

FIRST RECORD OF PARASTENOCARIDIDAE FROM THAILAND AND DESCRIPTION OF A NEW GENUS (COPEPODA: HARPACTICOIDA)

Veziro Cottarelli, Maria Cristina Bruno, and Raffaella Berera

(VC, cottarel@unitus.it; RB, raffaella.berera@unitus.it) Dipartimento di Scienze Ambientali, Università degli Studi della Tuscia, Largo dell'Università snc, Viterbo, I-01100 Italy;

(MCB, correspondence, cristina.bruno@iasma.it) Fondazione Edmund Mach, IASMA Research and Innovation Centre, Environment and Natural Resources Area, Via E. Mach, 1, S. Michele all'Adige (TN), I-38010 Italy

ABSTRACT

Asiacaris n. gen. is described to accommodate *Asiacaris dispar* n. sp., collected in the interstitial of the banks of a river on Pha-ngan Island, in the Gulf of Thailand. *Asiacaris* belongs to Parastenocarididae Chappuis, 1940, based on the following characters: leg 3 sexually dimorphic, modified in the male into a grasping organ; presence of sexual dimorphism on the endopod of leg 4; presence of a dorsal integumental window on cephalothorax and dorso-elliptical integumental windows on tergites of urosomites 2 to 5 in male and on genital double-somite and urosomites 4 and 5 in female; antennule 8-segmented, with an inner process on the 7th segment, first leg with 2-segmented endopod and unarmed exopod-2, and mouthparts armature and segmentation. The apomorphic characters of *Asiacaris* are represented by the sexual dimorphism of P2 (stronger in male than in female), the fusion of the P5 to the intercoxal sclerite and to the somite and, mostly, by the overall transformation of P4 in the male, which is the longest and strongest leg, a feature never recorded before in any male of freshwater or marine free-living harpacticoids: the endopod is missing, the exopodal segments are all enlarged, and the apical seta is transformed into a hook longer than the last segment of the exopod. The P4 project laterally, creating not only a characteristic habitus, but also possibly a locomotion pattern different from that of all other Parastenocarididae. This modified P4 could be used to grasp the female during coupling, because it forms a second set of pincers, longer and stronger than the one created by the P3.

KEY WORDS: *Asiacaris dispar*, Harpacticoida, interstitial fauna, Thailand

DOI: 10.1651/09-3201.1

INTRODUCTION

Parastenocarididae Chappuis, 1940 is a family highly specialized for life in groundwater and is almost exclusively restricted to this habitat (Galassi and De Laurentiis, 2004). The first described representative of the family is *Parastenocaris brevipes* Kessler, 1913, described almost a century ago from Germany. The family currently contains 278 species and subspecies, accommodated in ten genera: *Parastenocaris* Kessler, 1913; *Forficatocaris* Jakobi, 1969; *Paraforicatocaris* Jakobi, 1972b; *Potamocaris* Dussart, 1979; *Remaneicaris* Jacobi, 1972a; *Pararemaneicaris* Jacobi, 1972a; *Murunducaris* Reid, 1994; *Simplicicaris* Galassi and De Laurentiis, 2004; and *Monodicaris* Schminke, 2009. Finally, *Kinneicaris* Jacobi, 1972a, was recently redefined by Schminke (2008). Apart from these accepted genera there are 21 additional ones, which had been proposed by Jakobi (1972a, b), but which have not been conventionally accepted, although valid, being in full compliance with the ICZN (1999). Recently, Corgosinho and Martínez Arbizu (2005) and Corgosinho et al. (2007) proposed the adoption of all the genera described by Jakobi (1972a, b), pending the revision of them and test of their monophyly. Taxa of the parastenocaridids are in fact being gradually revised (see Dussart, 1979; Reid, 1991, 1994, 1995; Galassi and De Laurentiis, 2004; Karanovic, 2005; Corgosinho and Martínez Arbizu, 2005; Corgosinho et al., 2007; Corgosinho et al., 2008; Schminke, 2008, 2009). *Parastenocaris* is the most diverse and widely distributed genus of Parastenocarididae, but it has become a “taxo-

nomie repository”: most species are currently assigned to morphological species-groups, the phylogenetic relationships of which are unclear, and which are in some case polyphyletic [see for instance the discussions of the *minuta*-group Lang, 1948 in Berera and Cottarelli (2003), Galassi and De Laurentiis (2004), Karanovic (2005)]. The phylogenetic analysis of this genus is also made difficult by convergence (Karanovic, 2005). Galassi and De Laurentiis (2004) proposed to retain “within *Parastenocaris* sensu stricto only those species belonging to the *brevipes*-group Lang, 1948 (as revised by Reid, 1995), and to relegate the remaining species presently assigned to this genus to *Parastenocaris* s. l., pending a much-needed but not yet accomplished revision of the family.” However, although formally the sensu stricto group should be included within the sensu lato one, this terminology was used by several researchers (Corgosinho and Martínez Arbizu, 2005; Cottarelli et al., 2008; Ranga Reddy and Defaye, 2009) and is adopted here as well.

At the genus level, the highest diversity of Parastenocarididae occurs in the Neotropics: six of the ten accepted genera (namely *Remaneicaris*, *Pararemaneicaris*, *Paraforicatocaris*, *Potamocaris*, *Forficatocaris*, and *Murunducaris*) are exclusive to this region. The genus *Remaneicaris* is so far the most diverse taxon of Parastenocarididae in Latin America, including 31 described species (Corgosinho et al., 2007), several of which were previously assigned to *Parastenocaris*. The exclusively Neotropical genera *Forficatocaris* and *Potamocaris* are mainly known from psammic habitats (Ahnert, 1998) with 11 and 6 species

respectively in South America (Brazil, Paraguay, Peru, and Venezuela for the former genus, Argentina and Brazil for the latter) (Reid, 1991; Ahnert, 1998). *Paraforicatocaris* includes one hyporheic species from Brazil, and *Pararemanecaris* has one psammic and one hyporheic species from El Salvador and Brazil respectively. *Murunducaris* currently (Corgosinho et al., 2008) includes three species from Brazil and one from Peru, from semi-terrestrial and freshwater interstitial habitats. *Simplicaris* is so far endemic to central Italy, where it is represented by two species from interstitial habitats. *Kinnecaris* is known from psammal and hyporheic habitats, ranging from Africa (10 species) and Madagascar (three species) to India (two species), Western Australia (two species), and Papua New Guinea (one species) (Schminke, 2008; Ranga Reddy and Schminke, 2009). *Monodicaris* is endemic to Africa, with three species in Sierra Leone, Guinea, and Mali, respectively (Schminke, 2009).

In this paper, we describe and discuss *Asiacaris dispar* n. gen., n. sp., with particular regard to the status of some phylogenetic informative characters.

MATERIAL AND METHODS

Specimens were collected using the Karaman-Chappuis method (Delamare-Deboutteville, 1960), fixed in 5% buffered formalin solution, sorted, and mounted in Faure's medium between two cover slips, to allow observation from two sides, with fragments of human hair to avoid deformation of non-dissected specimens (Karanovic, 2005). Once the medium was dry, the cover slips were fixed to a microscope slide with pieces of adhesive tape. Drawings were made at a magnification of 1250 X, using a drawing tube mounted on a Zeiss Axioskop® phase-contrast microscope.

The following abbreviations are used throughout the text and figures: Enp = endopod; Exopod = exopod; A1 = antennule; A2 = antenna; P1-P5 = first to fifth thoracic limbs. The nomenclature and descriptive terminology follow Huys and Boxshall (1991).

Specimens are deposited at the Natural History Museum, London (NHM), and at the Dipartimento di Scienze Ambientali, Università degli Studi della Toscana (DISA).

SYSTEMATICS

Parastenocarididae Chappuis, 1940

Asiacaris n. gen.

Type and Only Species.— *Asiacaris dispar* n. sp.

Diagnosis.—Interstitial Parastenocarididae. Body cylindrical, elongated, without clear demarcation between prosome and urosome; depigmented. Eye absent. Hyaline frills of cephalothorax, thoracic and abdominal somites, and urosome smooth. Cephalothorax and certain somites with dorsal sensilla. Genital somite and third urosomite of female completely fused to form double genital somite. Genital field of female located in the anterior half of double-somite. Integumental window on cephalothorax of both sexes, on genital somite, and urosomites 2 to 5 in male, on double genital somite and urosomites 4-5 in female. Anal somite smooth, tapering distally; anal operculum convex and smooth. Caudal rami cylindrical, elongated, with six setae and one pore in both sexes. Spermatophore kidney-shaped, very large. Sexual dimor-

phism in caudal rami, antennule, P1-P5, and genital segmentation; male smaller than female.

Rostrum short, fused to cephalothorax, with two sensilla on tip. Antennule eight-segmented in male and seven-segmented in female; with geniculation between segments 6 and 7 and aesthetasc on segments 5 and 8 in male, 4 and 7 in female. Antenna with allobasis; exopod one-segmented with one seta, apparently fused to allobasis. Mandible with a coxal gnathobasis bearing one seta and a palp with two setae; Mx1 with precoxal arthrite with six elements, coxa with one seta and basis with three setae endopod and exopod absent; Mx2 with two syncoxal endites, endopod with two setae; Mxp prehensile, distal segment with one claw-like seta. P1: with three-segmented exopod and two-segmented endopod, basis with inner seta in male, without seta in female. P2: sexually dimorphic, coxa, basis, and intercoxal sclerite hypertrophied, coxa and basis apparently only partially fused; exopod-1 to exopod-3 of unusual shape and length; exopod-2 short in males (unusually armed with a small outer seta in both sexes). P3: transformed into a clasping appendage in male; with two-segmented exopod and one-segmented endopod in female, endopod missing in male. P4: with three-segmented exopod, exopod-1 with lateral seta inserted 2/3 of the segment in males, exopod-2 bare; exopod of male very long and strong, apically with strong transformed hook-like spine and small seta; exopod-3 inwardly bent, forming clasping structure with the hook-like spine. Exopod-3 with two normal apical setae in female; endopod lacking in male, one-segmented and very long in female, approximately of the same length of exopod-1-2 altogether. P5: without intercoxal sclerite, the pair being represented by two plates fused at their bases and with the somite, size, shape, and armature differing between the sexes.

Etymology.— The generic name is derived from Asia, and karis = shrimp (gender: feminine), to emphasize that this is the first new genus of this family collected in the continent of Asia.

Asiacaris dispar n. sp.

(Figs. 1-6)

Type Locality.— Hyporheic habitat on left bank of Than Sadet River, near Than Sadet waterfall, Pha-ngan Island, Thailand, at 124 m a.s. l. (9°44'74"N, 100°03'54"E).

Material Examined.— Holotype male, dissected and mounted on slide labeled: "*Asiacaris dispar* holotype: male, Pha-ngan Island (Koh Pha-ngan), Thailand, 11 Feb 2008" (NHM 2010.262). Allotype female, dissected and mounted on slide labeled: "*Asiacaris dispar* allotype: female, Pha-ngan Island, Thailand, 11 Feb 2008" (NHM 2010.263). One dissected and two undissected male paratypes, each mounted on a slide labeled: "*Asiacaris dispar* male paratype, Pha-ngan Island, Thailand, 11 Feb 2008" (NHM 2010.266, 2010.267; DISA 2010.262); three dissected and one undissected female paratypes, each mounted on a slide labeled: "*Asiacaris dispar* female paratype, Pha-ngan Island, Thailand, 11 Feb 2008" (NHM 2010.264, 2010.265; DISA 002, 003). All material collected by V. Cottarelli.

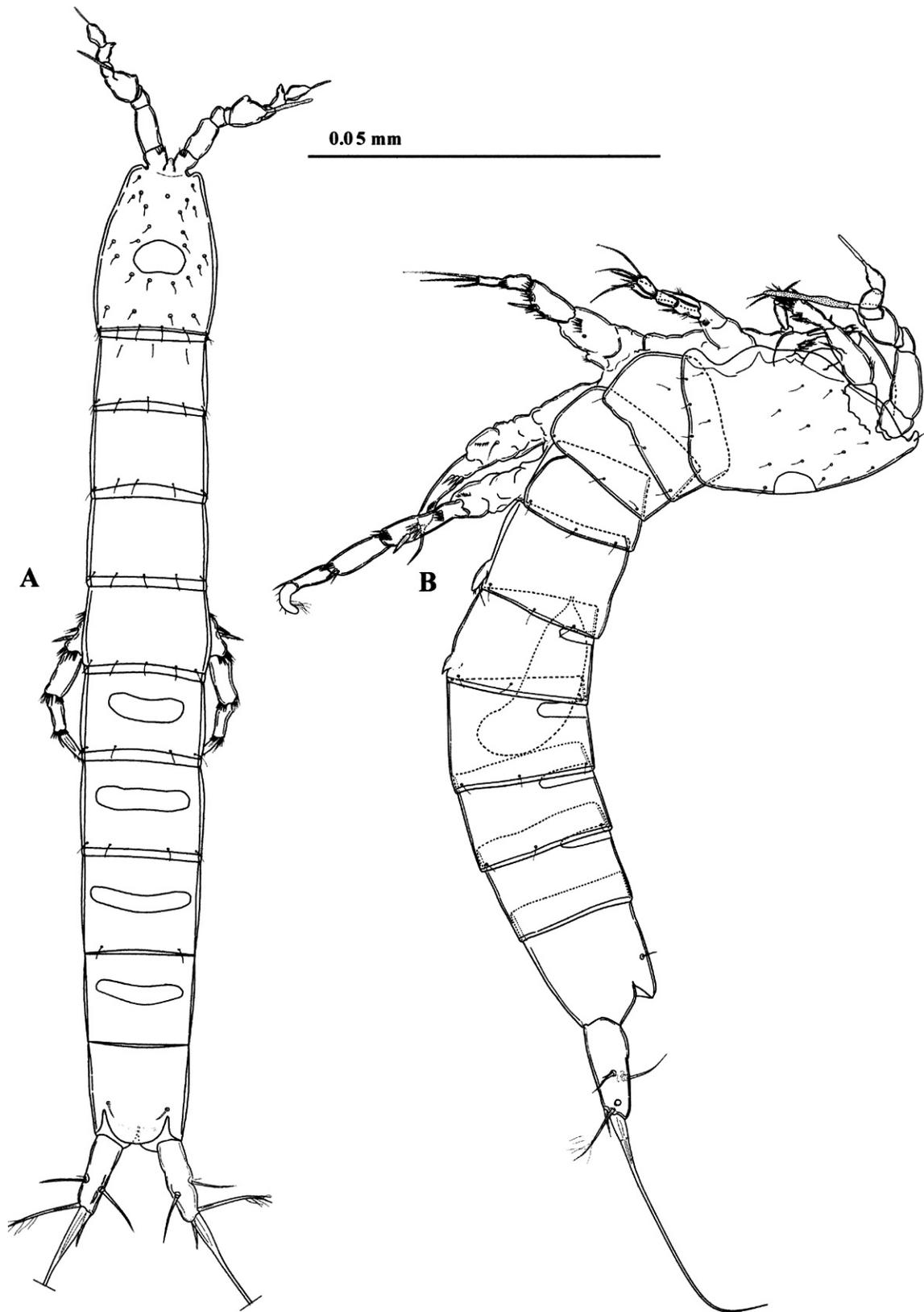


Fig. 1. *Asiacaris dispar* n. gen., n. sp. A, B: male. A (DISA 2010.262), habitus, dorsal view; B (NHM 2010.267), habitus, lateral view.

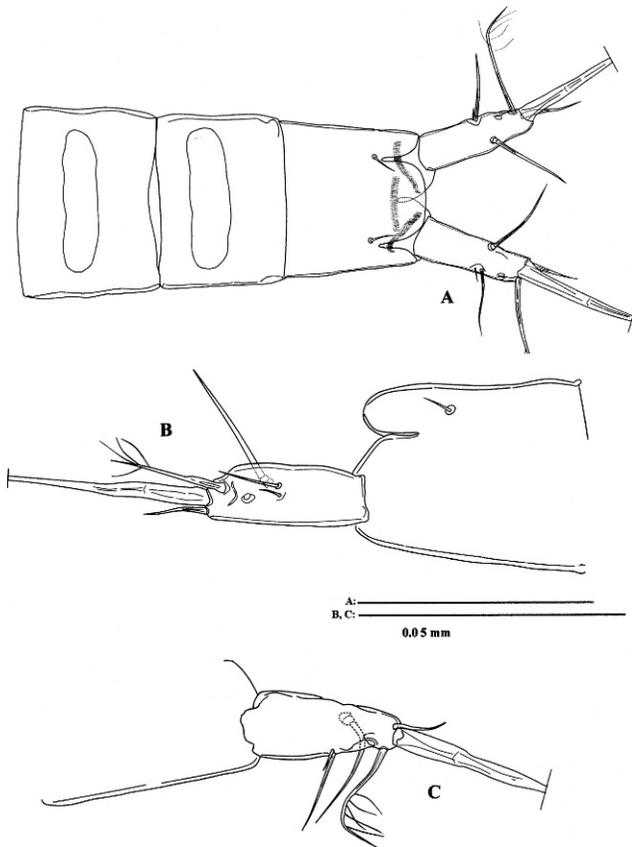


Fig. 2. *Asiacaris dispar* n. gen., n. sp. A: male; B, C: female. A (NHM 2010.262), fourth and fifth urosomites, anal somite and caudal rami, dorsal view; B (NHM 2010.265), anal somite and caudal ramus, lateral view; C (NHM 2010.263), caudal ramus, ventral view.

Description of Male.— Body vermiform, slender, unpigmented, eyeless, habitus as in Figs. 1A and 1B. Length, measured from tip of rostrum to apex of caudal rami; mean length 380 μm ($n = 4$). Hyaline frills of cephalothorax, thoracic somites, and urosome smooth. Cephalothorax with elliptical dorsal integumental window, one pore and numerous sensilla (Figs. 1A, 1B). In dorsal view, tergites of three free thoracic somites with 8, 5, 5 sensilla, respectively; urosomites 1 to 5 with 5, 4, 4, 2, 0 sensilla, respectively (Fig. 1A). Urosomites 2 to 5 with dorsal elliptical integumental window, that of urosomite 2 being the smallest (Fig. 1A, B). Anal somite (Figs. 1A, 2A) with proctodeal rows of spinules, and paired sensilla on dorsal side; anal operculum convex, with smooth distal margin and ventral transverse row of spinules (Fig. 2A). Caudal rami (Figs. 1A, 1B, 2A) smaller than last abdominal somite, approximately cylindrical, divergent; length/width: 2.85; one pore at 3/4 length of the ramus. One lateral seta missing (III?); anterolateral accessory seta (I) very short, about 1/5 as long as lateral seta (II?), both inserted slightly distal to mid-length of ramus. Outer terminal seta (IV) short (length of seta/length of caudal ramus: 1.00), pinnate. Inner terminal seta (V) without fracture plane. Terminal accessory seta (VI) short (length of seta/length of caudal ramus: 0.54) and smooth. Dorsal seta (VII) articulate, long (length of seta/length of caudal ramus: 1.1), slightly distal to setae I and II. Spermatophore kidney-shaped, very large (Fig. 1B).

Rostrum (Fig. 3A, B): fused to cephalothorax, small, with two apical sensilla.

Antennule (Fig. 3A, B): eight-segmented; geniculation between sixth and seventh segments. First segment with spinule row. Second segment with seven setae, the longest uniseriably plumose. Third segment with four distal setae. Fourth segment represented by U-shaped sclerite with two short setae. Fifth segment much enlarged, with a proximal inner triangular and pointed apophysis; four ventral setae, two of which very short and curved, and a distal tubercle with one seta and one aesthetasc of about same length, both reaching beyond end of antennule. Sixth segment partially merged with fifth segment, bare. Seventh segment short, bare, sickle-shaped, apically with bilobate apophysis. Eighth segment with eight setae and acrothek carrying one seta and one short, thin, apical aesthetasc, about half as long as aesthetasc on segment 5. Armature formula: 1-[0], 2-[1 uniplumose + 6 bare], 3-[4 bare], 4-[2 bare], 5-[4 bare + (1 + ae)], 6-[0], 7-[0], 8-[9 bare + ae].

Antenna (Fig. 3C): coxa unarmed; allobasis with two transverse rows of three and two spinules on inner margin. Exopod represented by small segment merged with allobasis, with short, pinnate apical spine. Endopod bearing on apex two lateral and five distal elements, two middle one geniculate, innermost one transformed, all elements with spinules near their insertions.

Mandible (Fig. 3E): coxal gnathobase bare, cutting edge with four apical bifid teeth and four spinules, and one subapical curved seta. Palp one-segmented, with two distal setae of equal length.

Maxillule (Fig. 3F): praecoxal arthrite with three curved robust spines, three thin anterior subterminal setae, and one subdistal composite seta; one seta on coxal endite; basis with three naked setae; endopod and exopod absent.

Maxilla (Fig. 3G): syncoxa with two endites: proximal endite short, with one seta, and distal endite longer, with three apical elements, one of these pinnate; allobasis prolonged into apical pinnate claw; endopod represented by a small segment with two short setae of equal length.

Maxilliped (Fig. 3H): prehensile. Syncoxa small and unarmed; basis slim and elongate, unarmed; endopod represented by distally unipinnate claw.

Basis of P1-P4 with one pore in the distal part, basis of P1, P3, and P4 with lateral seta and spinule row.

P1 (Fig. 4B): with small intercoxal plate; basis with inner seta, one spinule row near insertion of endopod; exopod as long as endopod, exopod-1 with distal lateral pinnate seta and two spinule rows, exopod-2 bare, with distal spinule row, exopod-3 with two normal and two geniculate setae, all unipinnate, and spinule row; endopod-1 as long as first two segments of exopod, endopod-1 bare with two outer spinule rows and one row at 2/3 length of inner margin; endopod-2 with one long, geniculate, unipinnate apical seta, and one normal unipinnate apical seta, and apical spinule row. Inner spinule rows of endopod with spinules longer than those of outer rows.

P2 (Fig. 5A, B): legs separated by wide intercoxal plate, coxa and basis very strong. Coxa with two transversal, distal spinule rows; basis with one spinule row and pore; exopod-1 as long as following two segments, strongly

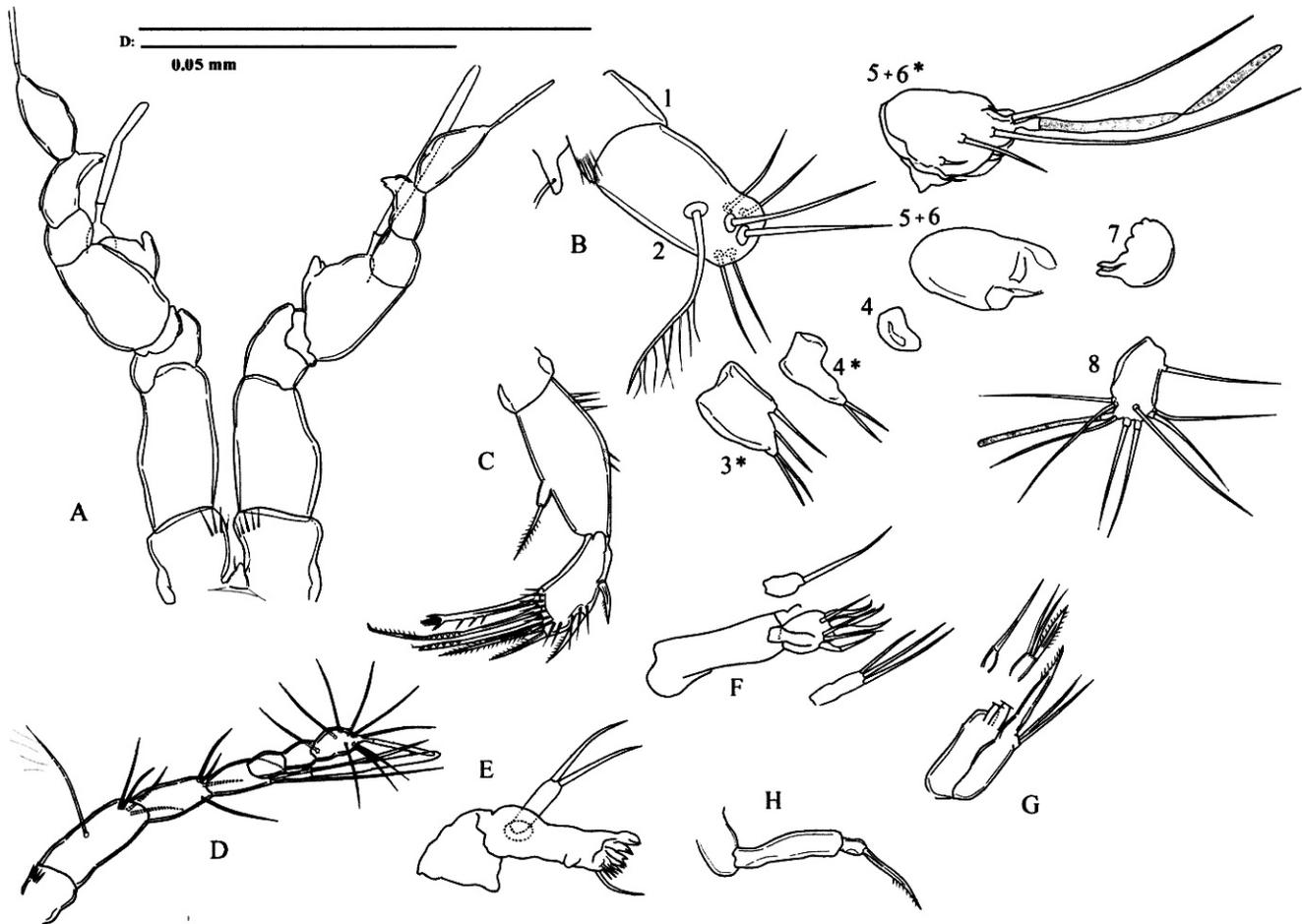


Fig. 3. *Asiacaris dispar* n. gen., n. sp. A-C, E-H: male; D: female. A (NHM 2010.262), rostrum and antennule without armature except sensilla, dorsal view; B (NHM 2010.262), rostrum and disarticulated antennule, dorsal view (except third, fourth, fifth + sixth segments, in ventral view, marked with asterisks); C (NHM 2010.262), antenna; D (NHM 2010.263), antennule; E (NHM 2010.262), mandible; F (NHM 2010.262), maxillule (coxal endite and basis disarticulated); G (NHM 2010.262), maxilla (syncoxal endites disarticulated); H (NHM 2010.262), maxilliped.

enlarged, with strong subdistal outer spine, proximally with two outer spinule rows of two and three spinules respectively, one distal row of spinules and a hyaline frill on the distal inner corner; exopod-2 shortest of all exopodal segments, squat, with one distal spinule row and one short subapical outer seta; exopod-3 squat, with hyaline frill on distal inner corner, apical spinule row, and one unipinnate spine and two pinnate setae distally. Endopod cylindrical, small, less than half as long as exopod-1, with apical seta and four spinules.

P3 (Fig. 5C): basis with outer spinule row composed of long, thin spinules and one transverse row of small spinules below outer seta; one inner row of acute laminar denticles. Exopod-1 slightly curved inward, with a laminar expansion along the inner margin and two longitudinal spine rows on outer margin: proximal row composed of three spines, distal one of five spines. Exopod-2 fused with exopod-1 and prolonged into apophysis ending in rounded tip; thumb longer than apophysis, thin and elongated, apically slightly curved. Endopod missing.

P4 (Figs. 5E, 5F), exopod-1 with outer seta inserted at 2/3 length, two outer spinule rows at 1/3 and 2/3, respectively, and distal spinule row. Exopod-2 bare, with

distal spinule row and distal outer tube-pore (arrowed in Fig. 5F). Exopod-3 with thin apical outer seta, apical spinule row, transformed hook-like apical spine longer than exopod-3. The spine has spaced spinules of same length on the outer margin, and a cluster of thin and long hair-like spinules starting at 3/4 of the way along inner margin.

P5 (Fig. 4C): fused to intercoxal sclerite and to somite, elongated, sub-rectangular, bearing from inner to outer corner one curved subapical spine, two setae of subequal lengths, very small spiniform process, and long seta.

P6: small plate without armature.

Description of Female.— Body vermiform, slender, unpigmented, eyeless. Length, measured from tip of rostrum to apex of caudal rami; mean length 388 μm ($n = 5$). Hyaline frills of cephalothorax, thoracic somites, genital double-somite, and urosomites smooth. Cephalothorax with elliptical dorsal integumental window and 36 sensilla. Genital somite and third urosomite fused, forming genital double-somite (Fig. 6A). Genital double-somite and succeeding two urosomites with dorsal elliptical integumental windows similar to those of male. First urosomite with ventral cuticular ridges (Fig. 4D). Female genital field:

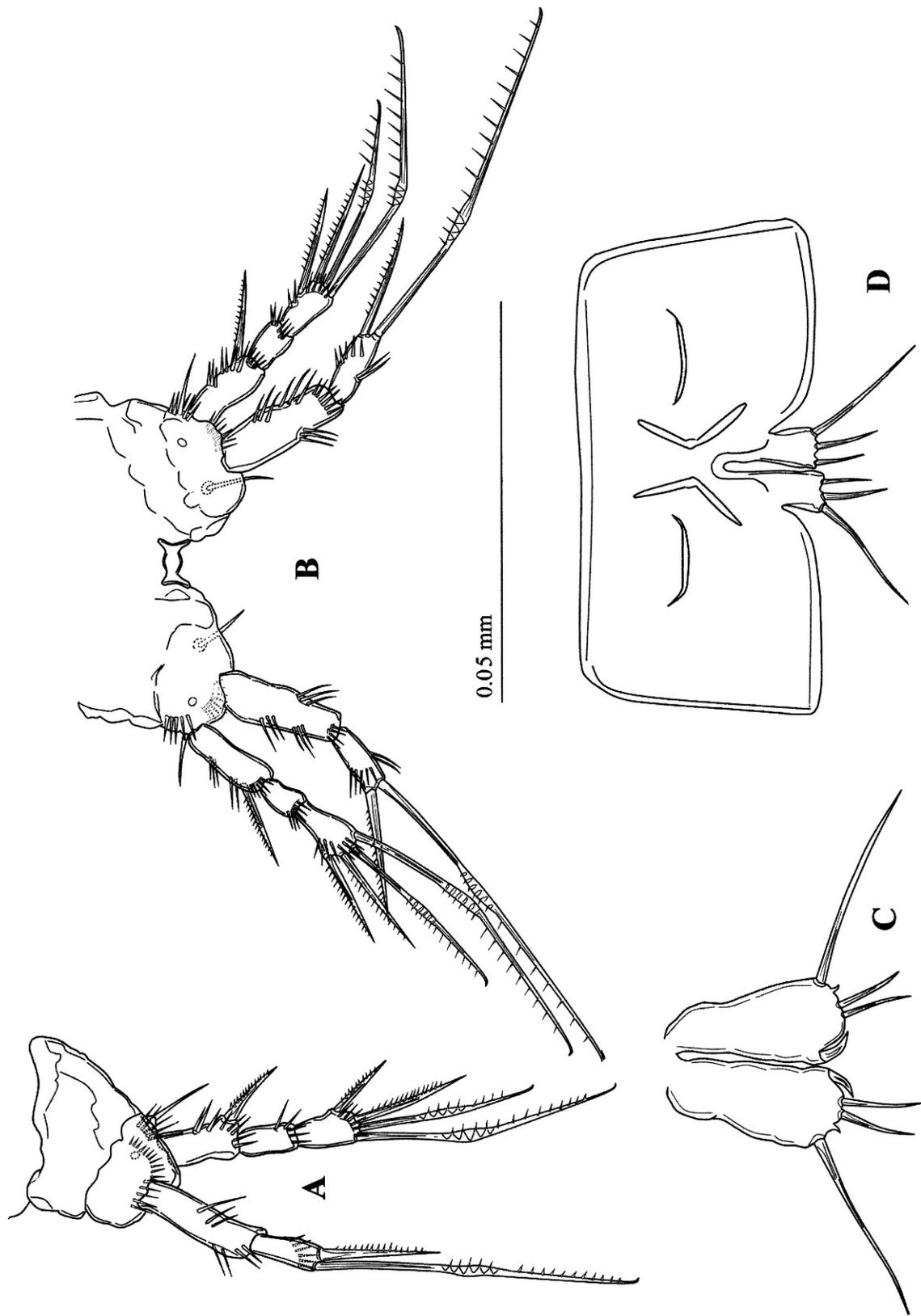


Fig. 4. *Asiaticaris dispar* n. gen., n. sp. B, C: male; A, D: female. A (NHM 2010.263), P1, inner view; B (NHM 2010.262), right and left P1 and intercoxal sclerite; C (NHM 2010.263), first urosomite and P5, ventral view.

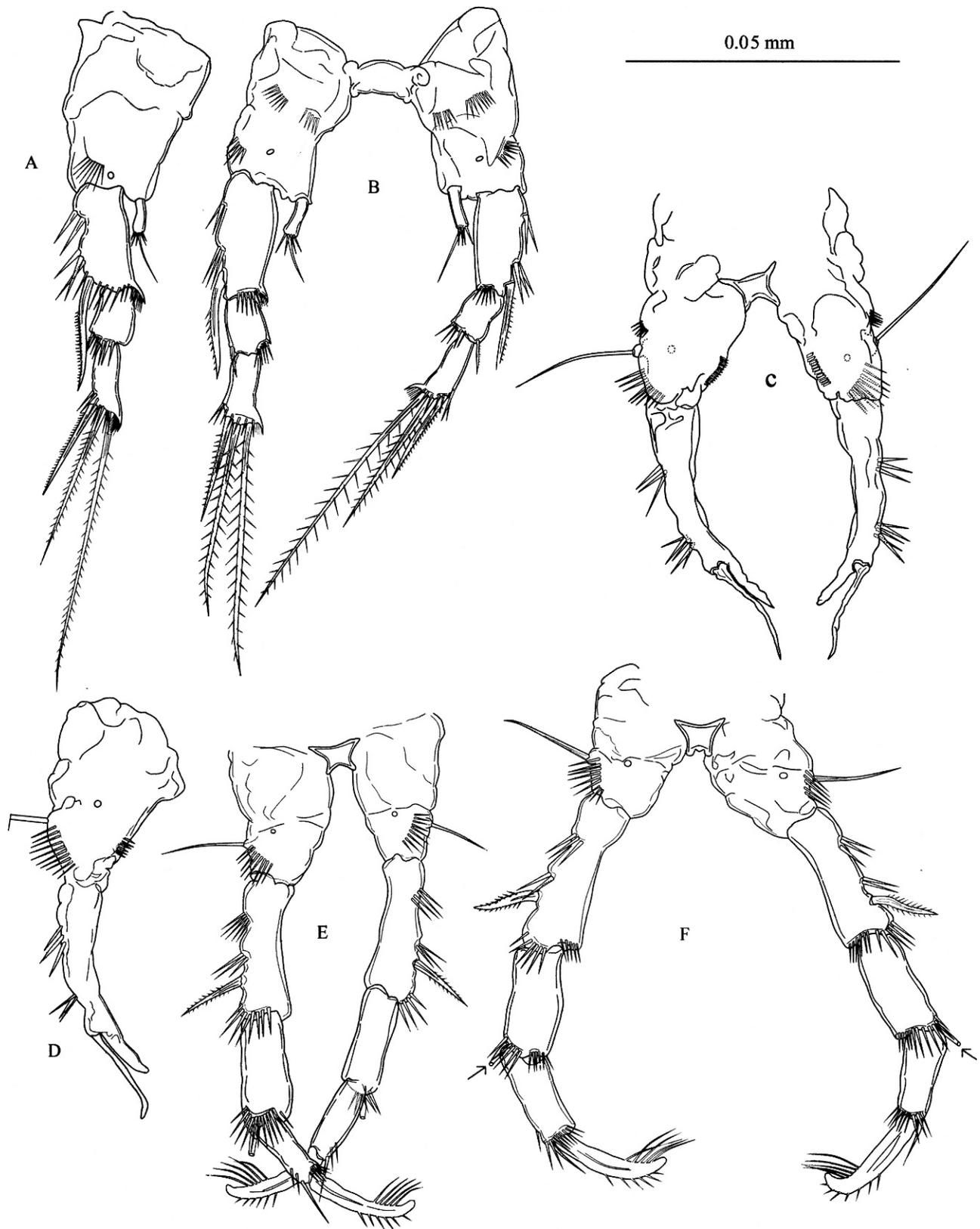


Fig. 5. *Asiacaris dispar* n. gen., n. sp. A-F: male. A (NHM 2010.266), P2, lateral view; B (NHM 2010.262), right and left P2 and intercoxal sclerite; C (NHM 2010.262), right and left P3 and intercoxal sclerite; D (NHM 2010.266), P3, lateral view (exhibiting variability); E (NHM 2010.266), right and left P4 in closed position, and intercoxal sclerite; F (NHM 2010.262), right and left P4 in open position, and intercoxal sclerite, tube-pore arrowed.

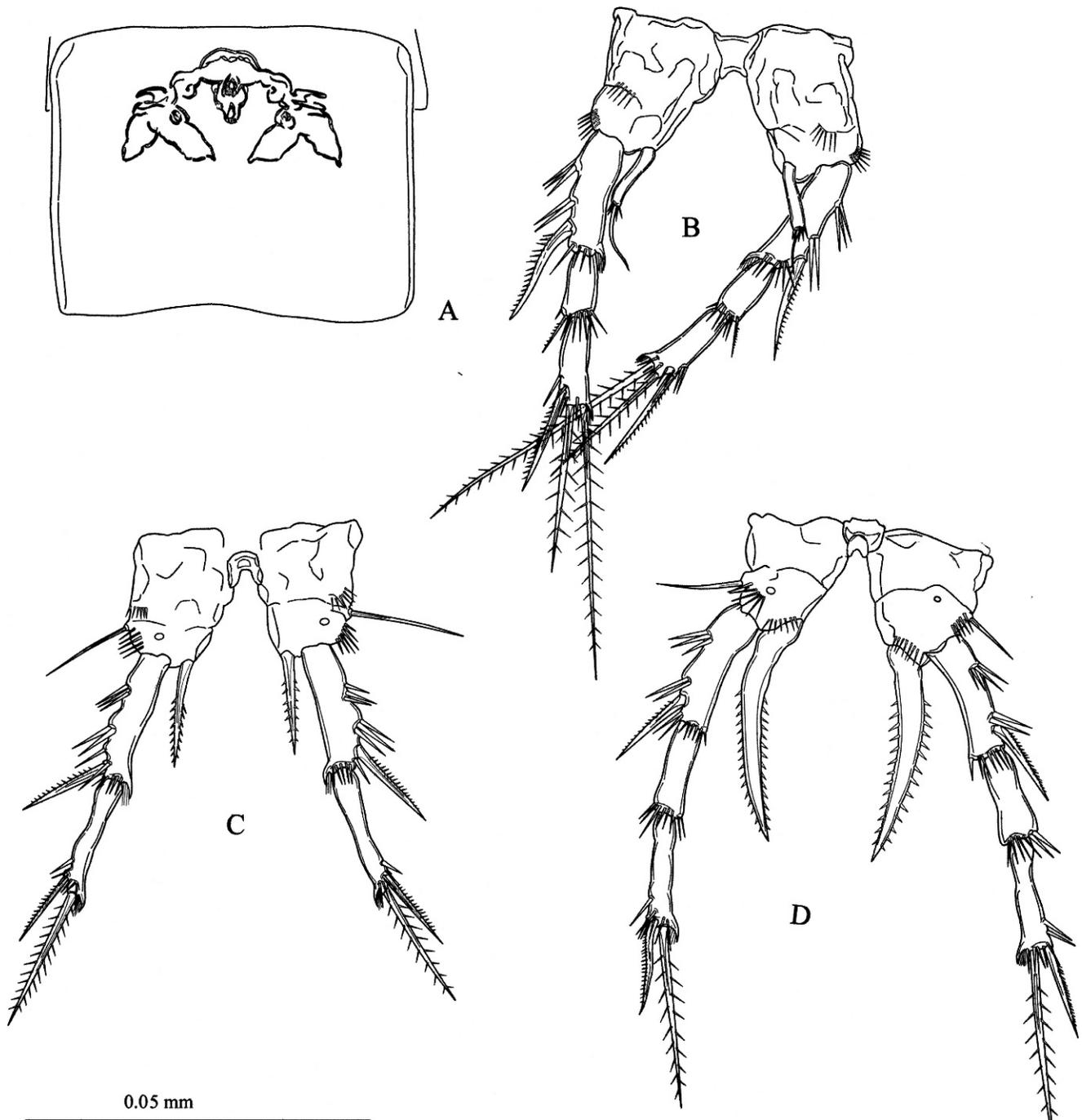


Fig. 6. *Asiacaris dispar* n. gen., n. sp. A-D female. A (DISA 2010.263), genital somite and genital field, ventral view; B (NHM 2010.264), right and left P2 and intercoxal sclerite; C (NHM 2010.264), right and left P3 and intercoxal sclerite; D (NHM 2010.263), right and left P4 and intercoxal sclerite.

L/W 0.74; copulatory pore not covered by operculum, opening at 1/5 of way from anterior end of double-somite (Fig. 6A). Anal somite, anal operculum, rostrum, antenna, mouth appendages, maxilliped, P1 exopod and endopod (Fig. 4A), as in male.

Caudal rami (Fig. 2B, C) smaller than last abdominal somite, conical, less divergent than in male, length/width 2.18; same armature as in male.

Antennule (Fig. 3D): seven-segmented, aesthetasc on fourth segment similar to that of male, reaching beyond end

of seventh segment. First segment with row of short spinules. Armature formula: 1-[0], 2-[1 uniplumose + 4 bare], 3-[4 bare], 4-[2 bare + ae], 5-[0], 6-[0], 7-[9 bare + ae]. Apical acrothek similar to that of male.

P1 basis (Fig. 4A): without inner seta.

P2 (Fig. 6B): legs separated by narrow intercoxal plate, less than half as wide as that of male; coxa and basis less developed than in male; coxa with distal transversal spinule row; exopod proportionally thinner than in male, with same ornamentation and armature including subapical outer seta,

with segments not enlarged and exopod-2 shortest of all exopodal segments. Endopod cylindrical, longer than half exopod-1 length, proportionally longer and thinner than in male, with apical seta and spinules.

P3 (Fig. 6C): coxa with distal transversal spinule row; basis with pore, outer seta about half as long as male one, and spinule row. Exopod-1 with outer distal seta and two outer spinule rows, with hyaline frill on distal inner corner, and apical spinule row. Exopod-2 with distal inner hyaline frill, distal spinule row, and two pinnate short apical setae. Endopod represented by pointed pinnate segment, slightly shorter than exopod-1.

P4 (Fig. 6D): coxa bare; basis with outer pore, seta, and spinule row; another spinule row near endopod insertion. Exopod-1 with distal outer seta longer and thinner than in male, remaining armature of exopod-1 and armature of exopod-2 as in male, but without tube-pore on exopod-2. Exopod-3 with two short apical setae, one pinnate, distal inner hyaline frill and spinule row. Endopod longer than exopod-1 and exopod-2, represented by strong, pointed, and inwardly curved pinnate segment.

P5 (Fig. 4D): fused to intercoxal sclerite and to somite, small, quadrangular, much smaller than in male, with three apical setae of different lengths.

Variability.— All features appear to be constant in the type series except for one male with a reduced number of spines in the distal outer row of exopod-1 of P3 (Fig. 5D).

Etymology.— The specific name from the Latin adjective “dispar” meaning “different”, it refers to the peculiar shape of the male P4, a morphological feature never described so far for any Parastenocarididae. The epitheton is an adjective in feminine singular.

Remarks on the Ecology of *Asiacaris*.— Three sampling campaigns in Pha-ngan Island, conducted from 2006 to 2009, allowed us to sample most of the running waters of the island, which belong to different typologies: small permanent creeks running through rainforest on the hill slopes (200–300 m a.s. l.) and through plantations of *Cocos nucifera* in the low plain; and larger torrents in the headwaters. Such streams run through all the vegetation types of the island. We sampled 18 stations, and the several taxa of Parastenocarididae listed in the introduction were collected at 11 of them. *Asiacaris dispar* was collected at only one station (Fig. 7) located where the Than Sadet River runs among large granitic boulders, with small sand deposits along the banks. The specimens were collected with the Karaman-Chappuis method at a depth of about 25 cm. The water pH was 5.5, the air temperature at 9:30 a.m. was 27.4°C, and the hyporheic water temperature was 25.7°C. The few specimens of *A. dispar* were collected together with numerous specimens belonging to two more new taxa of Parastenocarididae the study of which is in progress.

DISCUSSION

Taxonomic Affinities

Parastenocarididae is a monophyletic group within Harpacticoida characterized and easily distinguished by the



Fig. 7. Photograph of the *locus typicus*, small sandy area on the left bank of the Than Sadet River, near the Than Sadet waterfall, Pha-ngan Island, Thailand.

sexual dimorphism of the third pair of legs (Corgosinho et al., 2007), which are transformed in the males to allow grasping the female during copulation (Glatzel, 1991, 1996; Martínez Arbizu and Moura, 1994). In addition to this apomorphy (Corgosinho et al., 2007), the males of Parastenocarididae show other modifications, mainly in the endopod of the fourth leg and, sometimes, in the first, second, and fifth legs and the caudal rami (Schminke, 1991). These modifications are important and useful in distinguishing species and supra-specific taxa (Corgosinho et al., 2007). The phylogenetic informative characters, useful to assess relationships between *Asiacaris* and other taxa of Parastenocarididae, are listed and discussed below.

Cuticular Pores and Sensilla.— According to Corgosinho et al. (2007), the probable ground pattern of cuticular pores for Parastenocarididae is one dorsal pore on each somite and one outer pore on each side of the anal somite, as it has been recorded in some species of *Remaneicaris* and in *P. hispanica* Martínez Arbizu, 1997. *Asiacaris dispar* has only one pore on the cephalothorax and the pores on the P1–P4 basis in common with several Parastenocarididae (*Parastenocaris distincta* Cottarelli, Bruno and Berera, 2006; *P. reidae* Cottarelli, Bruno and Berera, 2007; *P. ranae* Stoch, 2000; *Remaneicaris tridactyla* Corgosinho, Martínez Arbizu and Santos-Silva, 2007; *R. paratridactyla* Corgosinho, Martínez Arbizu and Santos-Silva, 2007; *R. juliae* Corgosinho, Martínez Arbizu and Santos-Silva, 2007; *Kinneicaris giselae* Schminke, 2008; *Murunducaris loyolai* Corgosinho, Martínez Arbizu and Reid, 2008). The loss of the pores on each somite and anal somite represents an apomorphic character shared by these several taxa.

Comparative study of the sensillar pattern within Parastenocarididae has been mostly neglected, probably because the number and position of these structures is difficult to discern accurately (Corgosinho et al., 2007). The maximum number of sensilla described until now for a species of Parastenocarididae in males is 17/6/6/5/5/4/ 4/5/0/1 (Ahnert, 1994) counting unilaterally from the cephalothorax to the anal somite. *Asiacaris dispar* appears to

have a slightly lower number of sensilla than those reported for other genera.

Asiacaris dispar has no sensilla on the somite anterior to the anal somite, a condition reported by Corgosinho et al. (2007) as common to all Harpacticoida.

Dorsal Windows.— In *A. dispar*, dorsal windows are present in the same position in both sexes: one elliptical window on the cephalothorax, an elliptical integumental window on each tergite of the second through fifth urosomites in the male, and on the tergites of the genital double-somite and succeeding two urosomites in the female. This arrangement of integumental windows has been described for several species of *Parastenocaris* sensu lato and sensu stricto belonging to different species-groups, such as *P. brevipes* (Reid, 1994), *P. hispanica* (Martínez Arbizu, 1997), the species of the *P. hera*-group Berera and Cottarelli, 2003, *P. altitudinis* Cottarelli, Bruno and Berera, 2008, *P. reidae*, and *P. muvattupuzha* Ranga Reddy and Defaye, 2009. The same arrangement of windows is present in *Simplicaris lethaea* Galassi and De Laurentiis, 2004, in most of the species of *Forficatocaris* and *Potamocaris*, in *Murunducaris loyolai* Corgosinho, Martínez Arbizu and Reid, 2008, and in *Remaneicaris ignotus* (Dussart, 1983). This condition represents “the most common pattern in parastenocaridids” (Galassi and De Laurentiis, 2004, but see also Reid, 1994; Cottarelli et al., 2006). According to Corgosinho et al. (2007), this window arrangement is also a character present in the ground pattern of Parastenocarididae that has been conserved in several lineages of this taxon. This is therefore a plesiomorphic character for *A. dispar*. Windows are laterally or ventro-laterally displaced on the fourth urosomite of females and on the fifth urosomites of males of *Remaneicaris*, *Monodicaris*, and *Kinnecaris* and such feature has been interpreted as homoplastic by Corgosinho et al. (2007).

Caudal Rami.— The caudal rami are sexually dimorphic in shape and size in *A. dispar*; both sexes have only six setae and have lost one outer seta (we could not confirm whether the missing seta is the anterior or the posterior one, although seta III is most likely the missing one). A similar reduction is present in two Australian species of *Parastenocaris* sensu stricto, namely *P. kimberleyensis* Karanovic, 2005 and *P. jane* Karanovic, 2006. Within the remaining genera of Parastenocarididae, species of *Potamocaris* have a number of setae that varies between sexes and between the two rami of the same individual (Reid, 1991): *Potamocaris bidens* (Noodt, 1955) lacks “a small caudal seta ventral to the 2 terminal setae” (Reid, 1991), whereas *P. cuiabaensis* Reid, 1991, clearly lacks setae I and II. However, because there is no loss of one or more outer setae in the ground pattern of the genus *Potamocaris* (*P. estevesi* Reid, 1991 in fact has seven setae), the reduction of the number of setae in *Potamocaris* and *A. dispar* is probably related to different setae.

The insertion of all the setae on the distal half of the ramus, and the presence of a pore, has been reported for some Parastenocarididae, such as *P. mangyans* Bruno and Cottarelli, 1999; *P. amalasuntae* Bruno and Cottarelli, 1998; and *P. pasquini* Cottarelli, 1972. The fact that this

feature is present in other interstitial families, such as several species of *Bereraia* (Cottarelli, 1971) [Leptopontidae Lang, 1948], suggests that these characters are probably homoplastic and have arisen independently in different lineages of highly specialized interstitial harpacticoids.

Antennule of Both Sexes.— According to Corgosinho et al. (2007), a 9-segmented antennule in males and 7-segmented in females is the ground pattern of the Parastenocarididae. Such antennular segmentation is present, for instance, in *Remaneicaris* and *Potamocaris*. *Parastenocaris*, *Simplicaris*, *Kinnecaris*, and *Monodicaris* have a derived condition with an 8-segmented antennule in the male, whereas the female still has a 7-segmented A1. The same derived condition occurs in the male of *A. dispar*, which for this character is related to *Parastenocaris* and *Simplicaris*. The morphology and armature of the male A1 of *A. dispar* is very similar to that of *Parastenocaris*. In fact, *A. dispar* has a small, U-shaped fourth segment, just as it has been recorded recently in *Parastenocaris* sensu lato and *Simplicaris* (Berera and Cottarelli, 2003; Galassi and De Laurentiis, 2004; Cottarelli et al., 2008). This segment has been described as “a small sclerite” in *Kinnecaris* and *Monodicaris* (Schminke, 2008, 2009); and it appears to be “widespread within the family” (Galassi and De Laurentiis, 2004). Its presence in *A. dispar* is a plesiomorphic character shared among these genera. The anterior proximal corner of the fifth antennular segment and the anterior distal corner of the seventh segment in *A. dispar* protrude to jointly form a prehensile structure, which is lacking in some Parastenocarididae (*P. hispanica*, *P. mangyans*). Galassi and De Laurentiis (2004) stated that this structure is also not present in *P. brevipes*, but their figure shows it, albeit slightly developed. Finally, this prehensile structure is strongly developed in all species of *Kinnecaris* (Schminke, 2008) and some species of *Parastenocaris* such as *P. gayatri* Ranga Reddy, 2001 and *P. distincta*. Galassi and De Laurentiis (2004) took into account only the transformation of the seventh antennular segment and considered it to be a “derived character state” that evolved by convergence several times within the family. The transformation of the seventh segment is probably related to the transformation of the fifth one, because together they produce “very powerful pincers” (Karanovic, 2005); the most parsimonious hypothesis is still the independent evolution of this character several times within Parastenocarididae. The strongest transformation of the A1 towards a grasping organ is the “pocket-knife” formed by segments 5 and 7 of the male antennule described by Schminke (2008) for *Kinnecaris*, which represents an autapomorphy for this genus. In this sense, *Asiacaris* has a “normally prehensile” (sensu Schminke, 2009) male A1.

The shape and size of the aesthetascs in *A. dispar* correspond to the usual plesiomorphic pattern of Parastenocarididae, i.e., without the specializations described by Galassi and De Laurentiis (2004) as adaptive features to groundwater life in lineages that “entered groundwater early in the evolution of the family”.

Mouthparts.—As was already observed by Galassi and De Laurentiis (2004), mouthparts differ among Parastenocarididae, but phylogenetic reconstructions based on such differences should be evaluated with caution, because several descriptions are unreliable. On the other hand, Corgosinho et al. (2007) stated that the mouthparts of Parastenocarididae seem to be very conservative within the family, although some important differences can be seen in some groups. The latter authors described the ground pattern of the mandible of the Parastenocarididae as having a coxal gnathobase bearing one seta and a palp with two distal setae. This pattern is in fact very conservative within the family and the same morphology is present in *A. dispar*; the morphology of the mandible of the latter is thus a plesiomorphic character.

The phylogenetic value of the morphology of the maxillula is, however, more complex to interpret because these appendages are often very difficult to examine and the chance of error is high. According to Corgosinho et al. (2007), the Mx1 ground pattern in Parastenocarididae is represented by a precoxal arthrite with five elements, a coxa with one seta, and a basis with three setae, and they expressed some doubts as to the validity of other ground patterns hypothesized by other authors (Bozic, 1978; Ahnert, 1994; Reid, 1995; Galassi and De Laurentiis, 2004) for various taxa of Parastenocarididae. Although it would certainly be advantageous to agree on one pattern for the mx1 of all Parastenocarididae, we do not think this can be achieved, at least for *Parastenocaris* sensu lato and *Simplicaris*.

The maxillular pattern differs from the ground pattern defined by Corgosinho et al. (2007) which is: five elements on the precoxal arthrite, one on the coxa, and three on the basis, is present in only few of the species of *Parastenocaris* sensu lato, and *Kinnecaris* that have been recently described (Berera and Cottarelli, 2003; Karanovic, 2005; Cottarelli et al., 2006, 2007, 2008; Ranga Reddy and Defaye, 2007, 2009; Ranga Reddy and Schminke, 2009) and is not present in *Simplicaris* (Table 1). In *A. dispar* the pre-coxal arthrite has seven elements, and the coxa has one element, such armature being very common in all Parastenocarididae; the basis has three elements as in several species of *Parastenocaris* sensu lato and in *Simplicaris*. If an increase in the number of elements on the precoxal arthrite is correlated to feeding habits, then it has likely arisen several times in different lineages of Parastenocarididae and the character is homoplastic. In conclusion, in our opinion the armature of the mx1 in Parastenocarididae is highly variable and might be due to different adaptations correlated to the feeding habits of the different taxa. The ground pattern for this appendage in the Parastenocarididae as described by Corgosinho et al. (2007) has probably been modified by gains/losses of elements in the various lineages.

The maxilla of *A. dispar* has a proximal endite with a bare seta and a distal endite with three apical elements, one of which is pinnate: this is a plesiomorphic condition (Corgosinho et al., 2007) for *Asiacaris*, *Simplicaris* and all other genera and species of Parastenocarididae but *Remaneicaris*. *Remaneicaris* show the most plesiomorphic

Table 1. Maxillular pattern of some recently-described taxa of Parastenocarididae.

Species	Number of elements on precoxal arthrite	Number of elements on coxa	Number of elements on basis
<i>Parastenocaris sibiritica</i> Berera and Cottarelli, 2003	5	1	3
<i>P. reidae</i> Cottarelli, Bruno and Berera, 2007	3	1	2
<i>P. distincta</i> Cottarelli, Bruno and Berera, 2006	5	1	2
<i>P. altitudinis</i> Cottarelli, Bruno and Berera, 2008	4	1	2
<i>P. luciae</i> Cottarelli, Bruno and Berera, 2008	7	1	2
<i>P. kimberleyensis</i> Karanovic, 2005	4	1	3
<i>P. manhadi</i> Ranga Reddy and Defaye, 2007	6	1	2
<i>P. curvispinus</i> Enckell, 1970	4	1	2
<i>P. muvattupuzha</i> Reddy and Schminke, 2009	6	1	3
<i>Kinnecaris eberhardi</i> (Karanovic, 2005)	6	2	3
<i>K. godavari</i> Ranga Reddy and Schminke, 2009	5	1	2
<i>Simplicaris veneris</i> (Cottarelli and Maiolini, 1980)*	8	1	3
<i>S. laethaea</i> Galassi and De Laurentiis, 2004	8	1	3

*: pattern based on the re-examination of specimens of both sexes from our collection.

condition for Mx2. The proximal endite has 2 setae and the distal endite 3 bare setae. All other parastenocaridids share the loss of one seta of the proximal endite and the transformation of one seta of the distal endite into a pinnate spine. Cottarelli et al. (2008) discussed the morphology and armature of the mx2 of several Italian species of *Parastenocaris* sensu lato, showing a wide range of variation, the most reduced being that of *P. tryphida* Cottarelli and Bruno, 1993, a cave species from Italy which has only a small endite with one seta and a reduced endopod with one seta.

The maxilliped of *Asiacaris* corresponds perfectly to the plesiomorphic “model” of all Parastenocarididae.

Legs P1-P5.—The armature of the P1-P4 coxae and bases of *A. dispar* is the apomorphic character of the parastenocaridids as a family (Martínez Arbizu and Moura, 1994) represented by the lack of the outer basal seta on the P2 basis of both sexes (although the presence of this seta has been reported in several descriptions, e.g., by Galassi and De Laurentiis, 2004: 249). *Simplicaris* is characterized by another apomorphic character, i.e., the loss of the outer basal seta on the P4 basis of both sexes; this seta is present in *A. dispar*.

In *A. dispar*, the P1 basis of males has an inner seta, which is lacking in females. This dimorphic condition occurs in some Parastenocarididae (see Cottarelli et al., 2006 for details on *Parastenocaris*). The phylogenetic value of the inner seta on the P1 basis has been much debated. Galassi and De Laurentiis (2004) considered the presence of this seta as the plesiomorphic condition, and its secondary loss in some independent lineages within Parastenocarididae as a derived state, based on the

evolutionary trends of the P1 postulated by Martínez Arbizu and Moura (1994) for Parastenocarididae and related families. Lately, Corgosinho et al. (2007) reported the presence of the seta in the ground pattern of the Parastenocarididae, based on its presence in *R. ignotus*, the most basal member of *Remaneicaris*. Recently, Corgosinho et al. (2008) reviewed the genus *Murunducaris*, characterized by the presence of a dimorphic spinule on the inner margin of the basis, which is not homologous to a spine and seta, and due to the scattered presence of the seta in not closely related species of *Parastenocaris*, proposed a more parsimonious hypothesis, i.e., that this seta has arisen independently within different lineages of the family, as also seem to be the case for *A. dispar*.

The remaining armature of the P1 of both sexes of *A. dispar* is similar to that of all Parastenocarididae, with the three-segmented exopod lacking a distal outer seta on exopod-2, the two-segmented endopod without any seta/spine on endopod-1, and endopod-1 with two distal setae.

The P2 have a set of structural and, probably, functional peculiarities, which are related to the transformation of these limbs in the male and which result in a sexual dimorphism such as has never been recorded in the parastenocaridids. This represents an important autapomorphy of *A. dispar*. These peculiarities are related to modifications of: 1) the position of the male P2 relative to the body, 2) the relative size of the segments of the exopod of the male P2, and 3) the intercoxal plate. Because the coxa and basis of the male P2 are very strong, the endopod relatively small, and the intercoxal sclerite wide, the P2 legs are spread farther apart than is usual in Parastenocarididae. The P2 exopod is three-segmented as in all other parastenocaridids, but the shape and size are peculiar: this ramus is strong, exopod-1 being the longest and exopod-2 the shortest segment, whereas in all other Parastenocarididae exopod-2 is either almost as long as the exopod-3 (in *P. brevipes*, *P. distincta*, *R. paratridactyla*, and *Murunducaris juneae* Reid, 1994), or slightly longer than exopod-3, e.g., in *Simpliocaris lethaea* and *Kinnecaris eberhardi* (Karanovic, 2005). The P2 of the male of *A. dispar* are separated by a wide intercoxal plate, which is proportionately larger than the intercoxal plate of all the other pairs of legs and is sexually dimorphic (being overall much smaller in the female than in the male). To our knowledge, the larger size in these limbs, and such sexual dimorphism as they show, are features not present in the other genera of Parastenocarididae, and thus are apomorphies for the new genus.

The P2 of the female of *A. dispar* is more “normal”, and the position of this pair relative to the body is the one typical of Parastenocarididae, due to the “normal” intercoxal plate. Another sexually dimorphic feature never recorded before in the Parastenocarididae is the thinner P2 exopod of the female (in other Parastenocarididae, the exopods are identical in the two sexes), with exopod-2 shorter than the remaining exopodal segments. A longer and thinner P2 endopod in the female is a feature rarely recorded in this family; *A. dispar* shares this state

with some species of *Parastenocaris* sensu lato, e.g., *P. reidae*, *P. tryphida*, *P. aesculapii* Cottarelli and Bruno, 1997; in most Parastenocarididae this appendage is either not dimorphic, e.g., in *Kinnecaris*, *Monodicaris*, *Simpliocaris*, *Remaneicaris*, and some *Parastenocaris*, or the endopod is smaller in the female, e.g., in *Murunducaris*. Another interesting feature of the P2 exopod in the present species is the short subapical outer seta on exopod-2. Such a seta is present in several other families of freshwater harpacticoids if the exopod is three-segmented; it is missing however in all the other genera of Parastenocarididae, and represents an important autapomorphy for *Asiacaris*.

The P3 of males of *A. dispar* well corresponds to the ground pattern of Parastenocarididae and shows the typical transformations related to mating. So far, such modifications have only been recorded for Parastenocarididae among all harpacticoids, except for the genus *Bereraria* in Leptopontidae, in which the male P3 is modified as a clasping organ (Cottarelli, 1971). Besides the acute laminar denticles on the inner margin of the basis, and the laminar extension on the inner margin of exopod-1, other morphological adaptations to improve the grasping function of these limbs are not present in *A. dispar*. On the other hand, several taxa of Parastenocarididae display various morphological peculiarities of the male P3: the inner triangular laminar process of *P. distincta*; the particularly strong spines along the inner side of the basal segment of *P. kimi* Dumont, 1981; the large triangular hyaline lobe, large dentate process close to it, and small chitinous knob of *P. gayatri*; the foliaceous hyaline structure proximal to the endopod on the inner margin of *Remaneicaris analuizae* Corgosinho and Martínez-Arbizu, 2005; and the hump typical of *Murunducaris* (Corgosinho et al., 2008). It can be inferred that a transformed P3 with a relatively simple morphology has remained so in *A. dispar*, because its function in mating was complemented and perhaps replaced by the main morphological changes occurring in the P2 and, mostly, the P4 of males (see below), which represent strong apomorphies of the genus. In the other Parastenocarididae, on the other hand, evolutionary pressure to improve the probability of successful mating acted mainly on the clasping function, which indeed seems to be the primary responsibility of the male P3 (as reported by Glatzel (1996) for *Parastenocaris phyllura* Kiefer, 1938: “when the male clasps the female with both third pereopods to press her to his body”), resulting in various modifications of the basic morphology.

The unique morphology and armature of the male P4 is probably the most important feature of *A. dispar*. The apomorphic characters related to these legs include: 1) the shape of the exopod and of its apical setae, 2) the size and position of the outer seta of exopod-1, and 3) the loss of the endopod. Such an overall transformation of these limbs has never been observed in any freshwater or marine free-living harpacticoid: the strong exopods form a pincer with their long and strong transformed apical seta that ends in a hook and is longer than the distal segment of the exopod. The “pincer” function is enhanced by the parallel strong reduction of the second apical seta. The three segments

of the exopod are very stout (the P4 exopods are stronger than the P3) and long; overall, the P4 is the longest and stoutest leg, a feature never recorded before in any male harpacticoid. The P4 project laterally, creating not only a characteristic habitus, but also possibly a different locomotion pattern from that of all the other Parastenocarididae where the differences in length of legs P2-P4 are never so pronounced and the legs never protrude laterally except for the P3 in a few species. The corresponding legs of the female correspond well to the typical parastenocaridid pattern, with a strong endopod similar to those of *P. brevipes*, several species of *Remaneicaris*, etc. We have not personally observed the mating behavior of members of Parastenocarididae, but an important function of the male P3 in the mating behavior was reported by Glatzel (1996) for *Parastenocaridis phyllura*, who also stated that the P4 pair of the male is important in the "stimulation phase", and that there is "a fourth fixing point using the ventro-frontal process of the male's fourth pereopods." Based on this, it can be assumed that the evolution of a second pincer to grasp the female during coupling, stronger and longer than that formed by the P3, would have provided such a large evolutionary advantage by improving the reproductive success that it would compensate for the possible increased difficulties in locomotion (which, however, have not been demonstrated to occur). Another apomorphic character of the male P4 of *A. dispar* is the reduced size and subdistal position of the outer seta of exopod-1 (in the female the seta is more distal); as a consequence, the transverse spinule row, which is usually aligned with the base of the seta, is also shifted proximally to a mid-segment position.

Finally, the P4 endopod in the male of *A. dispar* is missing. Such a loss has been recorded, although infrequently, in species of *Parastenocaridis*, e.g., *P. cf. glacialis* Cottarelli, Bruno and Berera, 2007; *P. clujensis* Chappuis, 1925; *P. nana* Chappuis, 1925; *P. glareola* Hertzog, 1936; *P. diana* Chappuis, 1955; *P. mateusi* Noodt and Galhano, 1969; *P. tyrrhenidis* Cottarelli, 1970a; *P. amatheia* Cottarelli, 1970b; *P. boulouensis* Apostolov, 2005; and *P. altitudinis*. According to Noodt and Galhano (1969), the P4 endopod of the male has disappeared independently in several lineages of Parastenocarididae. The independency of such loss is supported by the fact that the above-mentioned species belong to phyletic lineages which are very different. In the case of *A. dispar*, the loss of this ramus, which may be important in stimulating the female (Glatzel, 1996), would have been counterbalanced by the resulting reduced hindrance to the grasping action of the exopod. Moreover, because a male harpacticoid reaches its maximum fitness if the placing and fixation of the spermatophore to the female's genital openings is successful and effective, and the spermatophore of *A. dispar* is relatively large if compared with that of *Parastenocaridis* sensu lato, the presence of two clasping pairs of legs instead of one would aid in managing a large spermatophore.

The P5 are sexually dimorphic: in the male they have one tip and one spine more than in the female. A sexually

dimorphic condition is rare in *Parastenocaridis*, and within this genus it is most pronounced in the *P. brevipes*-group Lang, 1948. A sexually dimorphic P5 is not present in *Kinnecaris*, *Monodicaris*, or in the ground pattern of *Remaneicaris* (Corgosinho et al., 2007). The P5 are dimorphic in *Potamocaris*, although comparisons are difficult because for most of the species of this genus only one sex has been described; a strong dimorphism is typical of *Forficatocaris* and *Murunducaris*. One of the most striking characteristics of the former genus is a strongly chitinized complex structure in the P5, while there is a large, subconical, terminal spine on P5 of males of the latter genus (Reid, 1994; Corgosinho et al., 2008). The P5 of the sole species of *Paraforficatocaris*, *P. paranaensis* Jakobi, 1972b, were reported by the author (Jakobi, 1972b) as being strongly sexually dimorphic, with the P5 of the male constructed "like a penis." To our knowledge, no other male in Parastenocarididae has a sexual dimorphism as pronounced as this. From examination of the original drawings, we think that Jakobi either erroneously drew the male P4 endopod as the P5 (Jakobi, 1972b: 246, fig. 2I), or he interpreted an extruded spermatophore as part of P5. As a consequence, what the author described as a P6 is, in fact, the P5, which thus would be almost identical to that of the female [a plate with three setae, although Jakobi (1972b) drew the female P5 with 3 setae (Jakobi, 1972b: 246, fig. 2J), and erroneously described it as a plate with 4 setae]. Finally, the P5 are characteristically missing in *Simplicaris*. Corgosinho et al. (2007) excluded from the ground pattern of Parastenocarididae any sexual dimorphism of P5.

Another derived state of the P5 of *A. dispar* is its fusion to the intercoxal sclerite and to the somite itself. The ground pattern for Parastenocarididae is represented by P5 plates joined by a small intercoxal sclerite, as stated by Corgosinho et al. (2007), and the absence of an intercoxal sclerite is thus a derived state. The absence of the intercoxal sclerite of legs 5 is a character present in the ground pattern of *Remaneicaris*, and represents a synapomorphy for the genus (Corgosinho et al., 2007), while also being shared with *Potamocaris* and with most species of *Parastenocaridis* as a homoplastic character. In these last genus, the intercoxal plate is rarely described, although in some cases its presence can be deduced from drawings, for instance in *P. hispanica* (Martínez Arbizu, 1997: 221, fig. 6A). An intercoxal sclerite is present in both sexes of *Kinnecaris* and *Monodicaris*, and in the female of *Murunducaris* (whereas in the male the P5 are fused to the intercoxal sclerite; see Corgosinho et al., 2008). In *Forficatocaris*, the females do not seem to have an intercoxal plate; the male P5 is strongly transformed and is probably actually fused to the intercoxal plate. The fusion of the P5 to both the intercoxal plate and the somite occurring in *A. dispar* probably represents a homoplastic state, which has arisen independently in other families such as Arenopontiidae Martínez Arbizu and Moura, 1994, and Leptopontiidae sensu Martínez Arbizu and Moura, 1994 (Martínez Arbizu and Moura, 1994).

Biodiversity

Asiacaris dispar was collected in Thailand, in Pha-ngan Island, one of the islands of the Samui Archipelago, in the southern Gulf of Thailand. During three sampling expeditions, almost all typologies of freshwater habitat present on the island were investigated; as a consequence, several species of Cyclopoida and Harpacticoida were collected. Among the latter a new species of Ameiridae, three of Canthocamptidae, a new species of *Schizopera* Sars, 1906, a new species of *Kinnecaris*, five new members of *Parastenocaris* sensu lato (Galassi and De Laurentiis, 2004; Cottarelli et al., 2008), another possible new genus of Parastenocarididae still under study (Cottarelli, unpublished data), and, finally, the new genus described herein.

It seems appropriate to label Pha-ngan Island as a “biodiversity hot spot”, considering that in such a small area (island surface area: 167 km²) all the above-mentioned species were collected, whereas in other, wider areas of Asia only a few taxa of Parastenocarididae have been collected until now, almost all of them belonging to *Parastenocaris* sensu stricto and s. l. In fact, one species of *Kinnecaris* and twelve species of *Parastenocaris* sensu stricto and s. l. (Enckell, 1970; Ranga Reddy and Defaye, 2007, 2009) have been collected so far in the entire Indian subcontinent, five of which endemic of Sri Lanka, one species in Malaysia (Cottarelli and Mura, 1982), and two named species of the genus (Bruno and Cottarelli, 1999, Cottarelli et al., 2006) and two *Parastenocaris* sp. (Cottarelli, unpublished data) in the Philippines (an area which we have intensively investigated); two more *Parastenocaris* sp. have been collected in Taiwan (Cottarelli, unpublished data).

A second island, Samui island, located 8 km south of Pha-ngan Island, with a surface of 247 km², was partly sampled in 2009: samples were collected from the hyporheic habitat of four streams from 15 to 110 m a.s.l.; three of the samples yielded two new species of *Parastenocaris* s. l., one of which is very close to one of the undescribed species collected in Pha-ngan Island; it was collected together with several species of Ostracoda and Cyclopoida. This material is still under study, but it will surely add to the diversity of Parastenocarididae of South-East Asia.

Distribution

Based on the principle that the more ancient the colonization of freshwater habitats, the larger number of species in the lineage (Boxshall and Jaume, 2000), Parastenocarididae have been regarded as being among the first wave of copepods to have dispersed into, and colonized the freshwater habitats of Pangaea, while the current distribution of this family is due to tectonic events that have shaped the modern distribution through vicariance events (Boxshall and Jaume, 2000). The geological history of Koh Pha-ngan and the adjacent Koh Samui islands is quite complex. The two islands, which today are located respectively 47 km and 17 km offshore from the mainland just south of the trend of the Khlong Marui trend where it is projected into the Gulf of Thailand (Hall, 2002).

The islands are probably constituted of basement rock that has been exposed and separated by sedimentary fill, and it seems very probable that they have been emergent highs for a very long time. Even during periods of high sea level they would not have been submerged, and during periods of low sea level they were probably hills surrounded by rivers and forest (Hall, personal communication). Although there are published information concerning the tectonic events that shaped the islands per se, data inferred from the general tectonic and geological setting of SE Asia (Hall, personal communication) suggest that this area was emergent terrestrial for much of the Mesozoic and Cenozoic, i.e., before 45 Ma. Probably during the Eocene and Oligocene these granite highs were hills separated by flat plains with meandering rivers. There would have been occasional incursions of the sea, which became more frequent during the Miocene. During the Middle Miocene from about 16 Ma there was a marine incursion and the highs became islands, but during the Late Miocene the present offshore region may have been a marginal marine area, i.e., close to a coastline with deltaic and littoral deposits. Probably during the last 5 million years (from the Pliocene) this region was more marine than terrestrial, with possible intervals of emergence during the ice ages, if not before. From this short summary of the main geological events that shaped the biogeographic setting of Koh Pha-ngan and Koh Samui is clear that the reconstruction of the historical events leading to the origin of the new genus is complicated by the quite complex geological history of these islands, and by the lack of any information on the harpacticoid biocoenosis of the adjacent mainland. From our preliminary data, the two islands, and particularly Koh Pha-ngan, seem to host, at least for Parastenocarididae, phylogenetic and distributional relicts (a new genus of Parastenocarididae and some new species of *Parastenocaris*, respectively, Cottarelli, unpublished data).

We hope to present a more detailed interpretation of the biogeography once we have described the new species of *Parastenocaris* collected in Koh Pha-ngan and Koh Samui. Nonetheless, the first data on Thai parastenocaridids presented in this paper widen the knowledge of Parastenocarididae of Australasia, helping to fill the numerous gaps that hinder a biogeographic analysis. In fact, the inclusion of *Asiacaris* within the biogeographic pattern of the entire family Parastenocarididae is not feasible yet given the description thus far of only one species with a very restricted distribution. The family appears to have had an ancient origin, as supported by the recent discovery of a number of species in Australia (Karanovic, 2004, 2005, 2006) where in the past the supposed low number of species had suggested the colonization of Australia by dispersal from elsewhere after the breaking up of the Gondwana landmass (in the mid-Jurassic, about 167 MY) (Schminke, 1981). However, reconstruction of the phylogeography within the family is hindered by the surprisingly high diversification of genera in the neotropics, by new genera recently described from other zoogeographical regions (Schminke, 2008, 2009), and by the polyphyletic nature of the genus *Parastenocaris* (Galassi, 2001).

Conservation

“This is a critical time for organisms living in continental waters” (Naiman, 2008): aquatic fauna biodiversity is strongly threatened by habitat alteration and loss, climate change, pollution, and alien species invasions (Millennium Ecosystem Assessment, 2004; Sala et al., 2000). It has been estimated that between 1970 and 2002, freshwater biodiversity declined about 55% (Naiman, 2008). Groundwater fauna is even more at risk (Galassi et al., 2008), mainly due to the reduced geographical range of groundwater species compared to epigeal species (Gibert and Deharveng, 2002).

The effects of anthropic impacts are detectable even in relatively remote areas (Tang and Knott, 2009), and are obviously stronger in small and strongly-populated areas, such as Koh Pha-ngan and Koh Samui. The latter has been discovered by mass tourism in the 1970s, and Koh Pha-ngan about one decade later. The tourism-related structures and activities have developed very quickly; the number of beach resorts, hotels, and private homes has been constantly increasing, with consequent hazards related to waste management, surface and groundwater withdrawal, and pollution of water resources. In Koh Pha-ngan, some of the sites at which we collected a rich and diverse interstitial fauna, including the new genus and the other undescribed Parastenocarididae, are protected because they are with Than Sadet National Park, and some sites are in remote areas. Five sites, however, are near villages, and one is located 3 km from Thong Sala, the island chief town, with a risk for the populations of groundwater harpacticoids living there (including two new species of *Parastenocaris* sensu lato).

As previously mentioned, we collected harpacticoids in Koh Samui only once, and therefore we can not draw conclusions about the conservation status of the waterbodies of this island. However, tourism has been an economic factor there for a longer time than in Koh Pha-ngan, and we can expect that important ecological alterations have taken place. Fortunately, in Thailand public opinion has been shifting towards sustainable management of natural and cultural resources of the nation; we hope that protection and preservation measures will soon include marginal fauna (sensu Schram, 2008; i.e., faunal groups of ancient age, generalists, living in cryptic habitats, and with limited powers of dispersal), that are still mostly unknown to the general public, such as groundwater crustaceans. This importance of these organisms is related not only to the obvious need to conserve diversity, but also because these marginal faunas are better protected from faunal globalization, and are thus destined to gain an increasing biogeographic value (Schram, 2008).

ACKNOWLEDGEMENTS

We would like to thank the personnel of Than Sadet Ko Pha-ngan National Park for the kind welcome accorded to VC and for providing useful information and directions resulting in the collection of the present material. We are very grateful to Prof. Robert Hall, SE Asia Research Group, Royal Holloway University of London, for providing the geological plate and tectonics information and explanations, and to Dr.

Janet W. Reid, Virginia Museum of Natural History, for her constructive comments and for revising the English of an early version of the manuscript. Two referees greatly improved the manuscript with their comments. Research was partly supported by “MIUR ex-60%” funding to V. Cottarelli.

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), Christian-Albrechts-Universität, Kiel, PhD Thesis, 226 pp.
- . 1998. Has the main habitat of *Potamocaris* species been overlooked until now? (Harpacticoida, Parastenocarididae). *Journal of Marine Systems*, Special Volume 15: 121-125.
- Apostolov, A. 2005. Copépodes harpacticoides stygobies de France. 7. Description de deux nouveaux copépodes du genre *Parastenocaris* Kessler, 1913. *Crustaceana* 78: 95-112.
- Berera, R., and V. Cottarelli. 2003. Two new species of interstitial harpacticoids from southern Italy and proposal of a new *Parastenocaris* species-group. *Italian Journal of Zoology* 70: 261-268.
- Boxshall, G. A., and D. Jaume. 2000. Making waves: the repeated colonization of fresh water 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: 239-244.
- Bruno, M. C., and V. Cottarelli. 1998. Description of *Parastenocaris amalasuntae* n. sp. and new data on *Parastenocaris proserpina* and *Parastenocaris pasquini* from subterranean waters of central Italy (Copepoda, Harpacticoida). *Italian Journal of Zoology* 65: 121-136.
- , and ———. 1999. Harpacticoids from groundwaters in the Philippines: *Parastenocaris mangyans* new species, *Epactophanes philippinus* new species and redescription of *Phyllognathopus bassoti* (Crustacea, Copepoda). *Journal of Crustacean Biology* 19: 510-529.
- Chappuis, P. A. 1925. Sur les Copépodes et les Syncarides des eaux souterraines de Cluj et des Monts Bihar. *Buletinul Societatii de Stiinte din Cluj* 2: 157-182.
- . 1940. Die Harpacticoiden des Grundwassers des unteren Maintales. *Archiv für Hydrobiologie* 36: 286-305.
- . 1955. Notes sur les Copépodes. 18. Nouveaux Harpacticoides des Pyrénées. *Notes Biospéologiques* 10: 89-101.
- Corgosinho, P. H. C., and P. Martínez-Arbizu. 2005. Two new interstitial species of *Remaneicaris* Jakobi (Copepoda, Harpacticoida, Parastenocarididae) from the Ribeirão do Ouro river, Brazil, with a redefinition of the genus. *Senckenbergiana Biologica* 85: 147-162.
- , ———, and J. W. Reid. 2008. Revision of the genus *Murunducaris* (Copepoda: Harpacticoida: Parastenocarididae), with descriptions of two new species from South America. *Journal of Crustacean Biology* 28: 700-720.
- , ———, and E. N. Santos-Silva. 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 ground pattern of Parastenocarididae. *Zootaxa* 1437: 1-28.
- Cottarelli, V. 1970a. *Parastenocaris tyrrhenidis* n. sp., nuovo arpacticide interstiziale di Sardegna (Crustacea, Copepoda). *Fragmenta Entomologica* 7: 61-71.
- . 1970b. Una nuova *Parastenocaris* (Crustacea, Copepoda) della falda iporreica del fiume Liscia (Sardegna). *Rivista di Idrobiologia* 9: 93-107.
- . 1971. *Ichmusella eione* n. gen., n. sp. (Copepoda, Harpacticoida), nuovo Crostaceo di acque interstiziali Italiane. *Rendiconti dell'Istituto Lombardo di Scienze e Lettere (B)* 105: 57-70.
- . 1972. *Parastenocaris* (Copepoda, Harpacticoida) di alcune laghi vulcanici del Lazio. *Rendiconti dell'Istituto Lombardo di Scienze e Lettere (B)* 106:138-155.
- , and M. C. Bruno. 1993. Harpacticoida (Crustacea, Copepoda) from subterranean waters of Bue Marino cave, Sardinia, and St. Barthélémy cave, Corsica, and description of three new species. *International Journal of Speleology* 22: 97-119.

- , and ———. 1997. First record of Parastenocarididae (Crustacea, Copepoda, Harpacticoida) from subterranean freshwater of insular Greece and description of two new species. *International Journal of Speleology* 25: 43-57.
- , and B. Maiolini. 1980. *Parastenocaris veneris* n. sp., nuovo arpacticoido interstiziale del Lago di Vico (Crustacea, Copepoda). *Fragmenta Entomologica* 15: 243-252.
- , and G. Mura. 1982. *Parastenocaris arganoi* n. sp., a new trogllobian species from Malaysia. *Malayan Nature Journal* 35: 65-71.
- , M. C. Bruno, and R. Berera. 2006. A new species of *Parastenocaris* from Mindoro Island, Philippines: *Parastenocaris distincta* n. sp. (Crustacea: Copepoda: Harpacticoida: Parastenocarididae). *Zootaxa* 1368: 57-68.
- , ———, and ———. 2007. Interstitial harpacticoids from groundwater in Tuscany (Central Italy): *Parastenocaris reidae* n. sp., *Nitocrella ensifera* n. sp., and notes on the morphology of *Parastenocaris* cf. *glacialis* Noodt (Crustacea: Copepoda). *Italian Journal of Zoology* 74, 83-99.
- , ———, and ———. 2008. Two new *Parastenocaris* (Copepoda, Harpacticoida, Parastenocarididae) from groundwater of Sardinia and Sicily (Italy). *Crustaceana* 81: 537-555.
- Delamare Deboutteville, C. 1960. *Biologie des eaux souterraines littorales et continentales*. Hermann, Paris.
- Dumont, H. J. 1981. Cladocera and free-living Copepoda from the Fouta Djallon and adjacent mountain areas in West Africa. *Hydrobiologia* 85: 97-116.
- Dussart, B. H. 1979. Algunos Copépodos de America del Sur. *Publicación Occasional, Museo Nacional de Historia Natural, Santiago de Chile* 30: 1-13.
- . 1983. Sobre algunos Copépodos de America del Sur. 3. Comunicaciones Científicas del CECONAL (Centro de Ecología Aplicada del Litoral), Argentina 16: 1-8.
- Enckell, P. H. 1970. Parastenocarididae (Copepoda Harpacticoida) from Ceylon. *Arkiv für Zoologi* 22: 545-556.
- Galassi, D. M. P. 2001. Groundwater copepods: diversity patterns over ecological and evolutionary scales. *Hydrobiologia* 453/454: 227-253.
- , and P. De Laurentiis. 2004. Towards a revision of the genus *Parastenocaris* Kessler, 1913: establishment of *Simplicaris* n. gen. from groundwater in central Italy and review of the *P. brevipes*-group (Copepoda, Harpacticoida, Parastenocarididae). *Zoological Journal of the Linnean Society* 140: 417-436.
- , M. Petitta, and F. Stoch. 2008. Conservation and management, pp. 115-138. In: D. M. P. Galassi, M. Petitta, and F. Stoch (eds.), *Subterranean Waters—Hidden Biodiversity*. Museo Friulano di Storia Naturale, Udine, Italy.
- Gibert, J., and L. Deharveng. 2002. Subterranean ecosystems: a truncated functional biodiversity. *BioScience* 52: 473-481.
- Glatzel, T. 1991. Neue morphologische Aspekte und die Copepodid-Stadien von *Parastenocaris phyllura* Kiefer (Copepoda, Harpacticoida). *Zoologica Scripta* 20: 375-393.
- . 1996. Mating behaviour of the groundwater copepod *Parastenocaris phyllura* Kiefer, 1938 (Copepoda: Harpacticoida). *Contributions to Zoology* 66: 103-108.
- Hall, R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions and animations. *Journal of Asian Earth Sciences* 20: 353-434.
- Hertzog, L. 1936. Crustaceen aus unterirdischen Biotopen des Rheintales bei Strassburg. I. Mitteilung. *Zoologischer Anzeiger* 114: 271-279.
- Huys, R., and G. A. Boxshall. 1991. *Copepod Evolution*. The Ray Society, London. 468 pp.
- ICZN. 1999. *International Code of Zoological Nomenclature*, fourth ed. International Trust for Zoological Nomenclature, London.
- Jakobi, H. 1969. *Forficatocaris noodti* n. gen., n. sp. (Copepoda Harpacticoida) aus brasilianischem Limnopsammal. *Crustaceana* 17: 231-238.
- . 1972a. Trends (Enp. P4[♂]) innerhalb der Parastenocarididen (Copepoda Harpacticoida). *Crustaceana* 22: 127-146.
- . 1972b. Zur Kenntnis der *Forficatocaris*-Zoenose des Nhundiaquara (Parana - Brasilien). *Studies on Neotropical Fauna* 7: 239-251.
- Karanovic, T. 2004. Subterranean Copepoda from arid Western Australia. *Crustaceana Monograph* 3: 1-366.
- . 2005. Two new subterranean Parastenocarididae (Crustacea, Copepoda, Harpacticoida) from Western Australia. *Records of the Western Australian Museum* 22: 353-374.
- . 2006. Subterranean copepods (Crustacea, Copepoda) from the Pilbara region in Western Australia. *Records of the Western Australian Museum, supplement* 70: 1-239.
- Kessler, E. 1913. *Parastenocaris brevipes* nov. gen et nov. spec., ein neuer Süßwasserharpacticide. *Zoologischer Anzeiger* 42: 514-520.
- Kiefer, F. 1938. Neue harpacticoide Ruderfusskrebse (Crust. Cop.) aus dem Grundwasser von Aschaffenburg (Main). *Zoologischer Anzeiger* 123:142-147.
- Lang, K. 1948. *Monographie der Harpacticiden*. Nordiska Bokhandeln, Stockholm, 1682 pp.
- 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.
- , and G. Moura. 1994. The phylogenetic position of the Cylindropsyllinae Sars (Copepoda, Harpacticoida) and the systematic status of the Leptopontiinae Lang. *Zoologische Beiträge, Neue Folge* 35: 55-77.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, D.C. 86 pp.
- Naiman, R. J. 2008. *Freshwater Animal Diversity Assessment*. Foreword. *Hydrobiologia* 595: 1-2.
- Noodt, W. 1955. Eine neue *Parastenocaris* (Copepoda-Harpacticoida) als Vertreter in limnischen Mesopsammon aus Südamerika. *Archiv für Hydrobiologie* 50: 76-81.
- , and M. H. Galhano. 1969. Studien an Crustacea subterranea (Isopoda, Syncarida, Copepoda) aus dem Norden Portugals. *Publicações do Instituto de Zoologia "Dr. Augusto Nobre"* 107: 9-75.
- 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: 705-733.
- , and D. Defaye. 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.
- , and ———. 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.
- , and H. K. Schminke. 2009. Discovery of the genus *Kinnecaris* Jakobi, 1972 (Copepoda, Harpacticoida, Parastenocarididae) in south-eastern India, with description of a new species. *Crustaceana* 82: 311-326.
- Reid, J. W. 1991. The neotropical genus *Potamocaris* Dussart (Copepoda: Harpacticoida: Parastenocarididae) with description of two new species. *Journal of Crustacean Biology* 11: 463-472.
- . 1994. *Murunducaris juneeae*, new genus, new species (Copepoda: Harpacticoida: Parastenocarididae) from a wet campo in central Brazil. *Journal of Crustacean Biology* 14: 771-781.
- . 1995. Redescription of *Parastenocaris brevipes* Kessler and description of a new species of *Parastenocaris* (Copepoda: Harpacticoida: Parastenocarididae) from the U.S.A. *Canadian Journal of Zoology* 73: 173-181.
- Sala, O. E., F. S. III Chapin, J. J. Armeston, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. *Global Biodiversity Scenarios for the Year 2100*. *Science* 287: 1770-1774.
- Sars, G. O. 1906. Copepoda Harpacticoida. Parts XV & XVI. Diosaccidae (concluded), Canthocamptidae (part). *An Account of the Crustacea of Norway*, with short descriptions and figures of all the species. Bergen Museum, Bergen 5:173-196.
- Schminke, H. K. 1981. Perspectives in the study of the zoogeography of interstitial Crustacea: Bathynellacea (Syncarida) and Parastenocarididae (Copepoda). *International Journal of Speleology* 11: 83-89.
- . 1991. Sexual dimorphism in furcal rami of Parastenocarididae (Copepoda: Harpacticoida). *Bulletin of the Plankton Society of Japan, Special Volume* 573-584.
- . 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: 1241-1253.

- . 2009. *Monodicaris* gen. n. (Copepoda, Harpacticoida, Parasteno-
carididae) from West Africa. *Crustaceana* 82: 367-378.
- Schram, F. R. 2008. Does biogeography have a future in a globalized
world with globalized faunas? *Contributions to Zoology* 77: 127-133.
- Stoch, F. 2000. New and little known *Parastenocaris* (Copepoda,
Harpacticoida, Parasteno-
carididae) from cave waters in northeastern
Italy. *Bollettino del Museo Civico di Storia Naturale di Verona,
Botanica Zoologica* 24: 223-234.
- Tang, D., and B. Knott. 2009. Freshwater cyclopoids and harpacticoids
(Crustacea: Copepoda) from the Gngangara Mound region of Western
Australia. *Zootaxa* 2029: 1-70.

RECEIVED: 31 July 2009.

ACCEPTED: 4 November 2009.