

# 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)

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A new genus *Simplicaris* (Copepoda, Harpacticoida, Parastenocarididae) is established to accommodate two species collected from deep groundwater in Italy, *S. lethaea* sp. nov. and *S. veneris* (Cottarelli & Maiolini, 1980) **comb. nov.** *Parastenocaris hippuris* Hertzog, 1938 and *P. aedes* Hertzog, 1938 are ranked as *incertae sedis* within the genus. Members display complete absence of leg 5 in both sexes and an unusual elongation of the first exopodal segments of legs 1–4, in which exp-1 is distinctly longer than exp-2 or -3, or as long as exp-2 and -3 combined. As the systematic status of the family Parastenocarididae and of the type genus *Parastenocaris* is still in flux, a list of phylogenetically informative characters is proposed, along with a discussion of their various states in representative members of the family. The genus *Parastenocaris sensu stricto* is redefined to comprise only the *brevipes*-group. The remaining members of the genus are considered *Parastenocaris sensu lato* pending a thorough revision of the family. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 417–436.

ADDITIONAL KEYWORDS: copepod – harpacticoid – phylogeny – stygobiont – taxonomy.

## INTRODUCTION

The family Parastenocarididae currently contains 239 species and subspecies, accommodated in five genera: *Parastenocaris* Kessler, 1913, *Forficatocaris* Jakobi, 1969, *Paraforficatocaris* Jakobi, 1972, *Potamocaris* Dussart, 1979, and *Murunducaris* Reid, 1994. *Parastenocaris* is the most speciose and morphologically diverse genus, with 220 species presently known. It is considered cosmopolitan, whereas all the remaining genera are neotropical in distribution. From an ecological point of view most species are interstitial, and linked to freshwater, although some have been encountered in epigeal habitats, especially in the tropics (Rouch, 1986). Moreover, *Parastenocaris* has also been recorded from brackish environments such

as coastal lagoons, sublittoral sediments of estuaries, and brackish beaches (Wells, 1986).

The family name was first introduced by Chappuis (1933) as Parastenocarididae, although without justification or diagnosis. In a later paper, Chappuis (1940) explained the reasoning behind this course of action and indirectly provided the family diagnosis by designating *Parastenocaris* as sole genus. Noodt (1965) emended the spelling to 'Parastenocarididae'. Although most authors (e.g. Lang, 1948; Rouch, 1986; Dussart & Defaye, 1990; Janetzky, Enderle & Noodt, 1996) attributed the family to Chappuis (1933), with the exceptions of Borutskii (1952) and Damian-Georgescu (1970), according to ICZN (2000: Article 13.2.1), the family name proposed by Chappuis (1933) is merely a *nomen nudum*. As a matter of fact, Article 13.2.1 states that 'A family group name first published after 1930 and before 1961 which does not satisfy the provisions of article 13.1 is available from its original publication only if it was used as valid before 2000, and also was

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not rejected by an author who, after 1960 and before 2000, expressly applied Article 13 of the then current editions of the Code'. Reid (1994: 775) formally rejected Chappuis (1933) as unavailable stating that 'the name did not become available until a cursory diagnosis was eventually supplied (Chappuis, 1940), as correctly recognized by Damian-Georgescu (1970)'.

The family is notorious for its ill-defined genera. Most problems arise from the fact that the descriptions of many species of *Parastenocaris* are inadequate, omitting morphological details recently shown to be taxonomically significant. Serious impediments to the assessment of natural groups are also related to the mosaic distribution of characters within the presently recognized genera, and to the differential weights assigned by different authors to several morphological characters, including the male antennular segmentation pattern, the morphology of the penultimate antennular segment, the basic structure of the female genital field, the morphology and ornamentation of the male leg 3, the general morphology of the male leg 4 (including the ornamentation of the basis and the structure of the endopod), the morphology of leg 5 and its mediobasal seta, the relative position of the lateral and dorsal setae on the caudal rami, and the integumental window patterns.

Recent ecological investigations in Italian groundwaters resulted in the discovery of a new species of parastenocaridid, representing a new genus which shows affinities to *Parastenocaris*.

## MATERIAL AND METHODS

Specimens were collected from the interstitial habitat by using the Bou-Rouch method (Bou & Rouch, 1967) and filtering through a 60 µm mesh net. Specimens were preserved in 7% formalin solution and dissected in polyvinyl lactophenol. Drawings and measurements were made using a camera lucida on a Leitz Laborlux phase contrast microscope. Additional analyses of morphological details were performed by using a Confocal Laser Scanning Microscope (CLSM) (Saras-tro 2000, Molecular Dynamics equipped with Argon ion laser, 25 mW output) coupled with a Nikon Optiphot fluorescence microscope. The descriptive terminology of Huys & Boxshall (1991) is adopted. Abbreviations used in the text and figures are: P1–P6, first to sixth thoracopods; exp., exopod; enp., endopod; exp (enp) -1 (-2, -3) to denote the proximal (middle, distal) segment of a ramus.

### MATERIAL EXAMINED

*Parastenocaris trinacriae* Pesce, Galassi & Cottarelli, 1988. ♂ holotype, 5 ♀♀ paratypes, personal collection of G. L. Pesce, University of L'Aquila, Italy.

*Parastenocaris kalypso* Pesce, Galassi & Cottarelli, 1988. ♂ holotype, 1 ♀ paratype, personal collection of G.L. Pesce, University of L'Aquila, Italy.

*Parastenocaris veneris* Cottarelli & Maiolini, 1980. ♂ holotype, 4 ♂♂, 5 ♀♀ paratypes, personal collection of V. Cottarelli, University 'La Tuscia', Viterbo, Italy.

*Parastenocaris orcina* Chappuis, 1938. 2 ♂♂, 1 ♀, Castelcivita Cave, South Italy, personal collection of D. Galassi, University of L'Aquila, Italy.

*Parastenocaris* sp. 1 ♂, Pertosa Cave, South Italy, personal collection of D. Galassi, University of L'Aquila, Italy.

*Parastenocaris glacialis* Noodt, 1954. 1 ♂, 2 ♀♀, Val Fondillo, Abruzzo, central Italy, personal collection of D. Galassi, University of L'Aquila, Italy.

*Parastenocaris lorenzae* Pesce, Galassi & Cottarelli, 1995. 8 ♂♂, 6 ♀♀, Val Fondillo, Abruzzo, central Italy, personal collection of D. Galassi, University of L'Aquila, Italy.

*Parastenocaris andreji* Brancelj, 2000. ♀ holotype (2000–2252), 1 ♀ paratype (reg. no. NHM 2000–2253), Natural History Museum, London.

*Parastenocaris brevipes* Kessler, 1913. 1 ♀, 3 ♂♂, Onkimanjarvi Lake, Evo village, municipality of Lamni, South Hame, Finland, National Museum of Natural History, Smithsonian Institution, Washington, D. C. (reg. no. USNM 259764).

*Parastenocaris glareola* Hertzog, 1936. 1 ♂, 1 ♀, Miribel canal, alluvial plain of the River Rhône, France, personal collection of D. Galassi, University of L'Aquila, Italy.

*Parastenocaris fontinalis borea* Kiefer, 1960. 1 ♂, 1 ♀, Méant, alluvial plain of the River Rhône, France, personal collection of D. Galassi, University of L'Aquila, Italy.

*Parastenocaris* sp. 1 ♂, 1 ♀, Stiffe Cave, central Italy, personal collection of D. Galassi, University of L'Aquila, Italy.

*Parastenocaris crenobia* Galassi, 1997. 1 ♂, spring of the River Gizio, central Italy, personal collection of D. Galassi, University of L'Aquila, Italy.

*Forficatocaris schadeni* Reid, 1982. 2 ♂♂, 2 ♀♀, Fazenda Água Limpa, Campo Úmido da Onça, Distrito Federal, Brazil, National Museum of Natural History, Smithsonian Institution, Washington, D. C. (reg. no. USNM 250054).

## SYSTEMATICS

### FAMILY PARASTENOCARIDIDAE CHAPPUIS, 1940

#### *SIMPLICARIS* GEN. NOV.

*Diagnosis.* Parastenocarididae. Body vermiform, without clear demarcation between prosome and urosome; integument without surface pits, very feeble

sclerotization. Hyaline frills of cephalothorax and somites bearing P2–P4 and abdominal somites plain. Female genital and first abdominal somites completely fused forming a genital double-somite. Anal operculum smooth. Caudal ramus cylindrical, elongate; with seven setae in both sexes. Sexual dimorphism in body size, antennule, P3, P4 endopods and ornamentation of basis, and genital segmentation.

Rostrum small, not defined at base. Antennule 7-segmented in female, with aesthetasc on segments 4 and 7; 8-segmented and haplocer in male, with geniculation between segments 6 and 7, and aesthetasc on segments 5 and 8. Antenna with allobasis; free distal endopodal segment with two lateral and five distal elements, two of them geniculate, the outermost distally crenulate. Antennary exopod well defined at base, bearing one seta. Mandibular palp 1-segmented, with two apical setae. Maxillule: praecoxal arthrite with three curved robust spines plus four anterior subterminal setae; one element inserted on an apparent peduncle (or pedestal segment); one element on coxal endite; basis with three naked setae, endopod and exopod absent. Maxilla: maxillary syncoxa with two endites, proximal one not defined at base, bearing one seta, distal endite well developed, with two apical elements, one of which apically crenulate, and subapical element; allobasis drawn out into a crenulate claw; endopod incorporated into allobasis or rudimentary, with two setae. Maxilliped well developed, subchelate; syncoxa unarmed, basis elongate, endopod represented by claw, with one accessory seta.

P1, P2 and P4 with 3-segmented exopods in both male and female; exp-1 distinctly longer than segments 2 or 3, or as long as exp-2 and -3 combined. P1 basis without inner seta in both sexes; P2 and P4 basis without outer seta. P1: exp-1 with outer spine, exp-2 unarmed, exp-3 with two outer spines and two apical geniculate setae. Endopod 2-segmented; enp-1 unarmed, enp-2 with one apical geniculate seta and one spine. P2: exp-1 as long as exp-2 and -3 combined, with one outer spine; exp-2 unarmed, exp-3 with one outer spine and two apical setae; endopod 1-segmented. Female P3 with two-segmented exopod and 1-segmented endopod. Male P3 transformed, basis with or without rudimentary endopod; when present, endopod reduced to a simple and short seta; basal outer seta well developed, exopod slender in which former segments 1 and 2 are fused, former proximal segment representing largest part of leg; former distal segment represented by a short part extended from the insertion of outer spine to the subterminal constriction, ending with rounded apophysis, outer subdistal spine representing outer spine of former proximal exopodal segment, not longer than apophysis. P4: exp-1 with one outer spine, exp-2 unarmed, exp-3 with one outer spine and one apical seta. Female

endopod 1-segmented, male endopod transformed, ornamentation of basis consisting of two elements, located anterior to insertion of endopod. P5 absent in both sexes. P6 absent in the male; reduced in the female to form small genital operculum without any trace of armature.

*Type species. **Simplicaris lethaea** sp. nov.*

*Other species. *Parastenocaris veneris* Cottarelli & Maiolini, 1980 = *Simplicaris veneris* (Cottarelli & Maiolini, 1980) **comb. nov.***

*Species incertae sedis. *Parastenocaris hippuris* Hertzog, 1938; *Parastenocaris aedes* Hertzog, 1938.*

*Etymology.* The generic name is derived from the Latin *simplex*, alluding to the reduction in the number of legs, the fifth leg being completely absent in both male and female; combined with the Greek *caris* (= shrimp).

#### **SIMPLICARIS LETHAEA SP. NOV.**

*Material examined and type locality.* Male (holotype), female (paratype), completely dissected and mounted in polyvinyl lactophenol, deposited in the Natural History Museum, London (reg. no NHM.2004.48 holotype; NHM.2004.49 paratype). Other paratypes: 3 ♂♂, 1 ♀ deposited in the Natural History Museum, London. Other material: 3 ♂♂, 2 ♀♀ in the collection of D. Galassi (University of L'Aquila). The type specimens were collected from interstitial habitats of the Presciano Spring system (Capestrano, L'Aquila, central Italy), 150 cm below the spring bed, temperature 10.55°C, electrical conductivity (25°) 483 µS/cm, pH 7.28, dissolved oxygen 8.28 mg/L, sediment composed of gravel and coarse sand, 31.vii.1996, coordinates 42°16'05"N, 13°46'56"E. One ♂ collected from interstitial habitat of the same spring, 150 cm below the spring bed, on the right side of the spring, temperature 11.88°C, electrical conductivity (25°) 489 µS/cm, pH 7.36, dissolved oxygen 8.42 mg/L, sediment composed of a large amount of particulate organic matter (13.63 mg/L), fine sand and silt, 28.vi.1996. One ♀ collected from interstitial habitat in the same spring system (Abate Spring), 150 cm below the spring bed, temperature 11.31°C, electrical conductivity (25°) 516 µS/cm, pH 7.36, dissolved oxygen 8.80 mg/L, sediment composed of fine sand, 18.ix.1996, altitude: 330 m a.s.l., coordinates 42°16'04"N, 13°47'37"E, coll. A. Marcheggiani, P. De Laurentiis & D. Galassi.

#### *Description*

*Male.* Total body length of the holotype, measured from tip of rostrum to posterior margin of caudal rami, 279 µm (range: 260–304 µm, with mean of 284 µm based on eight individuals). Body vermiform, slender

(Fig. 1A). Integument without surface pits, only feebly sclerotized. Hyaline frills of cephalothorax, somites bearing P2–P4 and urosome smooth. Integumental windows, located dorsally, rounded on cephalic shield and elliptical on abdominal somites, excluding anal somite. Cephalothorax and both thoracic and abdominal somites with cuticular ornamentation apparently represented by reduced number of paired sensilla (Fig. 1A). Anal somite with paired sensilla on dorsal side only (Fig. 1B). Anal operculum rounded, not protruding beyond insertion line of caudal rami. Caudal rami with complete setal pattern (seven setae) (Fig. 1B). Anterolateral accessory seta (I), anterolateral seta (II) and posterolateral seta (III) inserted on distal third of ramus. Outer terminal seta (IV) short (length seta/length caudal ramus: 0.42–0.46) and naked, inner terminal seta (V) plumose and long (length seta/length caudal ramus: about 3); terminal accessory seta (VI) slightly longer than outer terminal seta; dorsal seta (VII) inserted dorsomedially on distal third of caudal ramus, longer than setae IV and VI (length seta/length caudal ramus: about 1). Fine spinules located on ventral distal margin of caudal rami. One pore located ventrolaterally to insertion of setae I–III.

Rostrum small, not defined at base; with two dorsal sensilla (Fig. 1A).

Antennule (Fig. 1C) elongate, 8-segmented. Segment 1 with one ventral spinule row. Segment 2 longest. Segment 4 represented by small U-shaped sclerite. Segment 5 largest, sclerotized. Segment 7 prolonged into an apophysis with rounded tip. Armature formula: 1-[0], 2-[5 bare + 1 unipinnate], 3-[3], 4-[0], 5-[3 + (1 + ae)], 6-[0], 7-[0], 8-[7 + acrothek]. Apical acrothek consisting of two setae of different length and a slender, short aesthetasc. Aesthetasc on segment 5 very large, reaching far beyond distal segment of antennule.

Antenna (Fig. 1D): coxa unarmed; allobasis with two transverse spinule rows on inner margin; exopod 1-segmented, well-defined at base, bearing one unipinnate spine; free endopod with inner spinule row, armature consisting of two outer spines, two apical spines, two apical geniculate setae and one apically serrate seta; a row of spinules at outer corner.

Mandible (Fig. 2A): coxal gnathobase elongate, cutting edge with two distally crenulate coarse teeth and row of smaller teeth; naked seta at dorsal corner. Mandibular palp uniramous, 1-segmented, with two apical setae.

Maxillule (Fig. 2B): praecoxal arthrite well developed, rectangular, with three strong curved spines accompanied by four tiny, bare setae; one anterior surface seta inserted on a sort of peduncle. Coxal endite with one seta. Basis with three apical setae. Exopod and endopod absent.

Maxilla (Fig. 2C): syncoxa with two endites. One setule inserted on proximal part of syncoxa. Proximal endite with one seta; distal endite with one naked and one distally crenulate setae, one flaccid seta subapically inserted. Allobasis drawn out into a strong claw, distally spinulose; endopod represented by two setae, subequal in length.

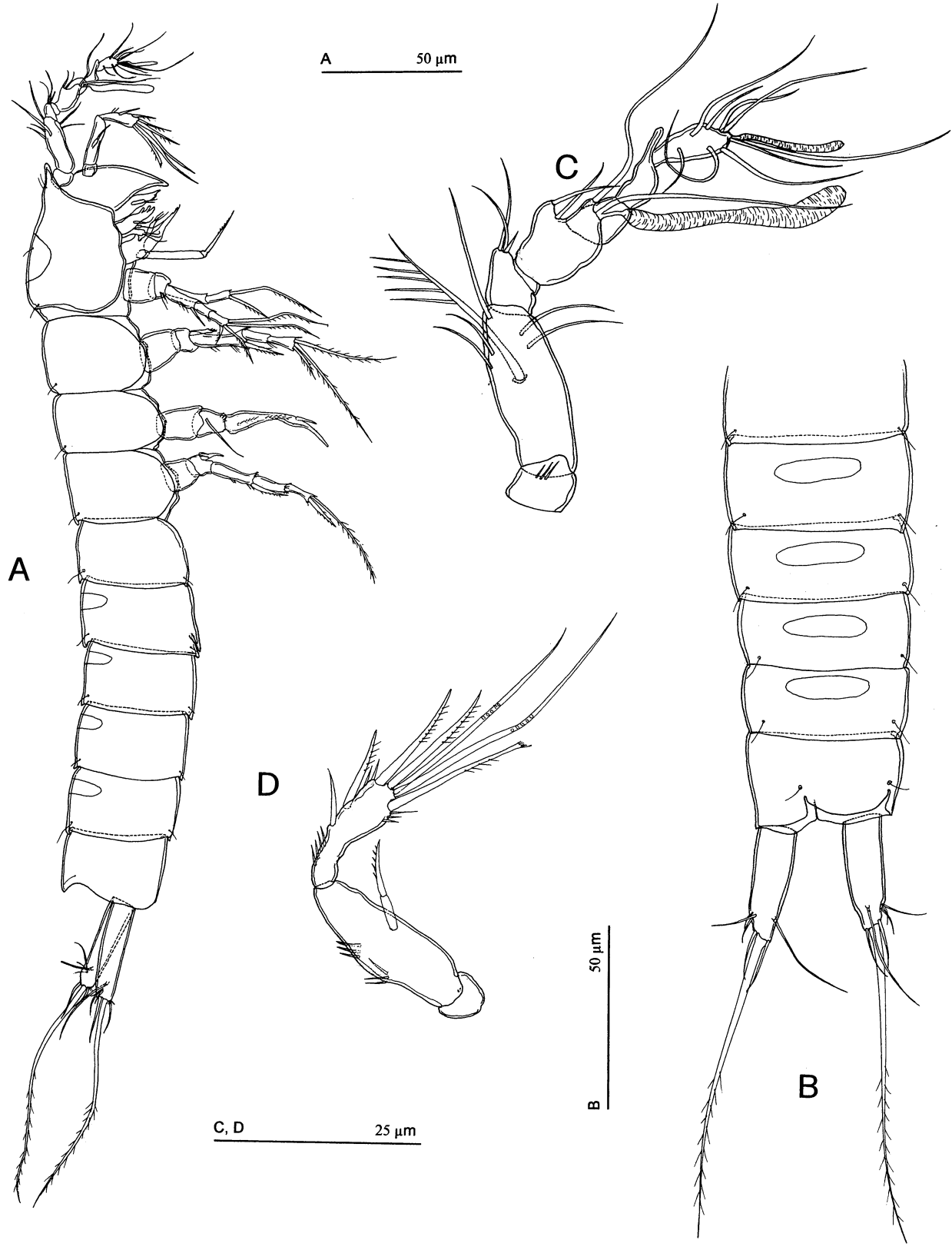
Maxilliped (Fig. 2D): very large, as long as leg 1; subchelate. Syncoxa small and unarmed; basis elongate and slender, unarmed; endopod represented by distally unipinnate claw accompanied by short seta basally.

P1–P2 and P4 with 3-segmented exopods. P1 with 2-segmented endopod; P2 and P4 with 1-segmented endopods. P3 transformed into a pincer-like structure. Intercoxal sclerites P1–P4 without ornamentation.

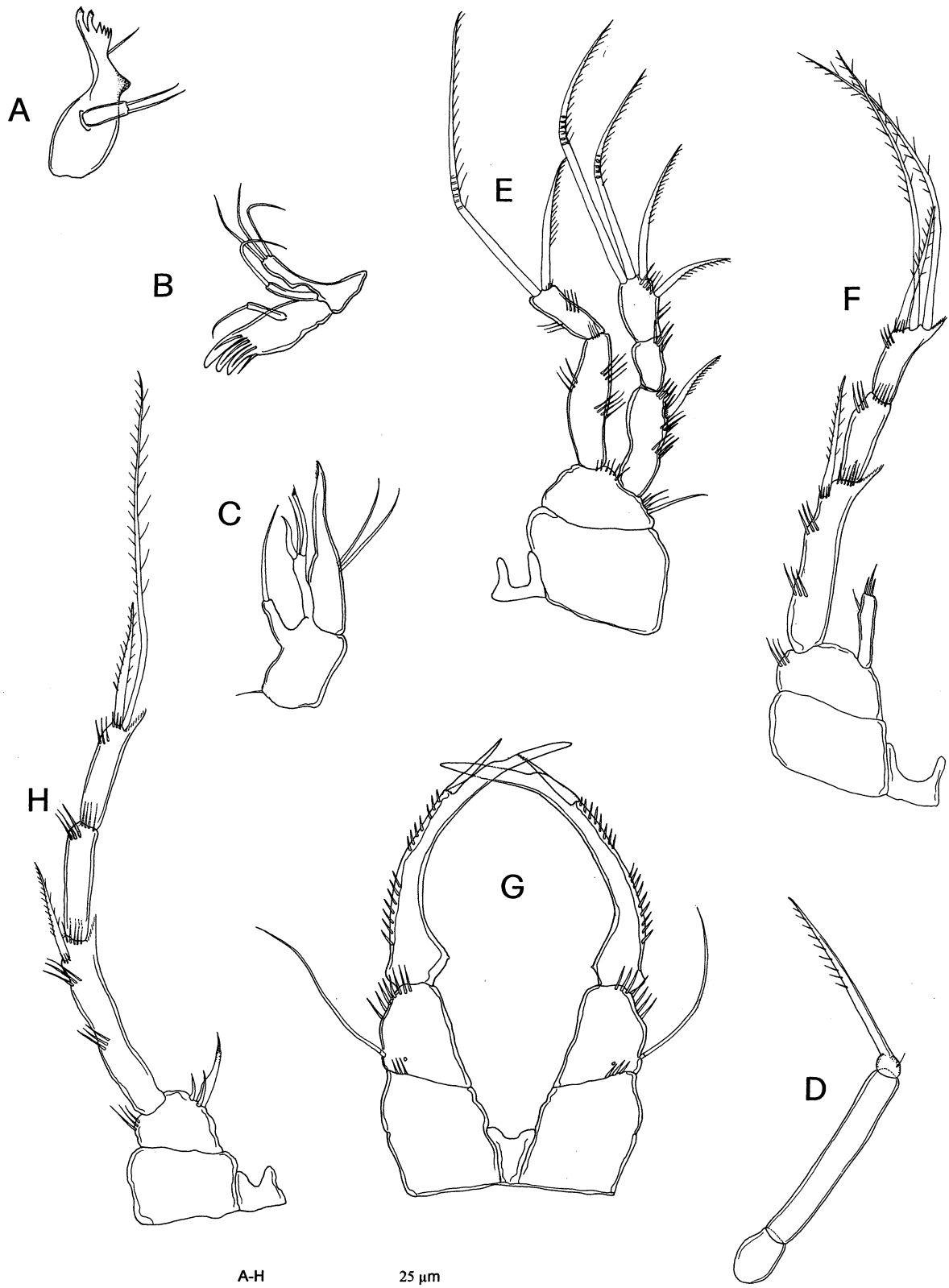
P1 (Fig. 2E): coxa without ornamentation. Basis with one outer seta, with spinule row along outer margin and row of fine spinules between exopod and endopod. Exopod about as long as endopod: exp-1 with one long and slender unipinnate outer spine and three transverse spinule rows on outer margin; exp-2 about half as long as exp-1, unarmed, ornamentation represented by distal spinule row on outer margin; exp-3 only slightly longer than exp-2, with two unipinnate outer spines, and two geniculate setae apically, with two outer spinule rows. Endopod: enp-1 only slightly shorter than exp-1 and exp-2 combined; with two transverse spinule rows along outer margin, one spinule row near about middle of inner margin, and a terminal row of fine spinules; enp-2 about half as long as enp-1, with one apical unipinnate spine and one geniculate seta, one outer and one inner spinule row.

P2 (Fig. 2F): coxa without ornamentation. Basis without outer seta, with spinule row along outer margin. Exopod elongate, exp-1 about as long as exp-2 and -3 combined; exp-1 with one bipinnate outer spine (densely spinulose along outer margin, and sparsely spinulose along inner margin), with two transverse spinule rows along outer margin, one spinule row distally and fine spinules around insertion of spine. Exp-2 unarmed; ornamentation consisting of one spinule row in distal third of outer margin and a terminal spinule row. Exp-3 about as long as exp-2, with one bipinnate outer spine and two subequal apical setae; all elements more densely spinulose along outer margin; one spinule row in distal third of outer margin and fine spinules around insertion of outer spine. Endopod 1-segmented, with one minute spinule in distal third of outer margin and three apical spinules, the medial one longer than the adjacent two.

P3 (Fig. 2G): coxa with one row of spinules distally. Basis with long outer seta and one row of spinules along outer margin; one anterior surface-pore. Exopod 1-segmented; former exp-1 elongate and slender, inwardly curved, with two spinule rows on outer



**Figure 1.** *Simplicaris lethaea* gen. et sp. nov. (A, C: ♂ paratype; B, D: ♂ holotype). A, habitus. B, urosome. C, antennule. D, antenna.



**Figure 2.** *Simplicaris lethaea* gen. et sp. nov. (A–C, G: ♂ paratype; D–F, H: ♂ holotype). A, mandible. B, maxillule. C, maxilla. D, maxilliped. E, P1. F, P2. G, P3. H, P4.

margin; inner margin with lobate expansion proximally; outer spine inserted close to the beginning of former exp-2; former exp-2 very short, ending with spinous apophysis with rounded tip. Endopod absent.

P4 (Fig. 2H): coxa without ornamentation. Basis without outer seta, with spinule row along outer margin, with two curved outward articulated spinules, located near insertion of endopod. Exopod elongate, exp-1 about as long as exp-2 and -3 combined. Exp-1 with one bipinnate outer spine (densely spinulose along outer margin, and sparsely spinulose along inner margin), with two transverse spinule rows, one spinule row distally and fine spinules around insertion of outer spine. Exp-2 unarmed; ornamentation consisting of one spinule row in distal third of outer margin and a terminal spinule row. Exp-3 about as long as exp-2, with one bipinnate outer spine and one apical seta, both being more densely spinulose along outer margin; one spinule row in distal third of outer margin and fine spinules around insertion of outer spine. Endopod 1-segmented, terminal seta incorporated into segment.

P5 and P6 absent.

*Female.* Total body length from 302 to 365 µm, with mean of 324 µm based on five individuals. Habitus similar to male. No sexual dimorphism in body shape, morphology and ornamentation of cephalothorax, and caudal rami. Integumental windows located dorsally on the cephalic shield, on the anterior surface of the genital double-somite, and the second and third abdominal somites. Cephalic appendages identical in both sexes, excluding antennules. Urosome 5-segmented. Female genital and first abdominal somites completely fused forming genital double-somite. Genital field located in anterior half of genital double-somite (Fig. 3A). Opercula well sclerotized, symmetrical, linear in shape and covering the copulatory pore (Fig. 3B).

Antennule (Fig. 3C) elongate, 7-segmented. Segment 1 with one ventral spinule row. Segment 2 longest. Armature formula: 1-[0], 2-[3 bare + 1 unipinnate], 3-[4], 4-[1 + (1 + ae)], 5-[1], 6-[1], 7-[7 + acrothek]. Apical acrothek consisting of two setae of different length and a slender, short aesthetasc. Aesthetasc on segment 4 reaching midlength of distal segment of antennule.

P2 (Fig. 3D): coxa without ornamentation. Basis without outer seta, with spinule row along outer margin. Exopod elongate, exp-1 about as long as exp-2 and -3 combined. Exp-1 with one bipinnate outer spine (densely spinulose along outer margin, and sparsely spinulose along inner margin), with two transverse spinule rows, one spinule row distally and fine spinules around insertion of outer spine. Exp-2 unarmed; ornamentation consisting of one spinule row

in distal third of outer margin and a terminal spinule row. Exp-3 about as long as exp-2, with one bipinnate outer spine and two subequal apical setae; one spinule row along distal third of outer margin. Endopod 1-segmented, with two minute spinules in distal third of outer margin and four apical spinules.

P3 (Fig. 3E): coxa without ornamentation. Basis with long outer seta, with spinule row along outer margin. Anterior surface-pore present. Exopod elongate, exp-1 about 1.5 times longer than exp-2. Exp-1 with one bipinnate outer spine (densely spinulose along outer margin, and sparsely spinulose along inner margin) with two transverse spinule rows, one spinule row distally and fine spinules around insertion of outer spine. Exp-2 with one bipinnate outer spine and one apical seta; one spinule row along distal third of outer margin and fine spinules around insertion of outer spine. Endopod 1-segmented, pointed at distal tip, with minute spinules in distal third.

P4 (Fig. 3F): coxa without ornamentation. Basis without outer seta, with spinule row along outer margin. Exopod elongate. Exp-1 long, but shorter than exp-2 and -3 combined; one bipinnate outer spine (densely spinulose along outer margin, and sparsely spinulose along inner margin); two transverse spinule rows, one spinule row distally and fine spinules around insertion of outer spine. Exp-2 unarmed, with one spinule row in distal third of outer margin and a terminal spinule row. Exp-3 about as long as exp-2, with one bipinnate outer spine and one apical seta, one spinule row along distal third of outer margin and fine spinules around insertion of outer spine. Endopod 1-segmented, with three distal subequal setules.

P5 absent. No trace of P6 armature.

*Etymology.* The species name refers to the Latin adjective *lethaea*, derived from *Lethe*, a mythical spring in Hell.

## DISCUSSION

### TAXONOMIC CONFUSION AT GENUS LEVEL

The new genus *Simplicaris* is placed in the family Parastenocarididae as defined by Lang (1948), showing the closest affinities with the genus *Parastenocaris*. Within this genus, Lang (1948) delineated seven species-groups. Besides the *proserpina*-group already defined by Kunz (1938), Lang recognized the *brevipes*-group, *minuta*-group, *nana*-group, *clujensis*-group, *muscolicola*-group, *fontinalis*-group, and *staheli*-group. These groups were based on the segmentation of the male leg 2 endopod (1-segmented vs. 2-segmented) and the gross morphology of the male leg 4 endopod, including the ornamentation of its basis. The same author emphasized the potential phylogenetic value of these groups, suggesting an evolutionary trend from

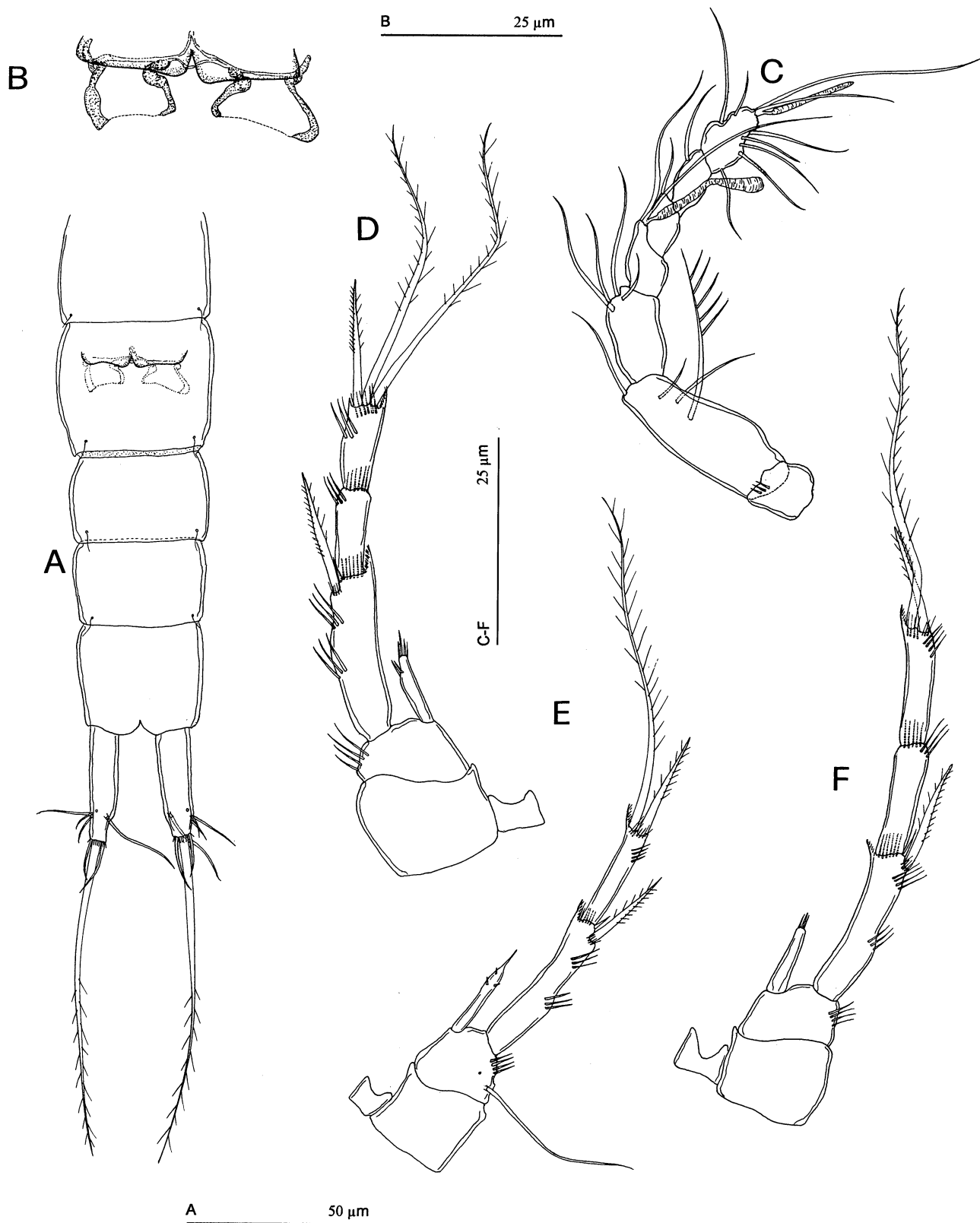


Figure 3. *Simplicaris lethaea* gen. et sp. nov. (♀ paratype). A, urosome. B, genital field. C, antennule. D, P2. E, P3. F, P4.



the more primitive *staheli*-group on the basis of the presence in *P. chelifer* Delachaux, 1923 of the outer spine on P1 exp-2 (absent in the remaining species of the genus), the presence of five elements on P1 exp-3 (vs. four in other *Parastenocaris*), the 2-segmented male leg 2 endopod (vs. 1-segmented in other *Parastenocaris*), and the weakly developed sexual dimorphism in the P4 endopod. Unfortunately, the low standard of Delachaux' (1923) drawings prevents us from assessing the real condition of these features and Lang (1948: 1227) himself doubted the accuracy of Delachaux' illustration of P1. Therefore, Martínez Arbizu & Moura (1994) and Martínez Arbizu (1997) questioned reports of a 2-segmented P2 endopod within Parastenocarididae, and voiced the opinion that a 1-segmented P2 endopod is a symplesiomorphy of the family.

According to Lang's (1948) division, *Simplicaris*, as defined herein, could potentially be assigned to the *minuta*-group due to the ornamentation of the male leg 4 basis (2–4 spinules) and the 1-segmented male P2 endopod. On the basis of these two diagnostic characters, at least 48 species and three subspecies are attributable to the *minuta*-group (Table 1).

As a matter of fact, the 1-segmented condition of the male P2 endopod is widespread in the Parastenocarididae and cannot possibly be considered an autapomorphy of this group. Similarly, the ornamentation of the male leg 4 basis is not necessarily indicative of phylogenetic closeness since species belonging to the *minuta*-group (Table 1), all showing 2–4 spinules, may differ significantly in robust morphological characters, such as the position of the lateral and dorsal setae on the caudal rami, the structure of P5, the sexual dimorphism in the morphology of the penultimate antennular segment in males, and the morphology of the female genital field. For instance, *P. pannonicus* shows a male leg 4 basis with two elements, in conjunction with a divergent arrangement of the lateral setae (inserted at the middle of the caudal ramus and the dorsal seta in a terminal position), and a male penultimate antennular segment which is not transformed. These characters suggest that *P. pannonicus* is only distantly related to most species of the so-called *minuta*-group. Similarly, *P. quollensis*, *P. lyncaea*, *P. aethiopica*, *P. impervia*, *P. cataractae*, and *P. kimi* show a robust and uncinat inner process on the P5, having a concave outer margin which is strongly protruding from the free distal margin of the laminar P5. In *P. kimi*, *P. lyncaea* and *P. cataractae* the latter condition is linked to a different position of the lateral setae of the caudal rami (inserted in the proximal third of the ramus). Additionally, the penultimate antennular segment in the male is not transformed in *P. lyncaea*, *P. hera*, *P. amyclaea*, *P. calliroe*, *P. federici*, and *P. etrusca*, whereas it is differently

**Table 1.** List of the species belonging to the *minuta*-group *sensu* Lang (1948)

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<i>P. acherusia</i> Noodt, 1955
<i>P. aethiopica</i> Cottarelli & Bruno, 1995
<i>P. amyclaea</i> Cottarelli, 1969
<i>P. andalusica</i> Enckell, 1965
<i>P. aphroditis</i> Cottarelli & Bruno, 1996
<i>P. balcanica</i> Petkovski, 1959
<i>P. calliroe</i> Cottarelli, 1969
<i>P. cataractae</i> Cottarelli, 1982
<i>P. cornuta</i> Chappuis, 1955
<i>P. crenobia</i> Galassi, 1997
<i>P. dentulatus</i> Chappuis & Rouch, 1959
<i>P. dubia</i> Kiefer, 1933
<i>P. elegans</i> Kiefer, 1933
<i>P. etrusca</i> Cottarelli, Bruno & Venanzetti, 1995
<i>P. federici</i> Stoch, 2000
<i>P. gracilis</i> Chappuis, 1954
<i>P. hera</i> Cottarelli, 1969
<i>P. hippuris</i> Hertzog, 1938
<i>P. impervia</i> Cottarelli & Bruno, 1995
<i>P. karamani brevicauda</i> Damian, 1958
<i>P. karamani karamani</i> Chappuis, 1937
<i>P. kimi</i> Dumont, 1981
<i>P. lorenzae</i> Pesce, Galassi & Cottarelli, 1995
<i>P. lyncaea</i> Cottarelli & Bruno, 1994
<i>P. macaco</i> Chappuis, 1952
<i>P. micheli</i> Chappuis & Rouch, 1959
<i>P. minuta</i> Chappuis, 1925
<i>P. minutissima</i> Chappuis, 1937
<i>P. narentina</i> Petkovski, 1959
<i>P. nertensis</i> Rouch, 1990
<i>P. numidiensis</i> Rouch, 1987
<i>P. oligoalina</i> Cottarelli, Bruno & Venanzetti, 1995
<i>P. orcina</i> Chappuis, 1938
<i>P. pannonicus</i> Török, 1935
<i>P. pasquini</i> Cottarelli, 1972
<i>P. phreatica</i> Chappuis, 1936
<i>P. quollensis</i> Cottarelli & Bruno, 1995
<i>P. ranae</i> Stoch, 2000
<i>P. rascana</i> Petkovski, 1959
<i>P. rivi</i> Cottarelli & Bruno, 1994
<i>P. silvana</i> Cottarelli, Bruno & Berera, 2000
<i>P. stammeri gallicus</i> Chappuis & Rouch, 1959
<i>P. stammeri stammeri</i> Chappuis, 1937
<i>P. stellae</i> Cottarelli, Saporito & Puccetti, 1981
<i>P. trichelata</i> Reid, 1995
<i>P. trinacriae</i> Pesce, Galassi & Cottarelli, 1988
<i>P. triphyda</i> Cottarelli & Bruno, 1993
<i>P. trisaetosa</i> Chappuis, 1954
<i>P. tumida</i> Kiefer, 1961
<i>P. vicesima dalmatina</i> Petkovski, 1959
<i>P. vicesima vicesima</i> Klie, 1935

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shaped in other species attributable to the *minuta*-group for which a description of the male antennule is available. Although for most species the current descriptions lack fundamental morphological details, the evidence already available strongly suggests polyphyletic origin of the *minuta*-group. Unfortunately, the original description of *P. minuta* by Chappuis (1925) was based on only a few drawings of poor quality, preventing us from refining the taxonomic concept of the *minuta*-group.

Jakobi (1972) divided *Parastenocaris* into 26 genera, but his orthogenetic revision was criticized by several authors (Schminke, 1976, 1986; Cottarelli & Maiolini, 1980; Dumont, 1981; Por, 1981; Dussart, 1984; Rouch, 1986; Dussart & Defaye, 1990; Reid, 1994) because it was almost exclusively based on the male leg 3 morphology and on supposed reductive trends shown by the male leg 4 endopod. Moreover, several of his proposed genera combined species that show a fundamentally different morphology in other characters, suggesting their polyphyletic nature. Only the genus *Cafferocaris* Jakobi, 1972 was considered valid by Schminke (1981, 1986), but nevertheless requires redefinition. It is, however, conceivable that some of Jakobi's (1972) genera may have to be reinstated in the future when revisionary work within the genus *Parastenocaris* becomes available. Kiefer (1976) assigned subgeneric rank to all of these genera.

On the basis of the diagnoses proposed by Jakobi (1972), the genus *Simplicaris* could be accommodated into the genus *Minutacaris* Jakobi, 1972, and to a lesser extent, into *Pannonicaris* Jakobi, 1972. The diagnosis of *Minutacaris* is largely a repetition of what was stated by Lang (1948) for the *minuta*-group. Jakobi (1972) added a third diagnostic character referring to the general morphology of the male P3, which he described as having a robust exopod, a characteristic spinule row on the basis, a robust apophysis longer than, or as long as, the distal part of the exopod. The male P4 endopod he described is either rectangular or represented by a pointed lamella. Since the morphology of the type-species *P. minuta* is inadequately documented, and the characters on which the generic diagnosis was based are ambiguous, it is preferable to treat *Minutacaris* as a *genus inquirendum*, pending a revision of the family. Similarly, the genus *Pannonicaris* (into which *P. aedes* is placed) is conceivably polyphyletic, comprising members showing a different position of the lateral and caudal setae. Jakobi's (1972) diagnosis of *Pannonicaris* is superficial and overlaps with that of *Minutacaris*.

A systematic reappraisal by Schminke (1993) led to the identification of two lineages within the family, which he recognized as different subfamilies, namely Parastenocaridinae and Fontinalicaridinae. However, according to ICZN (2000: Art. 13.2) these family group

names are unavailable and should be considered *nomen nudum*. The subfamily Fontinalicaridinae was also quoted by Martínez Arbizu (1997), who assessed the monophyletic *fontinalis* species-group, pending the formal establishment of the nominotypical genus within this subfamily.

Additionally, the phylogenetic status of the neotropical genera *Potamocaris* Dussart, 1979 and *Forficatocaris* Jakobi, 1969 within the family was discussed in depth by Ahnert (1994). He considered *Potamocaris* to be a paraphyletic subtaxon of the *Potamocaris-Forficatocaris* lineage, due to its lack of autapomorphies.

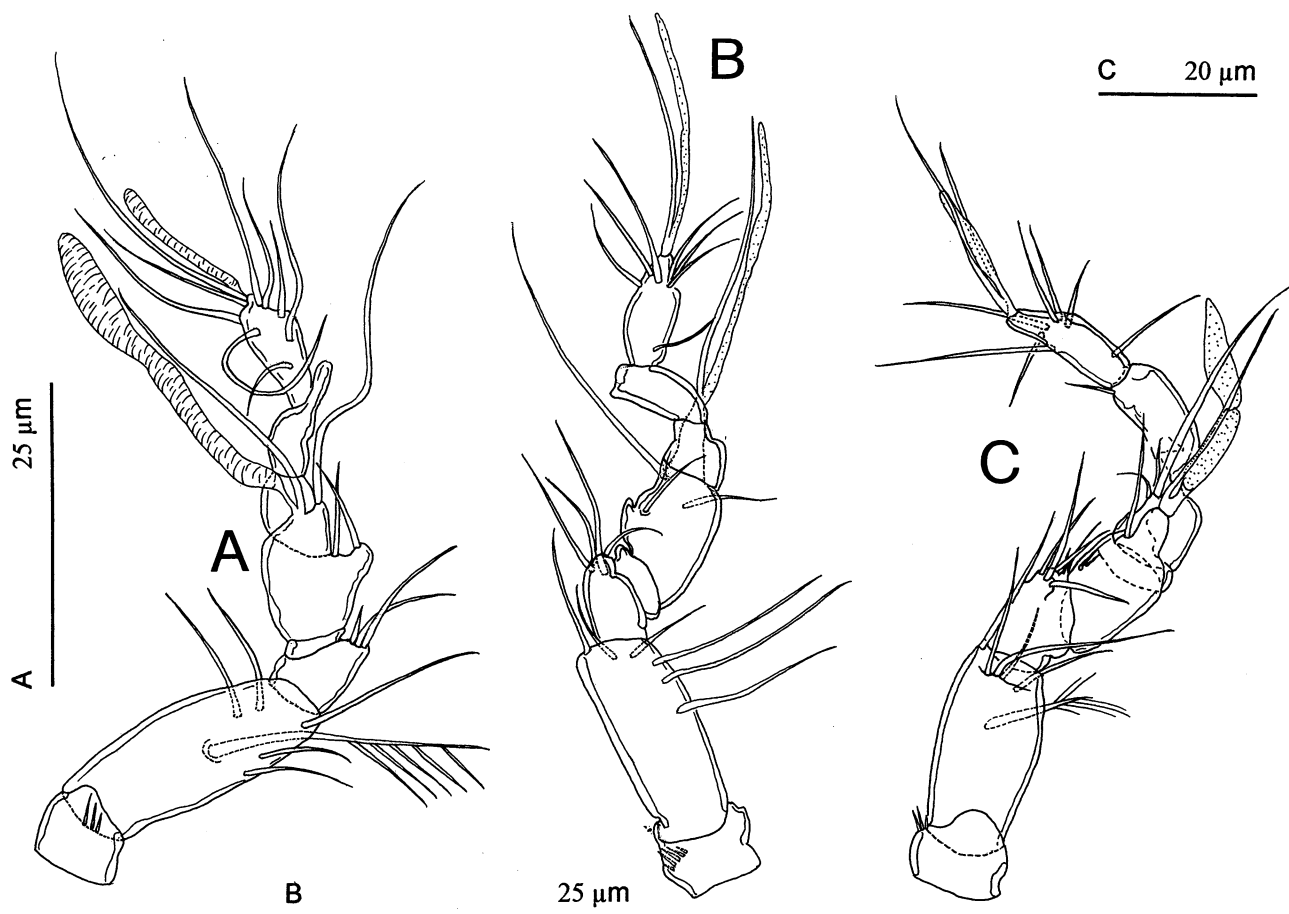
The systematic status of the Parastenocarididae as a whole is still in a state of flux, and the genus *Parastenocaris* clearly accommodates different morphological groups, possibly representing different evolutionary lineages. The relationships within the latter, as well as between the valid parastenocaridid genera presently recognized, are intricate and cannot be solved simply by comparison of available descriptions, since most are inadequate to assess differences in those morphological traits which may be useful for a phylogenetic analysis. Consequently, the formal establishment of the new genus *Simplicaris* is predominantly based on a direct comparison between the type-species *Simplicaris lethaea* sp. nov. (and the herein assessed congener) and the type-species of the genus *Parastenocaris*, *P. brevipes* Kessler, 1913. Morphological data of the latter were derived from Reid's (1995) redescription, as well as from direct observation of the Finnish material on which she based the redescription, since the type-material of *P. brevipes* is lost, and no neotypes were designated since 'it proved impossible to obtain specimens from the type locality in Germany' (Reid, 1995: 175). As part of this comparison, a review of the character states in representative members of the family is given below.

#### REVIEW OF PHYLOGENETICALLY INFORMATIVE CHARACTERS

##### *Male antennule*

*Simplicaris lethaea* gen. et sp. nov. displays an 8-segmented male antennule. A 7-segmented antennule was reported by Reid (1995) for the male of *P. brevipes*. This discrepancy relates to the third segment which was figured by Reid (1995) as divided into two segments and described as 'deeply incised'. Personal observations of Reid's material revealed the presence of a distinct U-shaped fourth segment in *P. brevipes*. Consequently, no differences are traceable in the segmental pattern of *S. lethaea* and *P. brevipes* (Fig. 4A, B).

Few descriptions have reported a distinct U-shaped fourth antennular segment in male *Parastenocaris*: *P. phyllura* Kiefer, 1938 (cf. Glatzel, 1991),



**Figure 4.** Segmental pattern of male antennule in representative members of Parastenocarididae. A, *Simplicaris lethaea* gen. et sp. nov. (♂). B, *Parastenocaris brevipes* Kessler, 1913 (♂), Onkimanjarvi Lake, Finland (USNM 259764). C, *Forficatocaris claudii* (♂) (after Ahnert, 1994; redrawn).

*P. hispanica* Martínez Arbizu, 1997, *P. corsica* Cottarelli, Bruno & Berera, 2000 and *P. silvana* Cottarelli, Bruno & Berera, 2000, *P. ranae* Stoch, 2000, *P. federici* Stoch, 2000 and *P. gertrudae* Kiefer, 1968 (cf. Stoch, 2000). Direct observations of additional species also demonstrated the presence of this segment in *P. crenobia*, *P. lorenzae*, *P. orcina*, *P. trinacriae*, *P. glareola* Hertzog, 1936, *P. fontinalis borea* Kiefer, 1960, and *P. kalypso* Pesce, Galassi & Cottarelli, 1988. The fact that it was never reported nor figured in the original descriptions suggests that the alleged absence of the U-shaped segment in many other described species can be attributed to observational errors.

Ahnert (1994) made an accurate analysis of the segmental pattern of the male antennule in the *Potamocaris*–*Forficatocaris* lineage. In both *Potamocaris* and *Forficatocaris* the male antennule is 8-segmented. However, the segments are not homologous to those identified in *Simplicaris* and in at least some *Parastenocaris* species. All *Potamocaris* and *Forficatocaris*

species observed by Ahnert (1994) lack the U-shaped segment but show an unfused condition of segments 4 (the segment bearing the proximal aesthetasc) and 5 (a short segment bearing a long seta on a protrusion) (Fig. 4C). The homologues of these segments are fused in the remaining members of Parastenocarididae except *Parastenocaris tapajosensis* Noodt, 1963, forming a large compound segment.

Ahnert (1994) also raised doubts about the existence of the U-shaped segment in the genus *Parastenocaris* referring to an unpublished report by Glatzel (Ahnert, 1994: 32–33), correcting his earlier observation (Glatzel, 1991) of the U-shaped segment in *P. phyllura*. Consequently, in his cladistic analysis Ahnert (1994) did not accept the existence of this segment in the Parastenocarididae as a whole. The presence of the U-shaped segment in *Simplicaris lethaea*, in several *Parastenocaris sensu lato* and in *Forficatocaris schadeni* (D. Galassi & P. De Laurentiis pers. obs.) suggests that the U-shaped segment is widespread within the family.

*Potamocaris estevesi* Reid, 1991, as redescribed by Rocha, Torres & Maia-Barbosa (1998), possesses a 10-segmented male antennule, diverging from the typical segmentation pattern of *Forficatocaris*–*Potamocaris* by the presence of an additional segment distal to the geniculation (Rocha *et al.*, 1998: fig. 37, p. 14). At present, this is the maximum number of segments recorded in the family.

Although the segmental pattern of the antennules of males may provide critical information for assessing relationships, numerous descriptions provide inadequate information, hampering any objective judgement on the relevance of reported differences between taxa. Any future assessment should be checked against direct consultation of available material.

#### *Penultimate male antennular segment*

*Simplicaris lethaea* and *P. brevipes* differ substantially in the morphology of the penultimate male antennular segment. It is cylindrical and not transformed in *P. brevipes*, but strongly transformed and asymmetrical in *S. lethaea*, showing a medio-distal protrusion prolonged into a long process, with a single rounded tip (Fig. 4A, B).

The significance of this segment, as well as its three-dimensional complexity were first noticed by Galassi (1997) when describing *P. crenobia*. In *P. crenobia* the segment is strongly sclerotized, and the pointed protrusion is curved downward. In several other species, a transformed segment has been observed or reported, although the modification is different. This is especially true for most species belonging to the artificial *minuta*-group. On the other hand, the segment is not transformed in several other *Parastenocaris* species, like *P. brevipes* and *P. hispanica*; it is very long, only slightly sclerotized and shows no trace of transformation or surface distortion. In species of *Potamocaris* and *Forficatocaris* the same segment does not seem to be transformed and is only slightly sclerotized. In *Murunducaris juneae* Reid, 1994 it is not transformed, without protrusions or irregularities in sclerotization. It is likely that transformation of the penultimate segment is a derived character state, which evolved convergently more than once in the family. This is in agreement with Dahms's (1988) view of the convergent origin of highly transformed (i.e. chirocer types) male antennules in harpacticoids in general.

#### *Morphology of the proximal aesthetasc of the male antennule*

The morphology of the proximal aesthetasc shows some variation within the family. It is typically bilobed in almost all parastenocaridids, although much more

pronounced in *Forficatocaris* (see *Forficatocaris schadeni* Reid, 1982) and *Murunducaris juneae*. In several descriptions it has been drawn as a linear baton with no constrictions along its length. Only rarely, as in *Simplicaris lethaea*, *S. veneris*, *P. aedes*, *P. hippuris*, *P. andreji*, *P. vandeli* Rouch, 1988, it appears as a large and long flaccid structure. Possibly this morphology may be considered an adaptive feature to groundwater life in stygobiont species that entered groundwater early in the evolution of the family.

#### *Antenna*

Coxa unarmed in *S. lethaea* vs. with one spinule row in *P. brevipes*. Two series of spinules are discernible along the inner margin of the allobasis in *S. lethaea*, whereas the proximal one is replaced by a single hair-like element in *P. brevipes*. It is difficult to assess the homology between them.

#### *Mouthparts*

Consistent differences are observable in parastenocaridid mouthparts, but any attempt to use such differences in a phylogenetic context should be subjected to scrutiny since many descriptions are unreliable. Moreover, differences in these characters have also been reported between closely related species of the genus *Parastenocaris* (Schminke, 1971; Cottarelli & Bruno, 1994; Cottarelli, Bruno & Venanzetti, 1995), potentially weakening their phylogenetic significance.

#### *Maxillule*

The maxillule of *P. brevipes* was neither drawn nor described by Reid (1995), although its structure was reported as 'like that of *P. ahaggarica* Bozic, 1978'. Marked differences are observable between the maxillule of *P. ahaggarica* and *S. lethaea*. As a rule, all parts of the maxillule are closely adpressed to each other, and it is difficult to discern individual elements. On the assumption that the additional elements are real, there are marked differences in their structure and setation. Nevertheless, it is not possible to make comparisons in view of the uncertainty surrounding the validity of these counts. The direct observation of the material on which Reid (1995) based her redescription failed to assess morphological details.

#### *Maxilla*

The proximal endite of syncoxa is unisetose and not well defined at the base in *S. lethaea* whereas it is bisetose and well defined at the base in *P. brevipes*. The distal endite has three elements in *S. lethaea* but only two in *P. brevipes*. The endopod is rudimentary in

*S. lethaea* but still discrete in *P. brevipes*. Interestingly, both *S. lethaea* and *P. brevipes* bear a tiny setule on the proximal part of the syncoxa, possibly representing the vestigial proximalmost endite of the maxilla syncoxa. An alternative explanation could be that it represents the tubular extension of the exit of the maxillary gland. A similar setule is displayed also by *P. ahaggarica*, and a spinule row is present in *Forficatocaris lilianae* Noodt, 1972 (in Ahnert, 1994), and *P. hispanica*, instead of the single setule.

#### Maxilliped

The structure of the maxilliped is virtually identical in all parastenocaridids for which it was described and figured. In *S. lethaea* the most striking feature is the size of the maxilliped; it is the largest observed in the family, as long as leg 1 and slightly shorter than legs 2–4. However, this atypical dimension has to be considered a species-specific attribute because in its congener *S. veneris*, as well as in the species *incertae sedis* of the new genus, *P. aedes* and *P. hippuris*, the maxilliped shows a length comparable to that of other parastenocaridids. A similarly large maxilliped is present also in *P. andreji* (cf. Brancelj, 2000), suggesting that it is possibly related to the trophic niche of the species.

#### Legs 1–4: structure and ornamentation

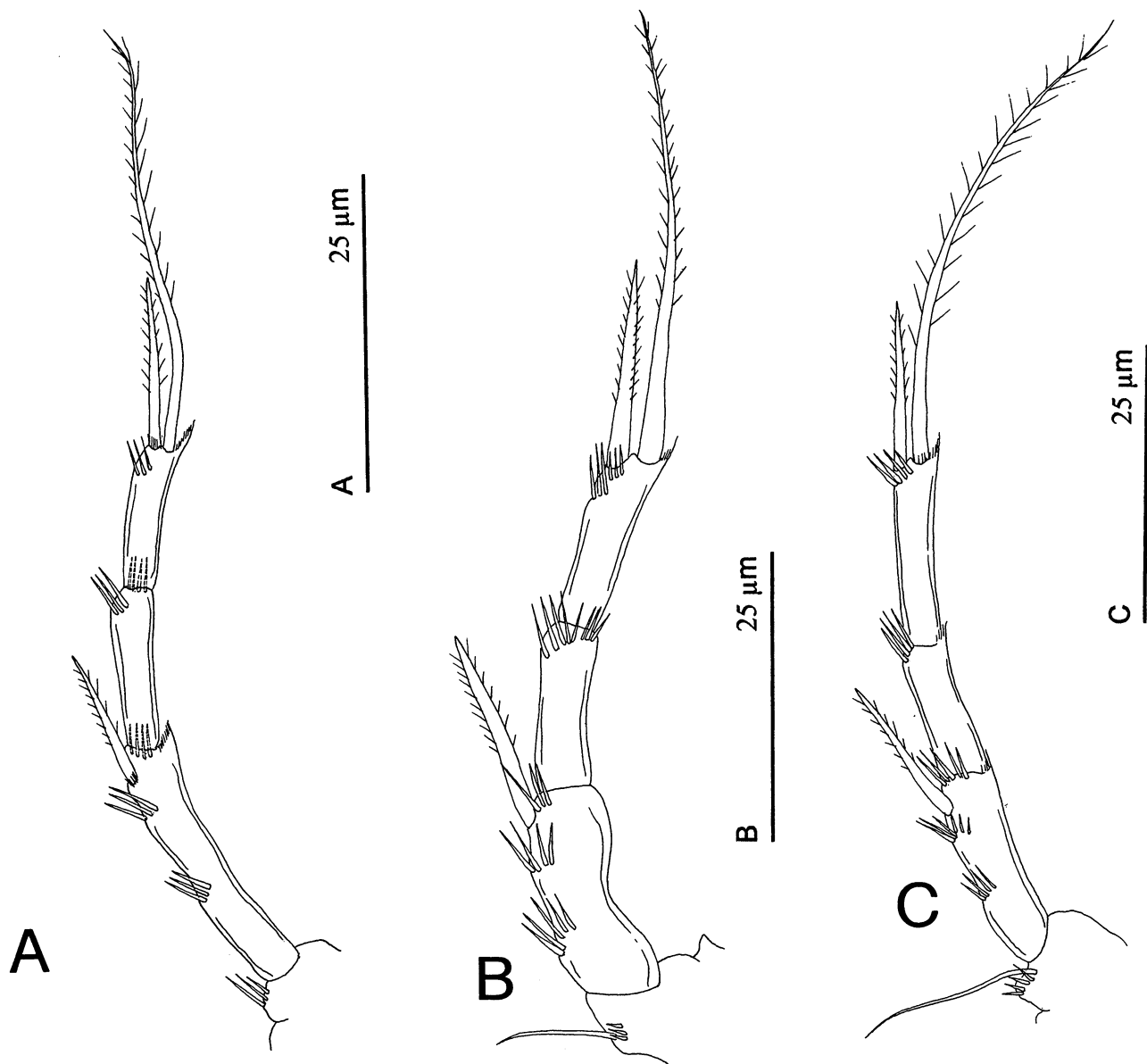
The coxa of P1–P4 is unarmed in both sexes of *S. lethaea*, whereas it is armed with one row of spinules in male P2–P3 and female P2 of *P. brevipes*. In *P. brevipes* the outer basal seta is lacking in male P2 only, and is always present in female P1–P4, although the re-examination of the Finnish material used in Reid's (1995) redescription revealed its absence in the female P2 also. In *S. lethaea* the basal outer seta is lacking in both male and female P2 and P4. Traditionally, the absence of the basal outer seta on P2 has been considered a synapomorphy of the Parastenocarididae (shared with *Psammonitocrella* Rouch, 1992; see Martínez Arbizu & Moura, 1994), but several descriptions reported its presence (i.e. *P. germanica* Kiefer, 1936, *P. acherusia* Noodt, 1955, *P. austriaca* Kiefer, 1976; *P. oligoalina*, *P. etrusca*, *P. mangyans* Bruno & Cottarelli, 1999, *P. lyncaea*) suggesting that this seta could be present in some species-groups at least. The basal outer seta of P4 has been reported for most parastenocaridids and is lacking in both male and female of *S. lethaea*, and in *S. veneris*.

Most parastenocaridids lack an inner seta on the P1 basis, as Martínez Arbizu & Moura (1994) postulated in the evolutionary trend of this leg in the Parastenocarididae and related families. Among the major

transformations recognized by these authors (their fig. 5), Parastenocarididae lack an inner seta on the leg 1 endopod and an inner seta on the leg 1 basis. Nevertheless, some parastenocaridids display an inner seta in both female and/or male P1 basis, although the species belong to different phylogenetic lineages. *P. tumida* (in Schminke & Notenboom, 1990); *P. mangyans*, *P. silvana*, *P. corsica*, *P. ranae*, *P. federici* and *P. trichelata* all show an inner basal seta, and a single spinule row (possibly homologous to the inner basal seta?) is present in several *Forficatocaris* species and in at least *Potamocaris bidens* (Noodt, 1955) (cf. Ahnert, 1994). The inner margin of the P1 basis is unarmed in both *S. lethaea* and *P. brevipes*. The ornamentation figured in Reid (1995)'s figure 2a–c is not to be considered homologous to the inner seta.

The male P1 basis is frequently ornamented with a transformed protrusion, apparently fused to the basis, and located very close to the coxa–basis boundary. This structure is never present in females, and is considered to be a sexually dimorphic feature, whose nature remains doubtful (supernumerary element? coxo-basis protrusion?). It may, or may not, accompany the genuine inner basal seta. This structure has been reported on the male P1 basis in a few descriptions [*P. crenobia*, *P. lorenzae*, *P. tumida*, *P. ranae*, *P. aphroditis*, *P. pasquinii* Cottarelli, 1972 (in Bruno & Cottarelli, 1998), *P. triphyda*, *P. etrusca*, *P. rivi* (in Bruno, Cottarelli & Berera, 1998), *P. trichelata* and in an undescribed *Forficatocaris* by Ahnert (1994)]. Although hypothesized by Bruno *et al.* (1998), the homology with sexual dimorphism displayed by the genuine inner basal seta (not transformed in the female, transformed in the male) in the Ameiridae is unlikely. This protrusion seems to be a transformation of the inner margin of the basis as in several Diosaccidae and Thalestridae, because in most cases the female shows an inner basal seta only when the inner protrusion, if present, is accompanied, in the male by an untransformed seta. To summarize, based on present knowledge, the maximum number of elements along the inner margin of the leg 1 basis in Parastenocarididae is represented by: one genuine inner seta (primitively present in both male and female, secondarily lost in several lineages) plus one transformed ornamentation element arising close to the coxa–basis boundary (primitively present only in males, secondarily lost in several lineages within the family). In some species whose males show the inner protrusion of the basis, the inner genuine seta was reported only in the female, probably because it was obscured by the protrusion in the male.

In *S. lethaea* an elongation of the proximal exopod segment is shown especially in legs 2 and 4 (both male and female) and in leg 3 (female) in which it is about as long as the remaining two combined. In *P. brevipes*



**Figure 5.** Male P4 exopod in representative members of the family Parastenocarididae. A, *Simplicaris lethaea* gen. et sp. nov. B, *Parastenocaris brevipes*, Onkimanjarvi Lake, Finland (USNM 259764). C, *Parastenocaris glareola* Hertzog, 1936, River Rhône, France.

the first exopod segment of all legs is as long as, or only slightly longer than the remaining ones, as in most parastenocaridids (Fig. 5A–C). Within the family, a tendency toward an important elongation of the first exopod segment of swimming legs is presently known only for *P. andreji*, and, to a lesser extent, for *P. vandeli*.

With regard to male legs 3–4, great emphasis has traditionally been placed on differences in morphology, armature and ornamentation. Most characters used to define natural groups are questionable (i.e.

ornamentation of P4 basis, relative length of the male P3 apophysis, presence/absence of male P3 endopod; robustness of the proximal part of the exopod) because similar states are frequently shared by species belonging to different groups.

In *S. lethaea* the former proximal segment of the male leg 3 exopod is slender and shows two spinule rows on the outer margin; the same segment is robust, stout, and naked in *P. brevipes*. Nevertheless the described morphology of the male leg 3 is not a strong autapomorphy for the *Simplicaris*, because

it is shared also by other parastenocaridids (i.e. *P. phreatica*; *P. acherusia*; *P. narentina*; *P. nolli alpina* Kiefer, 1960; *P. amyclaea*; *P. lorenzae*; *P. triphyda*, etc.). In *S. lethaea* the male P4 endopod is reduced; it has lost the shape of a typical segment and has incorporated the terminal seta into the segment. Conversely, in *P. brevipes* the male P4 endopodal complex is represented by four elements as described by Reid (1995), and accompanied by a marked concavity along the inner margin of the proximal exopodal segment, most probably lodging element 3 (Reid, 1995: fig. 3c).

#### Leg 5

In *S. lethaea* leg 5 is completely absent in both sexes. It is present in *P. brevipes*, as well as in all other members of the family, although it was reported as rudimentary in very few *Parastenocaris* species (*P. budapestiensis* Török, 1935; *P. amatheia* Cottarelli, 1970), as well as in *Murunducaris juneae*, in which the female shows a 'normal' leg 5 vs. a very reduced male leg 5, with the major part of this leg being represented by the inner strong coniform process (the transformed inner thorn/spine).

*Simplicaris* is remarkable for the complete absence of leg 5, which is unique within the family. Reductions and losses of parts of legs, especially endopods, occur frequently within the family. Gross reduction of the endopods in legs 2–4 has occasionally reported in the family (Rouch, 1988; Reid, 1991; Ahnert, 1994) reaching its extreme in *P. vandeli* where all three endopods are completely lost in both sexes. In all cases in which the endopods are reduced or completely lost in legs 2–4, leg 5 is always completely expressed, indicating that its development is decoupled from that of both exopods and endopods of legs 1–4. Typically, leg 5 appears at the third copepodid stage in harpacticoid development and attains its definitive structure in the adult (Huys, 1990; Glatzel, 1991; Huys & Iliffe, 1998). Reduction in the structure and armature of leg 5 is also reported in members of other harpacticoid families found in groundwater, such as Rotundiclipeidae Huys, 1988, the canthocamptid *Stygepactophanes jurassicus* Moeschler & Rouch, 1984, the ectinosomatid *Pseudectinosoma* Kunz, 1935, and in some Leptopontiidae (i.e. *Psammopsyllus* Nicholls, 1945, *Ichnusella* Cottarelli, 1971, *Sewellina* Krishnaswamy, 1956, *Parasewellina* Cottarelli, Saporito & Puccetti, 1986, *Arenopontia* Kunz, 1937), the latter possibly closely related to the Parastenocarididae. In all these cases, the reduction or the complete absence of leg 5 may be the result of arrested development before or at the time it begins to appear, and consequently a result of progenetic paedomorphosis. According to Huys & Iliffe (1998) its development is 'more labile since the functional con-

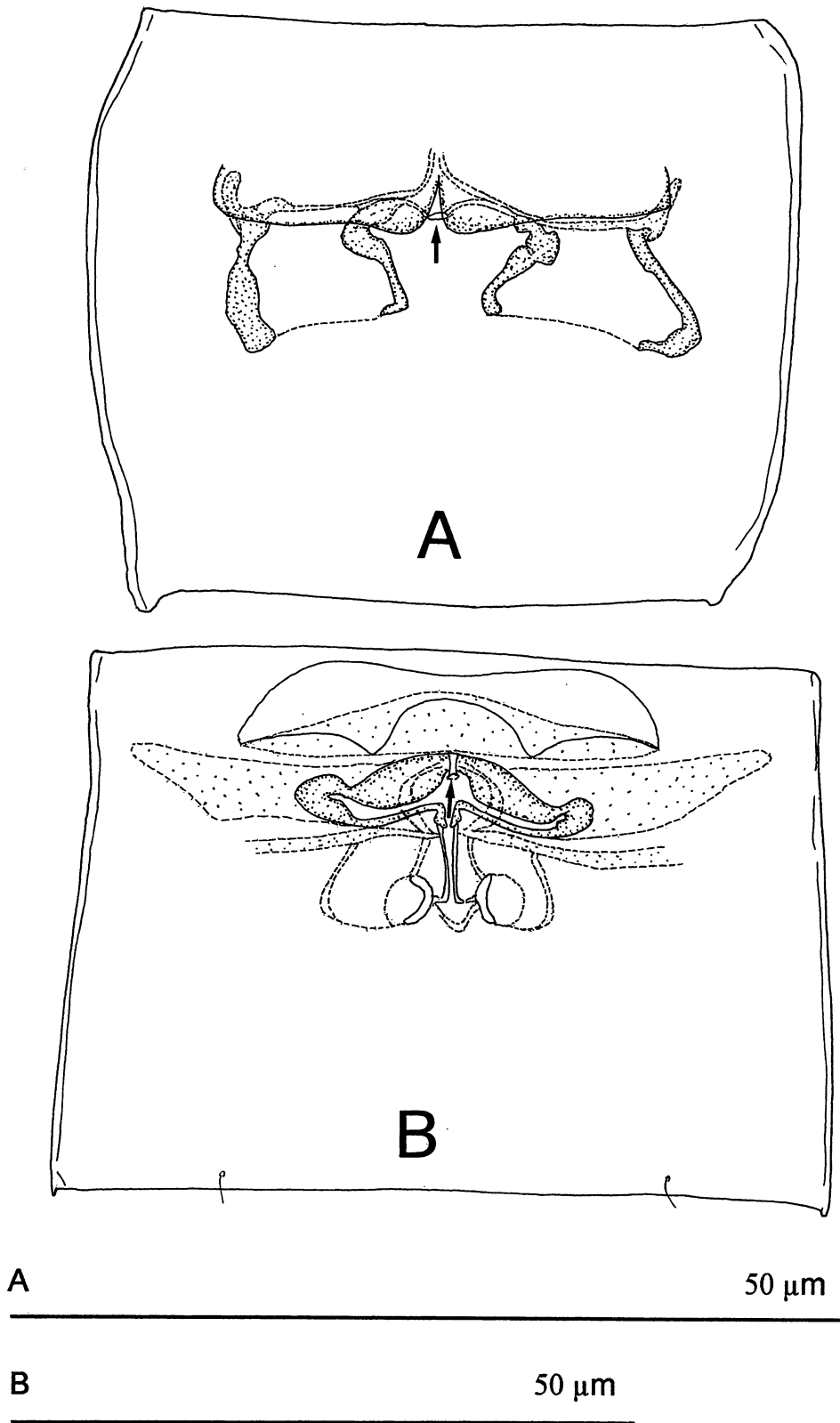
straints imposed on the morphology of genuine swimming legs are no longer present'. Its loss may be linked less to the loss of its primitive swimming function than to the fact that it is the last leg to be formed during ontogeny. Heterochronic events occurring during the terminal phases of ontogeny presumably have fewer consequences for the survival and fitness of the species.

Within the Harpacticoida the total loss of leg 5 has occurred only in *Simplicaris* and *Stygepactophanes*. Some members of the stygobiont order Gelyelloida share the loss of P5 accompanied by other remarkable reductions (Huys & Boxshall, 1991). In a phylogenetic context, the loss of P5, shared by members of *Simplicaris*, may be considered a weak argument to support their closer relationship, because it may be the result of adaptive pressure. We favour the alternative hypothesis, interpreting its loss as a preadaptive feature already present in the ancestor of the *Simplicaris*-lineage. The fact that the loss has also occurred in distantly related taxa can be most plausibly explained by assuming that progenetic paedomorphosis occurred convergently several times in different groundwater taxa.

#### Genital field

The female genital field is located between the first and the second third of the genital double-somite in *S. lethaea*, whereas it is located close to the proximal boundary of the double-somite in *P. brevipes*. In *S. lethaea* the copulatory pore is covered by a strongly sclerotized operculum represented by a single laminar plate running transversally across the genital double-somite, linear in shape, with medial incision as in Figure 6A. The genital apparatus (ducts of the receptaculum seminis or reinforced walls of the genital antra?) is simplified and condensed close to the copulatory pore. The receptaculum seminis is not visible. In *P. brevipes* the copulatory pore is not covered by the operculum, appearing as bilobate and symmetrical. Each lobe represents the rudimentary leg 6 and shows a concave free distal margin, although no trace of armature is visible (Fig. 6B). The remaining part of the genital apparatus (ducts of the receptaculum seminis?) is labyrinthine, and paired bulbs, strongly sclerotized along their medial half, are observable in the caudal part of the genital apparatus. Receptaculum seminis not visible but reported by Reid (1995).

The morphology of the genital apparatus may have great relevance in assessing differences among the phylogenetic lineages within the family. A thorough analysis is beyond the scope of the present study but it suffices to say that there are different structural plans of the genital field in the family.



**Figure 6.** Genital field in A, *Simplicaris lethaea* gen. et sp. nov. (♀). B, *Parastenocaris brevipes* (♀), Onkimanjarvi Lake, Finland (USNM 259764). Arrow indicates the copulatory pore.



*Caudal rami setation*

The lateral setae and dorsal seta are inserted in the distal third (terminal position) of the caudal ramus in both sexes in *S. lethaea*. In *P. brevipes* they arise from halfway along the outer margin of the caudal ramus.

Different arrangements of the lateral setae are recognizable within the family: (1) inserted halfway along the outer margin of the caudal ramus; (2) inserted in the distal third; (3) situated in the proximal third. Additionally, the relative position of the dorsal seta may be informative: it may be located around the middle of the outer margin or in the distal third of the caudal ramus. *Simplicaris* has both lateral setae and the dorsal seta in the distal third; the *fontinalis*-group *sensu* Martínez Arbizu (1997) has the lateral setae in the middle region of the caudal ramus and the dorsal seta in the distal third; the *brevipes*-group *sensu* Reid (1995) has both lateral and dorsal setae in the middle region of the caudal ramus. All of these features are shared by various members of *Parastenocaris s.l.* Other parastenocaridids (i.e. *P. germanica* Kiefer, 1936, *P. phyllura* Kiefer, 1938; *P. ruffoi* Chappuis, 1954, *P. admete* Cottarelli, Fasano, Mura & Saporito, 1980, and the *siolii*-group established by Noodt (1963), and subsequently raised by Jakobi (1972) to genus level as *Siolicaris* Jakobi, 1972) have the lateral setae in the proximal third of the caudal ramus and the dorsal seta in the distal third. Additionally, there are some species, e.g. *P. macaco*, placed by Jakobi (1972) in the genus *Macacocaris* Jakobi, 1972, in which the male has both lateral and dorsal setae in the distal third and the female has the lateral setae in the proximal third and the dorsal seta in the distal third. In this species, however, it is doubtful whether the specimens attributed to either sex are conspecific.

*Integumental windows patterns*

Reid (1994) gave an exhaustive survey of the integumental window patterns in the Parastenocarididae. It is known that integumental windows can differ between species in pattern, size and shape. However, it is impossible at present to reconstruct their evolutionary trends within the family. *S. lethaea* and *P. brevipes* show the most common pattern in parastenocaridids, as well as the same topology and morphology of the integumental windows, with no sexual dimorphism.

## RELATIONSHIPS

A re-examination of the type-material of *P. veneris* enabled us to improve the original description of the species in several morphological details, and to include it in the new genus *Simplicaris*. Supporting evidence for this generic assignment is found in the

relative length of the first exopodal segments of the legs, as well as in the complete absence of leg 5 in both sexes. The latter was reported as a kind of rudimentary bilobed protuberance in the original description by Cottarelli & Maiolini (1980; figs 13, 22), although it could not be found in any of the specimens we examined. In our estimation Cottarelli & Maiolini (1980) probably observed an artefact caused by medial collapsing of the ventral soft body wall.

*Simplicaris veneris* comb. nov. is closely related to the type-species *S. lethaea* in the following characters: tegument without pits and weakly sclerotized; fourth U-shaped segment of the male antennule present; aesthetasc flaccid and very large, reaching far beyond distal segment of antennule; penultimate male antennular segment prolonged in a rounded tip; maxillule similar in both structure and armature; elongation of first exopodal segment of legs (especially in P2 and P4); identical ornamentation and armature of P1–P4; P2 and P4 outer basal seta absent; male P3 with identical ornamentation; P5 absent in both sexes; genital field similar in general structure; lateral and dorsal setae inserted in distal third of caudal rami.

*S. lethaea* differs from *S. veneris* in the morphology of the penultimate segment in the male antennule (protrusion with a single rounded tip in *S. lethaea*, vs. bilobed in *S. veneris*); the endopod of the maxilla (reduced to two setae in *S. lethaea* vs. 1-segmented with two setae in *S. veneris*); maxilliped (very large in *S. lethaea* vs. minute in *S. veneris*); male and female P2 endopod (with an outer spinule in *S. lethaea* vs. slender and without outer spinule in *S. veneris*); the morphology and ornamentation of the female P3 endopod; the absence (in *S. lethaea*) vs. presence (in *S. veneris*) of the male P3 rudimentary endopod; the length of the caudal rami (about 3.2 times longer than wide in *S. lethaea*, vs. about 6.5 times longer than wide in *S. veneris*).

Among the known species of *Parastenocaris*, affinities are found with two other species, i.e. *P. aedes* Hertzog, 1938 and *P. hippuris* Hertzog, 1938, both described from the interstitial habitat of the river Rhine at Strasbourg. The type-material of both species is untraceable, and the apparent affinities are based exclusively on the original descriptions. Consequently, their provisional assignment to the new genus is based only on the relative length of the first exopodal segments of all legs and on the potential absence of leg 5, being reported for *P. aedes* as 'nicht zu sehen' ("not seen") (Hertzog, 1938: 51) and for *P. hippuris* as 'war nicht aufzufinden' ("was not found") (Hertzog, 1938: 53). For this reason, both species are placed as *incertae sedis* within the new genus. Other affinities are traceable in the large proximal aesthetasc on the male antennule, in the general structure of the male leg 3 (former proximal segment of the exopod elongate and

slender, with two spinule rows on the outer margin; former second segment (apophysis) with rounded tip); and in the relative position of lateral and dorsal setae on the caudal rami. *P. hippuris* also shares with *S. lethaea* the construction of the male leg 4 endopod and ornamentation of the basis, consisting of two untransformed spinules.

Both *P. hippuris* and *P. aedes* show an apparent inner spinule on the male leg 1 basis, whereas it is absent in both *S. lethaea* and *S. veneris*. However, the low standard of Hertzog's (1938) drawings prevents us from verifying whether this inner spinule is homologous to the inner basal seta or whether it represents a genuine ornamentation element. Additionally, *P. hippuris* shows also the presence of the outer basal seta on the male leg 4.

A tendency towards elongation of the first exopodal segments of P1–P4 legs has also been observed in *P. andreji* by Brancelj (2000). In respect of several characters, *P. andreji* may be considered a likely candidate for the more primitive outgroup of *Simplicaris*. Re-examination of the female holotype confirmed the presence of the flaccid and robust proximal aesthetasc of the female antennule, the large maxilliped, the relative length of the first exopodal segments (especially P2), the presence of leg 5; it also revealed a complete setal pattern of caudal rami (seven setae vs. six reported in the original description); the presence of the outer basal seta on leg 4, inserted close to the coxa–basis boundary (overlooked in the original description). Unfortunately, the missing male of *P. andreji* prevents us from analysing the potential relationships between *P. andreji* and the *Simplicaris* species-group in greater detail.

With regard to the allocation of *Simplicaris* within the family as a whole, we propose retaining within *Parastenocaris* only those species belonging to the *brevipes*-group (as revised by Reid, 1995), and to relegate the remainder presently assigned to this genus as *Parastenocaris s.l.*, pending the revision of the family. Reid (1995) identified a morphologically robust group around the type-species of the genus. Its members share the tapering caudal ramus with dorsal and lateral setae inserted at midlength, the long, distally serrate leg 4 endopod of the female, the leg 3 exopod of the male without a series of spinules along the outer margin of the exopod, and the leg 4 endopodal complex of the male with one or two large claws and a hyaline endopod bearing subterminal setae.

To this group belong *P. brevipes*, *P. arctica* Borutskii, 1952, *P. hinumanensis* Kikuchi, 1970, *P. longipoda* Shen & Tai, 1973 *P. feuerborni* Chappuis, 1931, *P. longicaudis* Chappuis, 1931, *P. brincki* Enckell, 1970, *P. irenae* Enckell, 1970, *P. lanceolata* Enckell, 1970, *P. noodti* Enckell, 1970, *P. singhalensis* Enckell, 1970, *P. oshimaensis* Miura, 1962, *P. savita*

Ranga Reddy, 2001, and *P. gayatri* Ranga Reddy, 2001.

Some of the characters shared by all members of this group are shared also with other species more distantly related to the *Parastenocaris*-group defined herein. This is the case for the position of the caudal setae, the distally serrate leg 4 endopod of the female, and the male leg 3 exopod without outer spinule rows. It is plausible that these characters, or at least some of them, may eventually be useful to identify suprageneric taxa within the family, in conjunction with others, such as the male antennular segmental pattern and the basic organization of the female genital field. In this regard, members of the *brevipes*-group, which we define here as *Parastenocaris s.s.*, share the following additional characters: (1) 8-segmented male antennule (U-shaped segment present, although not figured and described in most descriptions); (2) exopodal segments of legs 1–4 of about the same length, the proximal exopodal segment being only slightly longer than the middle and the distal segments; (3) leg 5 represented by a laminar plate with inner thorn more or less protruding but never uncinat, incorporated into the plate, or with inner spine (instead of a thorn) plus some setae, the outermost representing the outer basal seta, penultimate seta of leg 5 with tendency to be reduced, very short, and spinular in shape; (4) female genital field as in *P. brevipes*.

In our opinion the most robust autapomorphy of the *brevipes*-group is the peculiar morphology of the male leg 4 endopodal complex, involving also the morphology of the inner margin of the exopodal segment 1. The configuration of the P4 complex is not homologous to the male leg 4 morphology of *Forficatocaris fittkau* Jakobi, 1972. In this species the P4 endopod is strongly chitinized and curved into the inner concavity of the proximal exopodal segment; the characteristic ornamentation of the basis is completely absent. In general, in most species of *Forficatocaris*, the male endopod is curved outward and the inner margin of the proximal exopodal does not show the typical concavity of *F. fittkau*. In some species, the inner margin is linear [*F. amazonensis* (Noodt, 1963), *F. tetracantha* (Noodt, 1963), *F. forficata* (Noodt, 1963), *F. claudii* Noodt, 1972, *F. liliana* Noodt, 1972, as redescribed by Ahnert, 1994], whereas it shows two inner protrusions lodging the apex of the P4 endopod in *F. noodti* Jakobi, 1969.

This systematic scenario is even further complicated by the fact that *P. palmerae*, as already noticed by Reid (1995), combines the same morphology of the male P4 and the terminal position of both lateral and dorsal setae on the caudal ramus. *P. texana* Whitman, 1984, previously excluded by Reid (1995) from the *brevipes*-group, is more closely related to the Central American species *P. cuscatlanensis* Noodt, 1962,

*P. panamericana* Noodt, 1962, and *P. salvadorensis* Noodt, 1962, all of which show a male P4 complex which does not conform to that of the *brevipes*-group, as well as a different topology of both lateral and dorsal caudal setae (the lateral ones in the proximal third and the dorsal one in the distal third).

The phylogenetic affinity of the *Simplicaris*-species group to the *vandeli*-group, herein proposed with one species *P. vandeli* (pending the description of a new species belonging to the same group; V. Cottarelli, pers. comm.), may be supported by the following synapomorphies: penultimate antennular segment transformed in male, identical ornamentation of male leg 3, a tendency towards elongation of the first exopodal segment of the legs, lateral and dorsal setae in the terminal position, caudal rami slender, and possibly other characters (such as male antennular U-shaped segment present, ornamentation of leg 3, genital field) which we failed to verify in the untraceable type-material. These observations suggest that *Simplicaris* could be allocated to an evolutionary lineage, close to the *vandeli*-lineage (the potential sister group), both representing the terminal clades of a derived offshoot within the family. The *Simplicaris*-lineage proceeded towards the loss of P5, whereas in the *vandeli*-lineage the evolutionary loss of the P2–P4 endopods became much more pronounced.

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