material examined. 2 ♀♀ dissected and mounted on a single slide (Case 4, slide 14), identified by Noodt as *Parastenocaris* ♀♀ *digitata + jakobi*.

Sampling locality. Same as of *Siolicaris sioli* and *S. jakobi*.

Description. Female. Sexually dimorphic in A1, P3–P4 and genital somite.

A1 7-segmented (Fig. 5A), not geniculate; armature beginning with proximal segment as follows: 0/4/4/1+Ae/1/1/9+Ae.

P1 (Fig. 5B) basis and enp-1 without inner ornamentation.

P2 endopod as in Fig. 5C

P3 (Fig. 5F) exp 2-segmented, exp-1 with outer spine, exp-2 with two distal setae and hyaline frill at distal inner corner; enp represented by tiny spine.

P4 enp (Fig. 5D–E) spiniform, longer than exp-1, with scattered spinules along distal half.

Siolicaris sandhya (Ranga Reddy, 2001) comb. nov.

(Figs. 6–10)

Synonymy. *Parastenocaris sandhya* Ranga Reddy—Ranga Reddy (2001), Ranga Reddy & Defaye (2007), Ranga Reddy & Schminke (2008), Ranga Reddy & Defaye (2009).

Material examined. 3 ♂♂ and 3 ♀♀. Illustrations based on 1 ♂ and 1 ♀ dissected and mounted on 7 slides each.

Type locality. River Krishna at Vijayawada, South India (additional information in Ranga Reddy 2001).

Emended description. Male. Integumental window visible only on cephalothorax (Fig. 6A, B). Furca (Figs. 6A) with 7 setae; setae I–III proximally inserted, anterior to seta VII; seta II reduced; seta IV subdistal, inserting dorsally, on the outer margin of furca; seta V inserting on the distal margin of furca; seta VI shorter than seta V, inserting beneath it; seta VII approximately of the same size as seta VI, socketed at basis and inserting dorsally, on inner margin of furca.

A1 (Fig. 7A–C) haplocer, 8-segmented and prehensile, 7th segment without a distal inner apophysis; armature beginning with proximal segment: 0/6/4/2 [1 hyaline spine (dotted structure) and 1 seta]/5+Ae/2 [1 hyaline spine (dotted structure) and 1 seta]/2 [1 hyaline spine (dotted structure) and 1 distal seta]/9+Ae.

A2 (Fig. 7D) and Md (Fig. 7E) as described by Ranga Reddy (2001).

Mx1 (Fig. 7F) praecoxal arthrite with 5 elements (1 dorsal surface seta, 3 claw-like pinnate spines and 1 slender seta), coxa with 1 seta, basis with 3 setae.

Mx2 (Fig. 7G) basis with 2 endites, proximal endite with 1 seta, distal endite with 2 slender setae and 1 pinnate spine; proximal endopodal segment drawn into claw; distal endopodal segment with 2 setae.

Mxp (Fig. 7H) subchelate, composed of syncoxa, basis with 1-segmented endopod fused to the claw-like apical seta.

P1 (Fig. 7I) coxa bare, basis with outer seta and outer row of spinules, and row of spinules near the insertion of the enp. Exp 3-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with 2 outer spines and 2 geniculate setae of different lengths; enp 2-segmented, slightly bent inwards; enp-1 as long as the combined length of first 2 exopodal segments, with 2 long spinules inserted at inner distal third, enp-2 with 1 outer spine and 1 geniculate seta.

P2 (Fig. 8A–C) coxa bare; basis without outer seta, with outer pore and 1 row of spinules on outer margin; exp 3-segmented, exp-1 with long outer spine and hyaline frill on its distal inner corner; exp-2 without armature, with a distal row of long spinules and 3 superimposed series of long setules on inner margin; exp-3 with 3 setae, hyaline frill on distal inner corner, row of long spinules on outer distal corner and row of long setules proximally inserted on inner margin; enp 1-segmented, shorter than exp-1, obovate, with proximal and medial row of spinules, distally with long seta and large spinule with hyaline margin.

P3 (Fig. 8D–F) coxa naked; basis subquadrate, with row of strong spinules on outer margin, near the insertion of outer seta and pore; apophysis elongate, with distal claw and distal hyaline round tip, 1 large, outer spinule near the insertion of thumb; thumb strong, longer than apophysis, with a broad basis; enp represented by small seta.

FIGURE 6. *Siolicaris sandhya* (Ranga Reddy, 2001) **comb. nov.** A, male lateral habitus; B, female lateral habitus; C, female telson and furca, dorsal view; D, female telson and furca, ventral view; E, female telson,lateral view. Scale bar 1= 100 μm; scale bar 2 = 50 μm.

P4 (Fig. 8G) coxa naked; basis with outer seta, pore, row of small spinules near the outer margin and row of small spinules near the insertion of enp; exp 3-segmented, exp-1 with outer spine and hyaline frill on distal inner corner; exp-2 without armature and with distal row of long spinules; exp-3 with 2 setae and hyaline frill on distal inner corner; enp much reduced in size, 1-segmented, digitiform, bare.

P5 (Fig. 9A–C) trapezoidal, with slender inner process, connected by a small, triangular intercoxal plate. With a row of small spinules on inner margin and 4 setae, all distally inserted; proximal exopodal seta, adjacent to the outer basal seta tiny and inserted on a small protuberance.

P6 (Fig. 9A–B) as described by Ranga Reddy (2001).

Female. Sexually dimorphic in A1, P2–P5 and genital somite. Integumental window visible only on the cephalothorax (Fig. 6B). Furca (Fig. 6B, C, E) armature as in male; variation in furcal shape as described by Ranga Reddy (2001). Telson with ventral row of spinules near the insertion of each furcal ramus (Fig. 6D).

FIGURE 7. *Siolicaris sandhya* (Ranga Reddy, 2001) **comb. nov.**, male. A, A1segments I–V; B, A1 segments V–VIII; C, A1 segment IV; D, A2; E, Md; F, Mx1; G, Mx2; H, Mxp; I, P1. Scale bar = 20 μm.

FIGURE 8. *Siolicaris sandhya* (Ranga Reddy, 2001) **comb. nov.**, male. A, P2; B, P2 exp-2; C, P2 exp-3; D, P3; E, P3 exp with apophysis and thumb; F, outer basal seta of P3; G, P4. Scale bar = 20 μm.

FIGURE 9. *Siolicaris sandhya* (Ranga Reddy, 2001) **comb. nov.** A, male P5, lateral view; B, male P5, ventral view; C, male P5, ventrolateral view; D, female P5, and genital somite, ventral view. Scale bar = 20 μm.

FIGURE 10. *Siolicaris sandhya* (Ranga Reddy, 2001) **comb. nov.**, female. A, A1; B, A1 segment V; C, A2; D, P1; E, P2; F, enp P2; G, inner seta exp-3 P2; H, P3; I, J, P4 basis with enp and partially drawn exp-1. Scale bar = 20 μm.

A1 7-segmented (Fig. 10A), not geniculate; armature beginning with proximal segment as follows: 0/4/4/1+Ae/2/1/9+Ae.

P2 (Fig. 10E–F) inner margin of exp-2–3 without the series of long setules present in males. Enp claviform, with distal row of spinules and distal seta.

P3 (Fig. 10H) coxa bare. Basis with a long outer seta and inner row of spinules approximately where enp inserts in other species. Enp completely absent. Exp 2-segmented, exp-1 with outer spine and distally, with outer and inner row of small spinules; exp-2 with 2 distal setae, outer row of spinules and usual hyaline frill at distal inner corner.

P4 (Fig. 10I) coxa, basis and exp as in the male, with minor differences in ornamentation; enp reduced in size, smaller than exp-1, 1-segmented, digitiform, bare.

P5 (Fig. 9D) trapezoidal, with moderately pronounced inner process, 1 inner spinule and 3 setae, all distally inserted. Intercoxal sclerite not observed.

P6 (Fig. 9D) formed by 2 lateral and unarmed plates covering the gonopore. Single medially located copulatory pore.

Discussion

The phylogenetic relationships within the family Parastenocarididae are known only fragmentarily. The monophyly of the several genera proposed by Jakobi (1972) is still to be assessed. In South America, the family has 76 known species, 37 of them having been reported from Brazil (viz. Reid 1998; Corgosinho & Martínez Arbizu 2005; Corgosinho et al. 2007; Corgosinho et al. 2008, Corgosinho et al. 2010b). The species belong to nine nomenclaturally available genera, viz. *Parastenocaris*, *Remaneicaris*, *Brasilibathynellocaris*, *Forficatocaris*, *Pararemaneicaris*, *Siolicaris*, *Paraforficatocaris*, *Potamocaris*, and *Murunducaris*. Of these, six genera, viz. *Parastenocaris*, *Remaneicaris*, *Brasilibathynellocaris*, *Forficatocaris*, *Potamocaris,* and *Murunducaris* are considered valid (Corgosinho *et al.* 2010a).

The genus *Siolicaris* was proposed by Jakobi (1972) to accommodate Noodt's (1963a) Neotropical *Parastenocaris sioli*-group of species, which include *Parastenocaris sioli, P. jakobi* and *P. digitata,* based on the following diagnosis (translated from German): "Tiny Parastenocarididae with outer setae (setae I–III) of practically the same size at the proximal part of furca. These setae with sexual dimorphism of 1st grade (Jakobi & Silva 1962). Operculum weak, smooth, reaching the end of anal somite, without ornamentation. Terminal furcal seta basally thickened. P4 and P2 without sexual dimorphism. One-segmented P2 enp with outer seta. P3 as strong pincers, basis as a conic socket, with an outer row of spinules. Thumb longer than apophysis, apophysis sometimes hand-shaped (*P. digitata*). Enp. P3 present as a pen (seta). P4 basis with 2 fine bristles on the inner margin. Enp. P4 tiny or represented by a small seta (*P.siolii*)."

Much similar to what had initially happened to most of the genera erected by Jakobi (1972), the genus *Siolicaris* was not recognized by various authors (e.g. Löffler 1981; Rouch 1986; Dussart & Defaye 1990; Reid 1998), because of Jakobi's (1972) heterodox systematic method, in which similar complex structures were not considered *a priori* homologous to each other, but rather the result of convergence or parallelism within evolutionary trends (Corgosinho & Martínez Arbizu 2005). In fact, this artificial system was strongly criticized by Schminke (1976) and several other authors (e.g. Cottarelli & Maiolini 1980; Dussart & Defaye 1990; Rouch 1986; Reid 1994; Martínez Arbizu 1997; Galassi & De Laurentiis 2004; Corgosinho & Martínez Arbizu 2005; Corgosinho *et al.* 2010a). However, as has been mentioned in the introduction, the genus as such fulfills all the ICZN recommendations. Therefore, the genus-goup name *Siolicaris* is nomenclaturally available and can be used as valid.

Within the family Parastenocarididae, *Siolicaris* belongs to the phylogenetic lineage of Fontinalicaridinae Schminke, 2010 as evident from the following features: 1) the furcal setae I–III originate from almost the same region and anterior to seta VII; 2) male A1 is of coiled type, the penultimate segment bearing no apophysis; 3) presence of spinules at the inner margin of the coxa of male P4; 4) P5 of both sexes long, extending beyond its own somite; and 5) the female genital field is spherical in outline. However, as far as the morphology of the female P3 and the male P4 is concerned, *Siolicaris* presents a rather much reduced (derived) scenario within this subfamily (see below).

Here, we argue in favour of the revalidation of the genus *Siolicaris* on the basis of a unique combination of six major synapomorphies (abbreviated here as ap), which have resulted mostly from reduction of limb segments and loss of setation elements, and provide sufficient complexity to warrant the status of a monophylum:

Male P3: this limb provides a triple synapomorphy. The apophysis is short and robust (ap 1), one-segmented as in *Siolicaris sioli* and *S. sandhya* or probably two- segmented as in *S. jakobi*, with or without distal spine, and strongly bent inwards while in rest position (ap 2), thumb strong and longer than apophysis (ap 3), with or without distal hyaline membrane.

Female P3: enp is either reduced to a spinule or absent (ap 4);

Male P4 enp is greatly reduced in size or completely absent (e.g. *S. sioli*) (ap 5);

P5 in both sexes similar and trapezoidal, with 3–4 elements (when 4 elements, the proximalmost exp element is extremely reduced), all distally inserted (ap 6).

In this context, it is to be noted that Jakobi (1972) mentions in the diagnosis of *Siolicaris* one character that cannot be observed in any species within this genus, namely the presence of the dimorphism on the anterolateral setae (setae I to III). Noodt (1963a), however, does not depict anything of this, nor could we observe it in any of the specimens studied by us.

Some of the characters mentioned above can be found in other species within Parastenocarididae. What is worthy of note here is the presence of reduced P4 enp, or its complete absence within some of Lang's (1948) *Parastenocaris* groups, namely the *P. nana*-group and *P. clujensis*-group. Other species of *Parastenocaris*, i.e. *P. aedes* Hertzog, 1938, *P. glareola* Hertzog, 1936, *P. dianae* Chappuis, 1955, *P. mateusi* Noodt & Galhano, 1969, *P. tyrrhenidis* Cottarelli, 1970, *P. amatheia* Cottarelli, 1970, *P. altitudinis* Cottarelli, Bruno & Berera, 2008, *P. mateusi* Noodt & Galhano, 1969 also have the P4 enp reduced or absent. However, all these species are Parastenocaridinae (viz. Schminke 2010). Therefore, they are not closely related to *Siolicaris* and the similarities among these Parastenocaridinae species with the genus *Siolicaris* are considered the result of independent evolution. It is important to say that 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, with species belonging to Parastenocaridinae and Fontinalicaridinae occurring in the same groups. Therefore, here we reject Lang’s (1948) system, in favour of a more stable and natural one.

It has been a tradition followed by many authors to describe new Parastenocarididae species as belonging to the genus *Parastenocaris*. It is therefore undeniable that the most diverse genus *Parastenocaris sensu lato* is a “taxonomic repository” being composed of species belonging to different phylogenetic lineages, not closely related to each other. We consider as belonging to the genus *Parastenocaris sensu stricto* those species that exibit the characters used by Reid (1995) to define those species that are closelly related to *Parastenocaris brevipes*, and subsequently supported by Galassi & De Laurentiis (2004) and Karanovic (2005, 2006). No species of *Siolicaris*have the characters proposed by Reid (1995). Moreover, the species composing the genus *Parastenocaris sensu stricto* (as defined by Reid 1995) are typical Parastenocaridinae (viz. Schminke 2010), therefore not closely related to the species composing *Siolicaris*.

Interspecific relationships. Our observation of the type material reveals that *Siolicaris digitata* does not differ in any significant way from *S. jakobi* so it is considered a synonym of the latter. The differences in the shape of the P5 between the two species in the original drawings [in *S. jakobi* (fig. 74, p. 133), with a broader tip and pyriform in *S. digitata* (fig. 80, p. 134), tapering distally; see Noodt 1963a] are here considered an observational artifact. As already mentioned above, the morphology of the P3 of *P. digitata* is the result of a broken apophysis. *Siolicaris sandhya* fulfils all the above-mentioned generic criteria, but it is distinct from its South American congeners in P2 enp being dimorphic vs. isomorphic (Ranga Reddy 2001), male P4 coxa unornamented vs. ornamented, and female P4 endopod short vs. long. And we are of the opinion that the dimorphism of the P2 enp and the smaller enp of the female P4 are the result of independent evolution of the Indian lineage, with the apomorphic conditions occurring in *S. sandhya*.

Siolicaris chelifer*: *species inquirenda. *Parastenocaris chelifer* was described by Delachaux (1924) based on two specimens sorted by Chappuis from the same moss sample from which Menzel (1916) described *P. staheli* Menzel, 1916. It is puzzling that both these species were initially conceived to be very similar to each other, the striking differences in their male P3 and P5 notwithstanding. For example, Lang (1948) included them in his *Parastenocaris staheli*-group, on the basis of two controversial characters, viz. the P4 enp is constructed alike in both sexes, and the P2 enp of male 2-segmented. As already mentioned by Martínez Arbizu (1997) and Corgosinho *et al.* (2007), no Parastenocarididae have a 2-segmented P2 enp. Moreover, the P4 enp of the female is not described for *P. staheli* and in *P. chelifer* the male P4 enp is short, while it is longer than the exp 1 of P4 in the female. A P4 enp longer than exp-1 is described for the females of *Siolicaris* by Noodt (1963a). This shows that *P. staheli* and *P. chelifer* are not closely related to each other. In fact, the P3 of *P. staheli* is superficially similar to what can be seen in some *Remaneicaris* species, which probably influenced Jakobi (1972) to assign this species to *Remaneicaris*. However, Corgosinho & Martinez Arbizu (2005) excluded *P. staheli* from their concept of *Remaneicaris*. Until the rediscovery of this species and its redescription, nothing more can be said about its generic placement.

The inspection of the original illustrations of *Parastenocaris chelifer* leaves no room for doubt that *P. chelifer* is a true *Siolicaris* by virtue of its peculiar structure of the male P3, which is remarkably similar to what can be seen in *S. jakobi.* Of particular importance is the sturdy, rectangular basis, ornamented with a row of strong spinules at the outer margin, an exp strongly bent inwards, similar to *S. jakobi* in structure but 1-segmented instead of 2-segmented as in *S. Jakobi*, and a thumb strong, longer than apophysis. However, the presence of a P3 endopod in the female, the distinct shape of male P5 and the position of the setae precludes the definitive inclusion of this species within *Siolicaris*. Hence we prefer to maintain *P. chelifer* as *Siolicaris species inquirenda*, pending its full redescription.

Siolicaris xyrophora*: *species inquirenda. According to Ranga Reddy (2001) and Schminke (personal communication), pincers-like P3, similar to what occurs in *Siolicaris*, would appear also in *P. cruzi* Noodt & Galhano, 1969 from Portugal. One might hypothesize a close relationship between *Siolicaris* and *P. cruzi* on the basis of this character. However, in our view, the *Siolicaris* species have more in common with *P. xyrophora* than with the Portuguese *P. cruzi. P. xyrophora* has lost the enp of the male P4 (*cf.* Noodt & Galhano 1969; Schminke, 2010), and much like in *S. sandhya*, this species has a row of spinules inserted at the inner margin of the male P4 basis. The basis of the male P3 is long and rectangular and has a strong row of spinules at the outer margin; the apophysis is short, with an inner spine at midlength of the P3, marking the distal rim of this structure; finally, the thumb (a spatulate spine) is much longer than the apophysis, having a hyaline margin. The female P4 enp is longer than exp-1, similarly to the Brazilian species and the P5 in both sexes have all setae distally inserted, with a row of spinules on the inner margin. The female P3 has a short enp as in the case of *P. chelifer*.

Noodt & Galhano (1969) included *P. xyrophora* within the *Parastenocaris nana*-group. However, this species is a Fontinalicaridinae, while those included in the *P. nana*-group are all Parastenocaridinae (viz. Schminke 2010). Here we prefer not to include this species formally within *Siolicaris*, but treat it as *Siolicaris species inquirenda,* pending its redescription.

Putative *Siolicaris* affinities within South American Parastenocarididae. The monophyly of the Neotropical Fontinalicaridinae is still difficult to assess on the basis of the current data. In South America, we can find at least three different phylogenetic lineages with unclear interrelationships. The monophyly of *Forficatocaris/Potamocaris* is well established by such synapomorphies as the transformed spinule at the inner margin of the enp-1 of male P1, a P3 very similar in morphology and a P4 enp in male strongly sclerotized (for more details, see Ahnert 1994). A second phylogenetic lineage would be the one constituted by the species composing the *Parastenocaris columbiensis*-group Noodt, 1972 which includes *P. columbiensis* Noodt, 1972, *P. kubitzkii* Noodt, 1972, and *P rottgeri* Noodt, 1972 plus *P. tapajoensis* Noodt, 1963a, which share a similar ornamentation of the male P4 basis and the same structure of male P3. A third clade would be the one composed by the genus *Murunducaris* plus the closely related *P. santaremensis* Noodt, 1963a, and *P. itica* Noodt, 1962, the genus *Brasilibathynellocaris* and the Gondwanan *Siolicaris*. Within this group, *Siolicaris*, *Brasilibathynellocaris* and *Parastenocaris itica*, in particular, have close affinities, sharing a strong and rectangular basis and a short exp-1 on the male P3 (a long apophysis, giving the impression of elongate P3 that occurs in *Brasilibathynellocaris* and *P. itica*), a long thumb, tending to form a forceps with apophysis.

No doubt our present observations do not shed much light on the monophyly of the Neotropical Fontinalicaridinae. Hence, detailed morphological and DNA studies are badly needed to address this issue. And yet, we are of the opinion that the *P. columbiensis*-group is the missing link between the “first” and the “third” phylogenetic lineages proposed above. This could be supported by the long and rectangular shape of the basis of the male P3 in *P. columbiensis*, *P. kubitzkii* and *P. tapajoensis*, similar to what can be seen in *Brasilibathynellocaris*, *P. itica* and *Siolicaris*, and the structure of the enp of the P4 in *P. columbiensis*, *P. kubitzkii*
and *P. rottgeri*, closely resembling the situation in some *Potamocaris* species. In the present scenario, it is hard either to confirm or deny the close kinship of the Neotropical Fontinalicaridinae. However, the presence of a Gondwanan link (viz. *Siolicaris sandhya*) and the pending study of *P. xyrophora* from Portugal strengthen the hypothesis that the Neotropical species of Fontinalicaridinae do not constitute a monophyletic unity and that the missing link between these “phylogenetic clusters” must be found somewhere in the Neotropical region, the Afrotropical region or the Oriental.

Biogeography. In groundwater ecosystems, two groups of Crustacea are dominant, viz. Bathynellacea and Copepoda Harpacticoida. The bathynellaceans, the ancestors of which inhabited the tropical seas during the Carboniferous times, display the Gondwanan lineage rather spectacularly (Ranga Reddy 2011). This group as a whole might have achieved its worldwide distribution prior to the breakup of Pangaea (Schminke 1981), and its present day geographic distribution can more plausibly be explained by the vicariance model (Schram 2008) rather than by the classic dispersal model (Schminke 1981).

A great deal of genus-level congruence among bathynellaceans testifies to the Gondwanan connection between South America, Africa and India (viz. Noodt, 1963b, Noodt, 1969b, Ranga Reddy & Schminke, 2005, Ranga Reddy, Bandari & Totakura, 2011, Ranga Reddy & Totakura, 2012, Schminke, 1973).

As for the Parastenocarididae, at least three groups are of Gondwanan origin. The genus *Kinnecaris* can be found in Africa, the Oriental region *sensu* Morrone (2002) and Australia (Schminke 2008, Ranga Reddy & Schminke 2008, Karanovic & Cooper 2011); *Siolicaris* species have been recorded in South America and India and the genus *Remaneicaris* occurs in the Neotropical region. Moreover, should *P. ahaggarica* Bozic, 1978 prove to be a *Remaneicaris* (see Corgosinho 2007), the range of this genus would extend to Africa. And vast areas of the globe including Gondwana landmasses still continue to be *terra incognita* for groundwater fauna. In this context, it would be rather interesting to investigate the taxonomic affinities of the recent Indian record of *Parastenocaris tirupatiensis* Ranga Reddy, 2012 with *Remaneicaris,* considering that the latter species has some interesting characters in common with *Remaneicaris*, such as the ornamentation of the outer margin of the exp-1–3 of P2 and P4 and the presence of a 1-segmented enp in the P3 of male.

According to Noodt (1969a) and Schminke (1981), the Parastenocarididae, as compared with the Bathynellacea, is a much younger group, having originated possibly in the early Tertiary or even earlier. It is known that copepods, because of their small size and fragility, fossilize poorly and their fossil record was constituted solely by one Cretaceous (c. 115 Ma) parasite and a few Miocene (c. 14 Ma) fossils (Selden *et al.* 2010). However, the recent discovery of copepod fragments from a single bitumen clast in a glacial diamictite of late Carboniferous age (c. 303 Ma) from eastern Oman extends the fossil record of copepods by some 188 Ma, and of free-living forms by 289 Ma (Selden *et al.* 2010). The fossils provide evidence of the extant family Canthocamptidae, believed to have colonized freshwater in Pangaea during Carboniferous times (Selden *et al.* 2010).

Canthocamptid copepods together with parastenocaridids are the most diverse freshwater group of harpacticoids (see Boxshall & Defaye 2008, Table 01). They occur practically in all freshwater bodies, from the hyporheic zone to mosses in springs, in deep wells and aquifers, moist soils, phytotelmata and mountain streams. Despite the co-occurrence of Canthocamptidae and Parastenocarididae in the same habitats, there is no evidence in favour of the presence of Parastenocarididae from the Carboniferous (no evidence on the contrary, either). Considering that harpacticoids are as old as 310 Ma (Selden *et al.* 2010), it would not be unlikely that parastenocaridids are older than previously assumed, occurring on Gondwana landmass prior to its breakup.

Should Noodt (1969a) and Schminke (1981) be correct about the ancient origin of the Bathynellacea, i.e. back to the Carboniferous (360–270 Ma) and the younger age of Parastenocarididae, i.e. early Tertiary (70–25 Ma), the Parastenocarididae fauna might have evolved after the breakdown of India from the Western Gondwanaland (125–120 Ma) and the northern drift of this landmass followed by its crush against Eurasia (20–15 Ma). Parastenocaridids could have reached, therefore, in accordance with this scenario, the Oriental region by dispersion from the West Gondwanaland via some remaining connections with the Northern Eurasia.

A dispersion following this route could explain the actual distribution of *S. sandhya* in India and the South American species. It could also explain the presence of *Parastenocaris xyrophora* (if it is a true *Siolicaris* or a closely related species) in Northern Portugal. However, the dispersion hypothesis cannot be tested and dispersion biogeography itself is a paradigm in crisis (Crisci & Morrone 1992).

Likewise in the case of Bathynellacea, the vicariance events involving the continental drift rather than the subsequent dispersal events are believed to be responsible for the Parastenocarididae worldwide distribution (Boxshall & Jaume, 2000). In this scenario, we hypothesize the origin of the genus *Siolicaris* before the split of the Gondwana. If proved that *P. xyrophora* is a *Siolicaris*, this could call for a dispersionist hypothesis or even to a much earlier origin of *Siolicaris* during the Pangaea.

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References

Ahnert, A. (1994) *Eidonomie, Systematik und Entwicklung von Potamocaris Dussart, 1979 und Forficatocaris Jakobi, 1969 (Copepoda, Harpacticoida, Parastenocarididae) sowie Verteilung im Lebensraum und Verhalten zweier koexistierender Vertreter beider Gattungen an einem sandigen Flußabschnitt im Küstengebirge von São Paulo (Brasilien).* Unpublished D. Phil. Thesis, Christian-Albrechts-Universität, Kiel, 226 pp.

Boxshall, G.A. & Defaye, D. (2008) Global diversity of copepods (Crustacea: Copepoda) in freshwater. *Hydrobiologia*, 595, 195–207.

Boxshall, G.A. & Jaume, D. (2000) Making waves: the repeated colonization of freshwater by copepod crustaceans. *Advances in Ecological Research*, 31, 61–79.

Bozic, B. (1978) Une nouvelle *Parastenocaris* du Hoggar (Crustacea, Copepoda, Harpacticoida). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 514 (3), 239–244.

Brünnich, M.T. (1772) *Zoologiae fundamenta praelectionibus academicis accomodata. Grunde i Dyrelaeren. Hafniae et Lipsiae.* Copenhagen and Leipzig, Apud Friderich Christian Pelt, 254 pp.

Chappuis, P.A. (1940) Die Harpacticoiden des Grundwassers des unteren Maintales. *Archiv für Hydrobiologie*, 36, 286–305.

Chappuis, P.A. (1955) Notes sur les Copépodes. 18. Nouveaux Harpacticoïdes des Pyrénées, 19. Harpacticoïdes cavernicoles de Grèce. 20. Copépodes Harpacticoïdes des Iles du Pacifique. *Notes Biospéologiques*, 10, 89–101.

Corgosinho, P.H.C. (2007) *Phylogenetic systematic of Remaneicaris Jakobi (Copepoda, Harpacticoida, Parastenocarididae) from the Neotropical region.* Unpublished D. Phil. Thesis, Instituto Nacional de Pesquisas da Amazônia/ Universidade Federal do Estado do Amazonas, Manaus, 326 pp.

Corgosinho, P. H. C. & Martinez Arbizu, P. (2005) Two new interstitial species of *Remaneicaris* Jakobi 1972 from Ribeirao 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. & Reid, J.W. (2008) Revision of the genus *Murunducaris* (Copepoda: Harpacticoida: Parastenocarididae), with descriptions of two newspecies from South America. *Journal of Crustacean Biology*, 28(4), 700–720.

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.

Corgosinho, P.H.C., Martínez Arbizu, P. & Santos-Silva, E.N. (2010a) 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., Martínez Arbizu, P. & Santos-Silva, E.N. (2010b) Three new interstitial species of *Remaneicaris* Jakobi, 1972 (Copepoda: Harpacticoida: Parastenocarididae) from Southern and Southeastern Brazil. *Invertebrate Zoology*, 2010, 7(1), 1–28.

Cottarelli, V. (1970) *Parastenocaris tyrrhenidis* n. sp., nuovo arpacticide interstiziale di Sardegna (Crustacea, Copepoda). *Fragmenta Entomologica*, 7, 61–71.

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.

Cottarelli, V. & Maiolini, B. (1980) *Parastenocaris veneris* n. sp., nuovo arpacticoide interstiziale del Lago di Vico (Crustacea,
Copepoda). *Fragmenta Entomologica*, 15(2), 243–252.

Crisci, J.V. & Morrone, J.J. (1992) A Comparison of Biogeographic Models: A Response to Bastow Wilson. *Global Ecology*

Dahl, E. (1956) On the differentiation of the topography of the crustacean head. *Acta Zoologica*, 37, 123–192.

Delachaux, T. (1924) Zur Kenntnis der Copepodenfauna von Surinam. II. Harpacticiden. *Zoologischer Anzeiger*, 59, 1–16.

Dussart, B.H. (1979) Algunos Copépodos de America del Sur. *Publicaciones Ocasionales del Museo Nacional de Historia Natural, Santiago de Chile*, 30, 1–13.

Dussart, B.H. (1984) Some Crustacea Copepoda from Venezuela. *Hydrobiologia*, 113, 25–67.

Dussart, B.H. & Defaye, D. (1990) Répertoire mondial des crustacés copépodes des eaux intérieures III. Harpacticoides. *Crustaceana Supplement*, 16, 1–384.

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.

Hertzog, L. (1936) Crustaceen aus unterirdischen Biotopen des Rheintales bei Strassburg. I. Mitteilung. *Zoologischer Anzeiger*,
114 (9–10), 271–279.

Hertzog, L. (1938) Crustaceen aus unterirdischen Biotopen des Rheintales bei Straßburg. *Zoologische Anzeiger*, 123, 45–56.

Huys, R. & Boxshall, G.A. (1991) *Copepod evolution*. The Ray Society, London, 468 pp.

ICZN (1999) *International Code of Zoological Nomenclature, fourth ed.* International Trust for Zoological Nomenclature, London, xxix + 306 pp.

Jakobi, H. (1969) *Forficatocaris noodti* n. gen., n. sp. (Copepoda Harpacticoidea) aus brasilianischem Limnopsammal. *Crustaceana*, 17, 231–238.

Jakobi, H. (1972) Trends (Enp. P4 ♂) innerhalb der Parastenocarididen (Copepoda Harpacticoidea). *Crustaceana*, 22, 127–146.

Jakobi, H. & Silva, J.L. (1962) Two new species of *Parastenocaris* (Copepoda: Harpacticoidea) from Santa Catarina, Brazil. *Proceeding of the United States National Museum*, 113, 389–397.

Karanovic, T. (2005) Two new subterranean Parastenocarididae (Crustacea, Copepoda, Harpacticoida) from Western Australia.
Records of the Western Australian Museum, 22, 353–374.

Karanovic, T. (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, Crustaceana Monographs*, 16, 293–337.

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, 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, 1573–613.

Kessler, E. (1913) *Parastenocaris brevipes* nov. gen. et nov. spec., ein neuer Sübwasserharpacticide. *Zoologischer Anzeiger*, 42, 514–520.

Lang, K. (1948) *Monographie der Harpacticiden.* Vol I and II. Håkan Ohlsson's Boktryckeri, Lund, 1683 pp.

Löffler, H. (1981) Copepoda. *In*: Hurlbert, S.H., Rodríguez, G. & dos Santos N.D. (Eds.) *Aquatic Biota of Tropical South America*. *Part 1. Arthropoda*. State University press, San Diego, pp. 14–19.

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.

Menzel, R. (1916) Über das Auftreten der Harpacticiden-Gattungen *Epactophanes* und *Parastenocaris* in Surinam. *Zoologischer Anzeiger*, 47, 149–152.

Milne Edwards, H. (1840) Ordre des Copepodes. *In:* M. Milne Edwards (Ed.) *Histoire naturelle des Crustaces, comprenant l'anatomie, la physiologie et la classification de ces animaux.* Librairie encyclopédique de Roret, Paris, pp. 411–529.

Morrone, J.J. (2002) Biogeographical regions under track and cladistic Scrutiny. *Journal of Biogeography*, 29, 149–152.

Noodt, W. (1962) Limnisch subterrane Copepoden der Gattung *Parastenocaris* Kessler aus Mittelamerika. *Beiträge zur*

Neotropischen Fauna, 2 (3), 223–248.

Noodt, W. (1963a) Subterrane Crustaceen der zentralen Neotropis. *Zoologischer Anzeiger*, 171, 114–147.

Noodt, W. (1963b) Estudios sobre Crustaceos de aguas subterraneas, III. Crustacea Syncarida de Chile Central. *Investigaciones Zoológicas Chilenas*, 10, 151–167.

Noodt, W. (1969a) Die Grundwasserfauna Südamerikas. *In:* Fittkau, E.J., Illies, J., Klinge, H., Schwabe, G. H. & Sioli, N. (Eds.). *Biogeography and Ecology in South America*, *2. Monographiae Biologicae.* Dr. W. Junk N.V. Publishers, The Hague 19, pp. 659–684.

Noodt, W. (1969b) Bathynellidae vom Tropenrand in São Paulo. *Naturwissenschaften*, 56(3), 144–145

Noodt, W. (1972) Drei neue *Parastenocaris* aus Kolumbien (Crustacea Copepoda). 1 Mitteilung über kolumbianische Grundwasser-Crustaceen. *Studies on Neotropical Fauna*, 7, 101–112.

Noodt, W. & Galhano, M.H. (1969) Studien an Crustacea Subterranea (Isopoda, Syncarida, Copepoda) aus dem Norden Portugals. *Publicaçoes do Instituto de Zoologia 'Dr. Augusto Nobre'*, 107, 1–75.

Ranga Reddy, Y. (2001) Discovery of Parastenocarididae (Copepoda, Harpacticoida) in India, with the description of three new species of *Parastenocaris* Kessler, 1913, from the river Krishna at Vijayawada. *Crustaceana*, 74(8), 705–733.

Ranga Reddy, Y. (2011) Gondwanan heritage in groundwater crustaceans of peninsular India. *Current Science*, 101(2), 156–158.

Ranga Reddy, Y. (2012) A new phreatic species of genus *Parastenocaris* Kessler (Copepoda: Harpacticoida: Parastenocarididae) from southeastern India, with a key to species of Indian subcontinent. *Biosystematica*, 5(2), 31–37.

Ranga Reddy, Y., Bandari, E. & Totakura, V.R. (2011) First Asian record of the genus *Parvulobathynella* (Malacostraca: Bathynellacea) with description of two new species from Southeastern India and amendment of the generic diagnosis. *Journal of Crustacean Biology*, 31(3), 485–508.

Ranga Reddy, Y. & Defaye, D. (2007) Parastenocarididae (Crustacea, Copepoda, Harpacticoida) of India: description of *Parastenocaris mahanadi* n. sp., and redescription of *P. curvispinus* Enckell, 1970 from hyporheic habitats. *Zootaxa*, 1580, 1–26.

Ranga Reddy, Y. & Defaye, D. (2009) Two new Parastenocarididae (Copepoda, Harpacticoida) from India: *Parastenocaris muvattupuzha* n. sp. from a river and *P. kotumsarensis* n. sp. from a cave. *Zootaxa*, 2077, 31–55.

Ranga Reddy, Y. & Schminke, H.K. (2005) A new bathynellid from India with unusual mouthparts (Bathynellacea: Bathynellidae). *Journal of Crustacean Biology*, 25, 25–30.

Ranga Reddy, Y. & Schminke, H.K. (2008) Discovery of the genus *Kinnecaris* Jakobi, 1972 (Copepoda, Harpacticoida, Parastenocarididae) in Southeastern India, with description of a new species. *Crustaceana*, 82(3), 311–326.

Ranga Reddy, Y. & Totakura V.R. (2012) A new phreatic species of the genus *Parvulobathynella* (Malacostraca: Bathynellacea) from southeastern India, along with an updated key to the species. *Journal of Crustacean Biology***,** 32(5): 871–882.

Reid, J.W. (1994) *Murunducaris juneae*, new genus, new species (Copepoda: Harpacticoida: Parastenocarididae) from a wet campo in central Brazil. *Journal of Crustacean Biology*, 14, 771–781.

Reid, J.W. (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(1), 173–187.

Reid, J.W. (1998) Maxillopoda–Copepoda. Harpacticoida. *In:* Young P.S. (Ed.) *Catalogue of Crustacea of Brazil*. Museu Nacional/ UFRJ, Rio de Janeiro, pp. 75–127.

Rouch, R. (1986) Copepoda: Les Harpacticoïdes souterrains des eaux douces continentales. *In:* Botosaneanu L. *(*Ed.), *Stygofauna Mundi, a Faunistic, Distributional, and Ecological Synthesis of the World Fauna Inhabiting Subterranean Waters.* EJ Brill/Dr. W Backhuys, Leiden, pp. 321–355.

Rouch, R. (1988) *Parastenocaris vandelii* n. sp., nouvelle Copépode harpacticide psammique des Pyrénées. *Crustaceana*, 54(2), 163–170.

Sars, G.O. (1903) Copepoda Harpacticoida. Parts I & II, Misophriidae, Longipediidae, Cerviniidae, Ectinosomidae (part). *An Account of the Crustacea of Norway*, 5, 1–28.

Schminke, H.K. (1973) Evolution, System und Verbreitungsgeschichte der Familie Parabathynellidae (Bathynellacea, Malacostraca). *Mikrofauna Meeresboden*, 24, 1–192.

Schminke, H.K. (1976) The ubiquitous telson and the deceptive furca. *Crustaceana*, 30, 292–300.

Schminke, H.K. (1981) Perspectives in the study of the zoogeography of interstitial Crustacea: Bathynellacea (Syncarida) and Parastenocarididae (Copepoda). *International Journal of Speleology*, 11(1–2), 83–89.

Schminke, H.K. (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.

Schminke, H.K. (2009) *Monodicaris* gen. n. (Copepoda, Harpacticoida, Parastenocarididae) from West Africa. *Crustaceana*, 82(3), 367–378.

Schminke, H.K. (2010) High-level phylogenetic relationships within Parastenocarididae (Copepoda, Harpacticoida). *Crustaceana*, 83(3), 343–367.

Schram, F.R. (2008) Does biogeography have a future in a globalized world with globalized faunas? *Contributions to Zoology*, 77, 127–133.

Selden, P.A., Huys, R., Stephenson, M.H., Heward, A.P. & Taylor, P.N. (2010) Crustaceans from bitumen clast in Carboniferous glacial diamictite extend fossil record of copepods. *Nature Communications*, 1(50), 1–6.

Walter, T.C. & Boxshall, G.A. (Eds) (2012) *World Copepoda database.* Available from www.marinespecies.org/copepoda/