

## ***HIMALAYACARIS ALAKNANDA* N. GEN., N. SP. (COPEPODA: HARPACTICOIDA: PARASTENOCARIDIDAE) FROM THE HYPOREIC ZONE OF A HIMALAYAN RIVER, NORTHERN INDIA**

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### ABSTRACT

We establish *Himalayacaris* n. gen. to accommodate the type and only species, *Himalayacaris alaknanda* n. sp., collected in the Himalayan Alaknanda River, Uttarakhand, northern India. This species displays three principal autapomorphies of the male leg 4, which are considered diagnostic for the genus: 1) the enormous, conical, plate-like modified structure at the proximal inner corner of the coxa, bearing hair-like spinules at inner distal margin; 2) the condition of the endopod, a small, unornamented, plate-like structure ending in a tiny papilla fused to the basis; and 3) the short and somewhat modified first exopodal segment, ornamented with an additional row of obliquely directed spinules on its dilated inner margin. Another unique feature of this species is the row of long spinules on the proximal inner margin of the basis of the male leg 2. *Himalayacaris* is closely related to the Neotropical *Remaneicaris* Jakobi, 1972, but differs from it, inter alia, in the details of the setae of the caudal rami, 'pocket knife type' of the male antennules, the shape of the basis and the configuration of the exopod and endopod of male leg 3, the insertion of the outer spine of the third exopodal segment of male leg 4, the absence of additional ornamentation of endopod of the male leg 4 and the configuration and armature of leg 5. This is the first hyporheic species from the Ganges River system in the Garhwal Himalayas and the second one from the Himalayan rivers. The phylogenetic position of the new taxon within Parastenocarididae is discussed. In addition, a brief note is given on the ecology of the new species, especially on its skewed sex ratio resulting from the scarcity of males (spanandry), and also on its biogeography.

**KEY WORDS:** Alaknanda River, North India, *Himalayacaris*, Parastenocaridinae, phylogeny

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### INTRODUCTION

During a sampling campaign undertaken by us in November 2008 to study the hyporheic copepod and bathynellacean fauna of the Ganges River system from Badarinath to Haridwar in Garhwal Himalaya, Uttarakhand state, northern India, only a single copepod taxon, herein named *Himalayacaris alaknanda* n. g., n. sp., was encountered. This is the second species of copepod from Himalayan rivers, the first being *Parastenocaris sutlej* Ranga Reddy, 2011, from the River Sutlej in the Western Himalaya in Himachal Pradesh state. Up until now, Parastenocarididae Chappuis, 1940, to which these two species belong, has been known on the Indian sub-continent by 19 species in four genera (see Totakura et al., 2014).

This paper gives an illustrated description of *H. alaknanda* n. gen., n. sp. and discusses its phylogenetic position in Parastenocarididae. *Himalayacaris*, together with the south Indian *Parastenocaris tirupatiensis*-group of species (Ranga Reddy and Totakura, in prep.) and the Neotropical *Remaneicaris* Jakobi, 1972, forms a monophyletic unity with the character states as in the genus *Psammonitocrella* Rouch, 1992 and other basal genera within the out-group Ameiridae. Furthermore, a brief note is added on the ecology of the new species, with special reference to its skewed

sex ratio resulting from the scarcity of males (spanandry), and also on its biogeography.

### MATERIAL AND METHODS

The specimens of *Himalayacaris alaknanda* were obtained from core samples taken from coarse sand underneath cobbles and boulders of the hyporheic zone of the Alaknanda River, northern India (Fig. 1). A rigid PVC pipe (70 cm long, 4 cm in diameter) was used to extract cores from the sediment surface to a depth of 10-20 cm. The samples were pooled in a bucket filled with water from the site, and stirred vigorously. The supernatant was filtered through a bolting-silk plankton net (70  $\mu$ m mesh size) and the filtrate was fixed in 5% formaldehyde. The specimens were sorted into 70% alcohol and later transferred into glycerol.

Dissection was carried out in glycerol under a binocular stereo zoom microscope at a magnification of 90 $\times$ . Drawings were made with the aid of a drawing tube mounted on a Leica DM 2500 Trinocular Research Microscope equipped with a UCA condenser, an IC objective prism, and 1-2 $\times$  magnification changer. Permanent preparations were mounted in glycerol and sealed with wax and Araldite. All the type material has been deposited in the Muséum national d'Histoire naturelle, Paris (prefix MNHN).

In order to determine the position of the new genus within Parastenocarididae, the method of phylogenetic systematics of Hennig (1966) was followed. The cladograms (Figs. 9 and 10) were generated by computer using the program NONA (Goloboff, 1999) for cladistic parsimony, and in interface with WINCLADA (Nixon, 1999). This program uses a heuristic algorithm with unconstrained search and multiple TBR + TBR (searches for trees using tree bisection-reconnection method of branch-swapping, then repeats this process the number of times as indicated in the number of replications box) as search strategy for the best topology, and a Wag-

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prosoma and urosoma inconspicuous; genital field approximately rectangular, wider than high, occupying anterior ventral half of female genital double-somite; caudal rami cylindrical, divergent, about 5 times as long as wide, armed with 7 setae (3 lateral, 1 dorsal, 2 apical, and 1 lateral), and with distinct gap between lateral and dorsal setae; male antennule 8-segmented, of 'pocket-knife type,' segment 5 with spinous process proximally, and penultimate segment with apophysis at distal inner angle; female antennule 7-segmented. In male, leg 1 without inner armature element on basis; leg 2 endopod shorter than first exopodal segment, with 1 apical seta and 1 spinule, and basis with row of long spinules on proximal inner margin; male leg 3 strongly built and both legs of pair interlocking apically; basis relatively long, with strong, blunt cuticular process on distal border; endopod reduced to simple hook-like seta; ancestral proximal segment about as long as basis, sharply bent inwards and unornamented; apophysis short, somewhat conical with modified apical seta; thumb membranous, leaf-like, slightly shorter than apophysis; endopod of female leg 3 more slender than in male, with 1 rudimentary seta and 1 tiny subapical inner subapical spinule; inner proximal corner of coxa of male leg 4 with single enormous conical, plate-like structure, ornamented with row of hair-like spinules on inner distal margin; basis with spinular row between outer seta and first exopodal segment and also at base of first exopodal segment; first exopodal segment short, somewhat modified, sturdy, without any invagination at proximal inner corner, but distal inner margin dilated and ornamented with 3 anteriorly directed spinules; outer spine shorter than next segment; endopod simple and plate-like structure, ending in tiny papilla fused to the basis; endopod of female leg 4 fused to apical seta, imparting a spiniform shape, unornamented and as long as first exopodal segment; leg 5 small, fused to somite, identical in both sexes, unornamented, without intercoxal sclerite, and armed with usual outer seta but with only 1 seta on distal margin, close to inner angle; male sixth legs smooth, unarmed, unornamented, forming simple operculum and covering gonopore.

Type Species.—*Himalayacaris alaknanda* n. sp.

Other Species.—Currently none.

Etymology.—The generic name is derived from Himalaya and the Greek *karis* = shrimp (gender: feminine), to denote that it is the first parastenocaridid genus from a river in the Garhwal Himalaya.

*Himalayacaris alaknanda* n. sp.  
(Figs. 2-8)

Type Locality.—The Alaknanda River meets one of its main tributaries, the Pindar River, at Karanprayag and thereafter flows as the Alaknanda. The sampling site is located in the confluence area at Karanprayag city (30°15'37"N, 79°13'8"E, elevation 1451 m, water temperature 12°C and pH 9.6) in the Chamoli district of Uttarakhand state (Fig. 1). The Himalayan rivers are mostly fed by snow, ice melt and monsoon precipitation. The type locality is cradled in the much corrugated Garhwal Lesser Himalaya of the Himalayan mountain system. Lithologically, the Garhwal Kumaon zone is composed of Upper Carboniferous and Permian dolomitic limestones, slates, and glacial beds, which

are mostly of marine origin, but oscillate to freshwater and terrestrial conditions (Wadia, 1975a, b). The climate of Garhwal Himalaya is temperate (Singh, 1995).

Type Material Examined.—Holotype male (MNHN-IU-2013-11927), dissected on 4 slides, and allotype female (MNHN-IU-2013-11928), dissected on 2 slides; 131 paratypes, of which 1 female dissected on 2 slides (MNHN-IU-2013-11929); 1 male (MNHN-IU-2013-11930) and 3 females (MNHN-IU-2013-11931-11933) whole-mounted on 1 slide each; 100 females (MNHN-IU-2013-11934) preserved in alcohol in 1 vial; 25 females and 1 male in the second author's personal collection. November 4, 2008, coll. V. R. Totakura and Y. Ranga Reddy.

Description of Adult Male (Holotype).—Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 498  $\mu$ m. Preserved specimens colourless. Nauplius eye absent. Body (Fig. 2A) slender, somewhat cylindrical and without any demarcation between prosoma and urosoma; prosoma/urosoma length about 0.7 in lateral view; greatest width at posterior border of cephalothorax in lateral view. Body length/width ratio about 7.7; all somites connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, narrow. Integument smooth, ornamented with sensilla, spinules, pores and also with large dorsal simple cuticular window on each on cephalic shield, genital somite and 3 postgenital somites. Cephalothorax (Fig. 2A, B) elongate-oval, about 1.3 times as long as wide in lateral view (Fig. 2A), 1.5 times as long as wide in dorsal view (Fig. 2B), representing 17.7% of total body length; other somites gradually tapering posteriorly. Surface of cephalic shield ornamented with 9 scattered pairs of sensilla and single, trapezoidal cuticular window in posterior half. Second, third, and fourth pedigerous somites with 2, 3, and 3 pairs of large posterior sensilla, respectively.

Urosoma (Fig. 2A, C): gradually narrowing behind. First urosomite shorter than genital somite and with 3 pairs of sensilla posteriorly. Genital somite ornamented with 4 pairs of sensilla, of which 1 pair just anterolateral to elliptical cuticular window, and 3 pairs posteriorly. Third and fourth urosomites each with 3 pairs of posterior sensilla and 1 dorsal, elliptical cuticular window on anterior half, third one being shortest of all urosomites. Preanal somite longer than preceding somite, with largest dorsal cuticular window and no other surface ornamentation. Anal somite about 1.3 times as long as wide, ornamented with 2 large dorsal sensilla at base of anal operculum and 1 pair of proximo-lateral cuticular pores (Fig. 2A). Large, longitudinally placed spermatophore (Fig. 2C) visible within fifth pediger and genital somite. Anal operculum moderately developed, ornamented with transverse row of ventral spinules discernible through transparent operculum; distal margin slightly concave, not reaching posterior end of anal somite, representing 69.8% of somite's width. Anal sinus wide, ornamented with 1 row of fine spinules on either side. Rostrum (Fig. 2A, B) small, membranous, linguiform, with no demarcation at base, and ornamented with 2 dorsal sensilla.

Caudal rami (Fig. 2A, C): slender, cylindrical with somewhat wavy lateral margins, strongly divergent, space between their bases about equal to maximum width of one ramus, gradually tapering, about 5.6 times as long as greatest

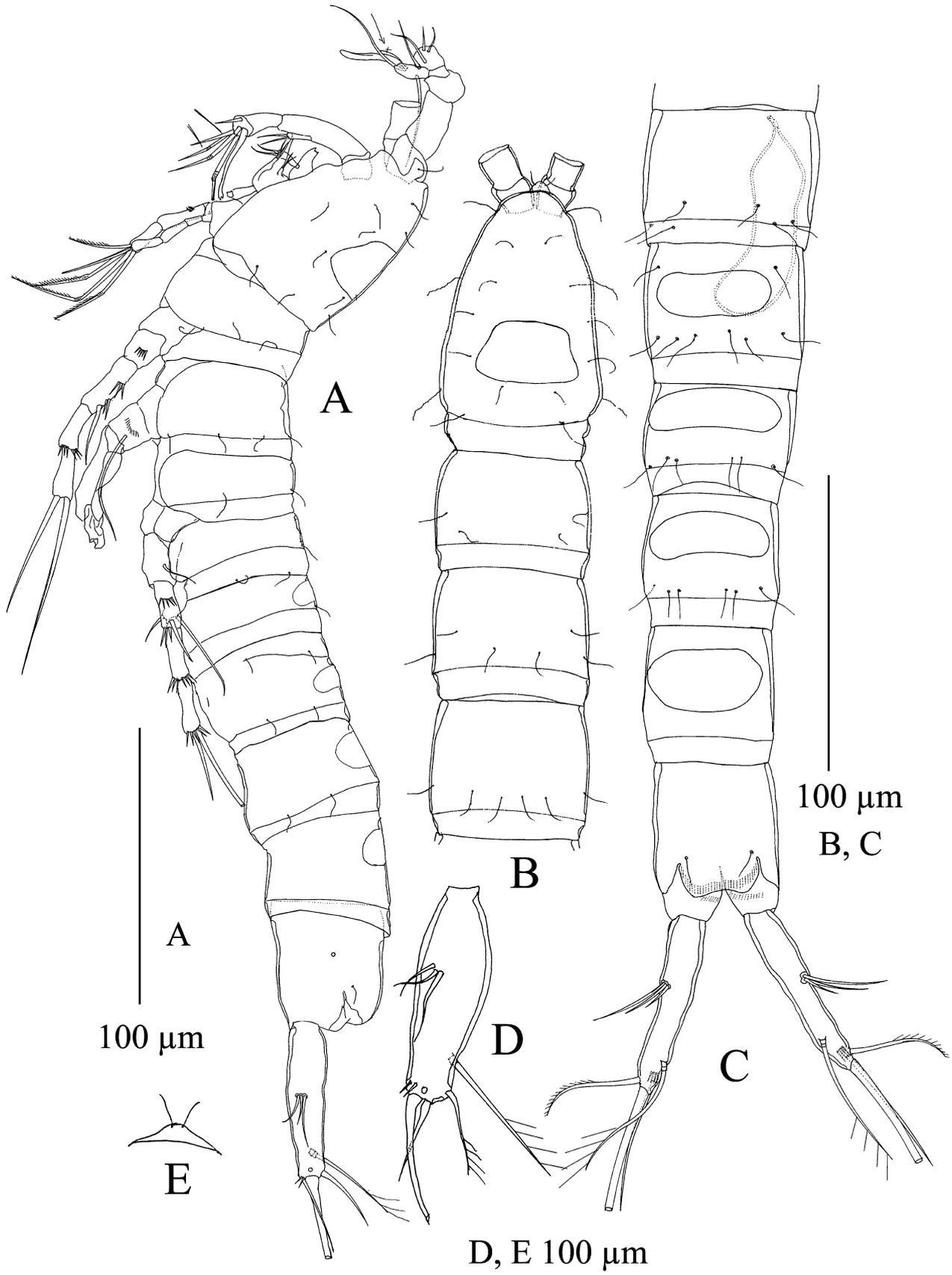


Fig. 2. *Himalayacaris alankanda* n. gen., n. sp. A, E, paratype male habitus, lateral. B, C, holotype male; B, prosome, dorsal; C, urosome, dorsal. D, paratype female caudal ramus, lateral; E, ventral ornamentation of third somite.

width in dorsal view, 4.2 times as long as wide in lateral view (Fig. 2D) and about 1.2 times as long as anal somite; cuticular pore located disto-laterally, and ventral row of spinules along posterior margin; with full complement of 7 setae (3 lateral, 1 dorsal, 2 apical, 1 subapical). Lateral setae (I-III) located proximally at 2/5 of length of ramus. Dorsal seta (VII) slender and plumose, inserted close to inner margin at about 4/5 of length of ramus, and biarticulate basally. Inner apical seta (VI) smooth, inserted close to ventral margin. Middle apical seta (V) strongest, about 2.6 times as long as ramus, lacking breaking plane, distal part unipinnate and curved inwards (Fig. 8K). Outer apical seta (IV) also lacking breaking plane and unipinnate, about half as long as ramus and directed postero-laterally.

Antennule (Fig. 3A): slightly longer than cephalothorax, slender, 8-segmented, prehensile, 'pocket-knife' type, digeniculate with geniculations between third and fourth, and between sixth and seventh segments. First segment very short, ornamented with 1 row of spinules; segments 5 and 6 strongly dilated; segment 5 with small proximal spiniform process and elongate aesthetasc, latter slightly overreaching distal end of appendage and fused basally to simple seta; shorter and more slender apical aesthetasc on eighth segment fused basally with 2 setae (as acrothec). Seventh segment with moderate-sized, triangular apophysis. Setal formula: 0.5.3.1.4 + aes.0.0.9 + aes. All setae slender and smooth, except proximalmost seta on second segment unipinnate with long setules along lateral margin. Length ratios of segments, from proximal to distal end and along caudal margin, 1.0:3.4:1.0:0.2:2.0:1.1:1.4:1.2.

Antenna (Fig. 3B): composed of coxa, allobasis, 1-segmented endopod, and 1-segmented exopod. Coxa very short, ornamented with arched row of short spinules, otherwise unarmed. Allobasis about 3 times as long as maximum width, ornamented with 2 rows of spinules, one each on anterior and posterior surfaces. Exopod small, cylindrical, about 2.6 times as long as wide, unornamented, and armed with 1 apical seta of length 2.9 times that of segment. Endopod 0.4 times as long as allobasis and 1.5 times as long as wide, with surface frill distally, ornamented with 2 longitudinal rows of spinules on inner margin, armed laterally with 2 unequal short spines and apically with 5 strong elements (2 spines, 2 geniculate setae, and 1 unipinnate transformed seta).

Labrum (Fig. 3C, D): hook-like in lateral view (Fig. 3C), subtriangular in ventral view (Fig. 3D), distal margin narrow cutting edge with minute denticles on free margin, and 1 row of fine spinules on ventral surface.

Mandible (Fig. 3E): with narrow cutting edge on elongate coxa, armed with 2 complex teeth ventrally, 1 unipinnate seta dorsally, and several smaller teeth. Palp 1-segmented, cylindrical, about 4.5 times as long as wide, unornamented and armed with 2 smooth apical setae.

Maxillule (Fig. 3F): praecoxal arthrite trapezoidal, about 2.1 times as long as wide in lateral view, armed with strong lateral seta and 3 apical elements. Coxal endite armed with 1 smooth seta apically. Basis twice as long as coxal endite, armed with 2 smooth apical setae.

Maxilla (Fig. 3G): composed of syncoxa, basis, and 1-segmented endopod. Syncoxa with 2 endites, basal one short and armed with 1 basally fused, smooth apical seta,

and distal one armed with 2 smooth apical setae. Allobasis prolonged into strong, unipinnate claw, with no seta at base. Endopod represented by small segment, armed with 2 smooth, subequal, apical setae.

Maxilliped (Fig. 3H): syncoxa short, unarmed and unornamented; basis slender, 4.5 times as long as wide, unarmed and unornamented; endopod small, with unipinnate claw about 0.6 times as long as basis.

Praecoxae of legs 1-4 unornamented and unarmed.

Leg 1 (Fig. 4A): coxa trapezoidal, unarmed, ornamented with arched row of small spinules near outer distal corner. Basis shorter than coxa, trapezoidal; ornamented with ventral row of small spinules close to bases of exopod and endopod, another row of spinules on inner margin ventrally, and also 1 pore on anterior surface; armed with weak outer seta. Exopod 3-segmented, first segment 0.6 times as long as next 2 segments combined, all segments ornamented with spinules along outer margin, first segment armed with 1 bipinnate outer spine; second segment unarmed and third segment with 4 elements (1 outer spine, 1 apical seta, and 2 apical geniculate setae). Endopod 2-segmented, about as long as exopod; first segment as long as proximal 2 exopodal segments, 3.6 times as long as wide, unarmed but ornamented with arched row of spinules on inner margin, 2 rows on outer margin, and 1 row at outer distal corner; second segment ornamented with 1 row of spinules on inner margin; armed with 1 short outer spine and 1 long, apical geniculate seta, latter being about as long as entire endopod, almost 2.3 times as long as neighbouring outer spine, and 0.9 times as long as exopod's inner geniculate seta. All exopodal and endopodal armature elements unipinnate along outer margin except for bipinnate spine on first exopodal segment.

Leg 2 (Fig. 4B): coxa larger than in leg 1, trapezoidal, ornamented with arched row of spinules near distal margin. Basis with row of small spinules on outer margin and row of long spinules on inner proximal margin. Exopod 3-segmented, bent inwards; ornamented with spinules along outer margins of all segments, row of spinules at inner distal corner second segment, and hyaline frill at inner distal corners of first and third segments. First segment 0.6 times as long as next 2 segments combined, armed with moderately long, bipinnate outer spine; second segment unarmed; third segment slightly longer than second segment, armed with unipinnate subapical spine and 2 bipinnate apical setae; innermost seta about as long as exopod. Endopod 1-segmented, incurved, 6.5 times as long as wide, 0.6 times as long as first exopodal segment, ornamented with 1 long subapical spinule; armed apically with 1 smooth seta, this being 0.9 times as long as segment and pointing outwards.

Leg 3 (Fig. 5A): strongly built with both legs of pair interlocking with each other apically. Coxa trapezoidal, shorter than basis, ornamented with 1 row of spinules on outer margin. Basis subquadrate, robust, in line with coxa and with strong, blunt chitinous lobe on distal border close to inner angle; ornamented with longitudinal row of small spinules on inner margin, row of somewhat long spinules at outer distal angle, and pore on anterior surface; armed with 1 long, slender, basally articulated outer seta. Endopod represented by small, hook-like seta inserted on inner margin of basis at 3/4 of its length. Exopod sturdy, about as

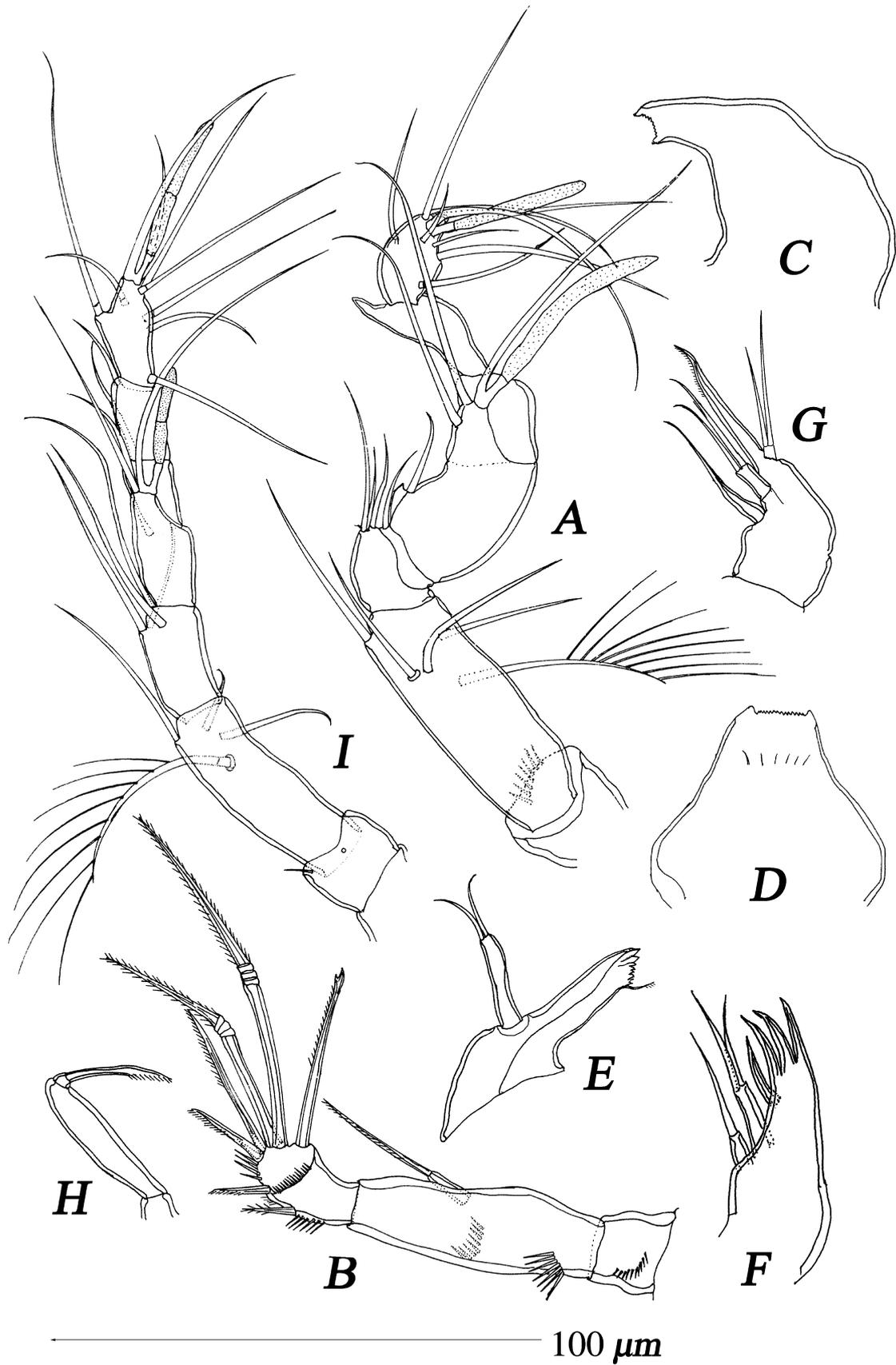


Fig. 3. *Himalayacaris alaknanda* n. gen., n. sp. A-G, holotype male; A, antennule, ventral; B, antenna, lateral; C, labrum, lateral; D, same, ventral; E, mandible, anterior; F, maxillule, posterior; G, maxilla, anterior. H-I, allotype female; H, maxilliped, anterior; I, antennule, ventral.

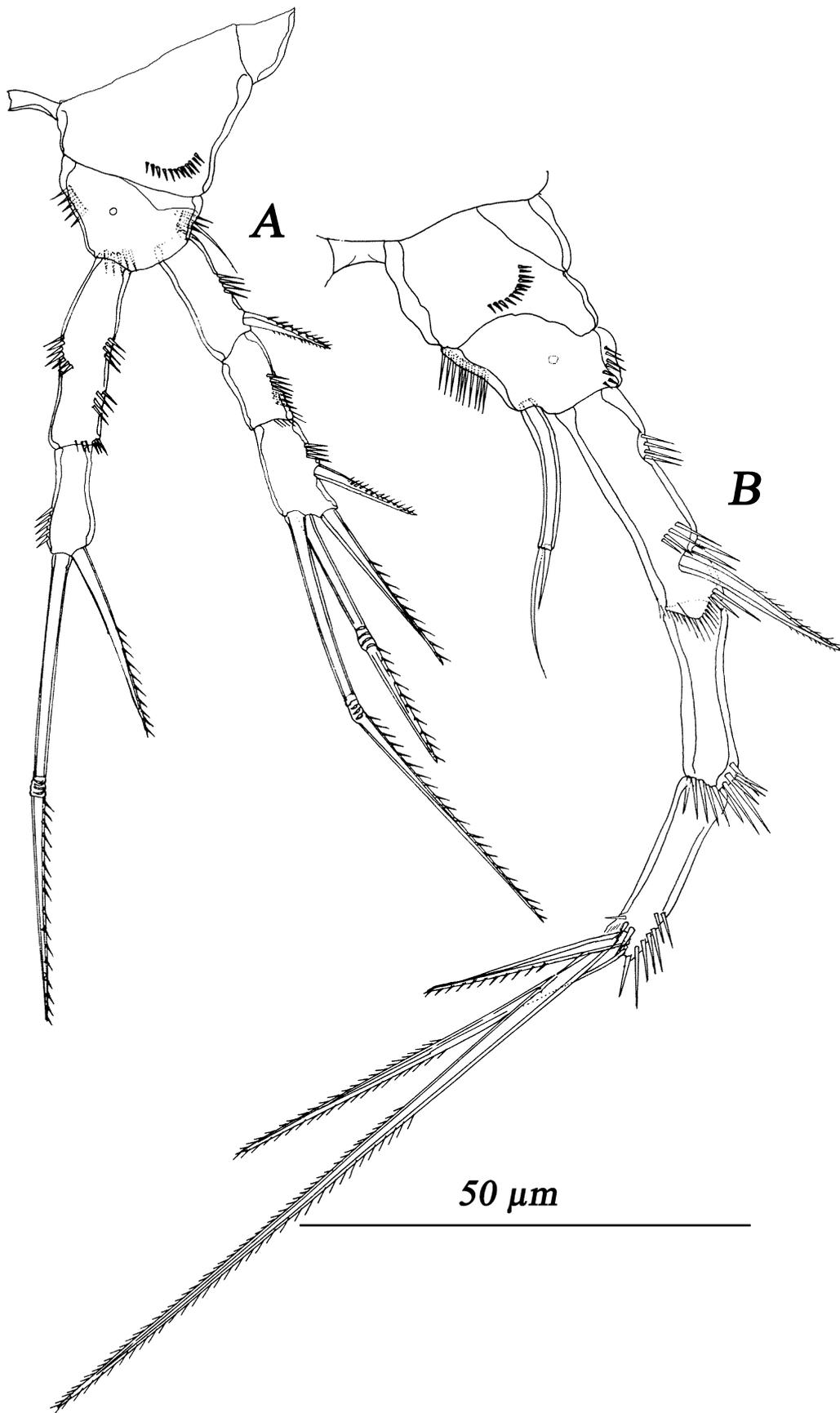


Fig. 4. *Himalayacaris alaknanda* n. gen., n. sp. A-B, holotype male; A, leg 1, posterior; B, leg 2, anterior.

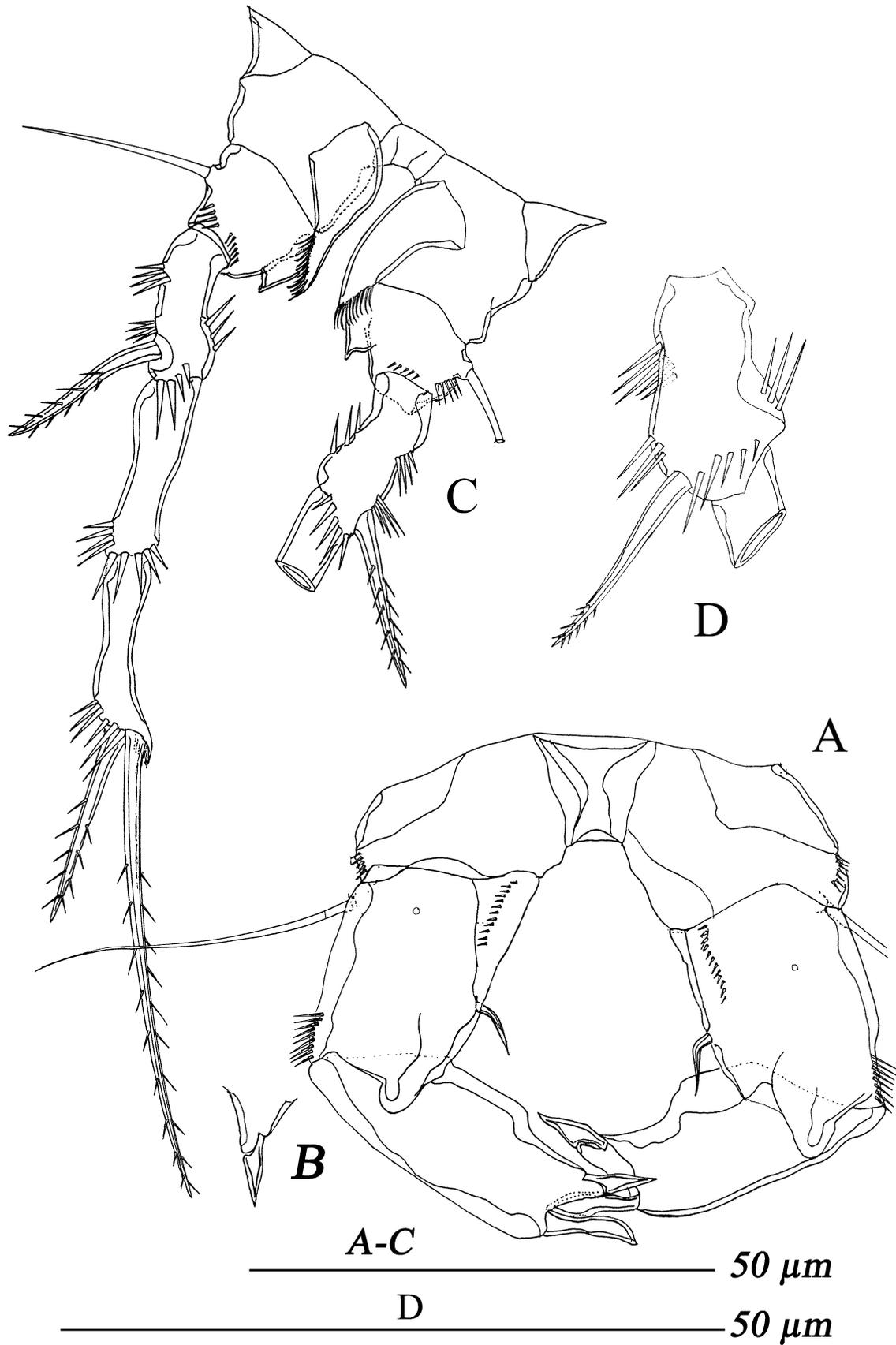


Fig. 5. *Himalayacaris alaknanda* n. gen., n. sp. holotype male. A, leg 3, anterior; B, apophysis, anterior; C, leg 4, anterior; D, leg 4, first exopodal segment, antero-lateral.

long as basis, sharply bent inwards with both segments completely fused; ancestral proximal segment subquadrate, stout, 1.7 times as long as wide in anterior view, with straight outer margin, and unornamented; ancestral distal segment (apophysis) (Fig. 5B) short, more or less triangular and with apical seta modified into conical hyaline lobe; thumb membranous, leaf-like, with hyaline margins, somewhat shorter than apophysis.

Leg 4 (Fig. 5C, D): coxa trapezoidal, bearing massive, conical, plate-like structure on inner anterior surface, this having spinulose inner distal margin and acuminate tip reaching base of endopod. Basis shorter than coxa in anterior view, ornamented with row of spinules on outer margin and another row at base of exopod; armed with moderately long, smooth outer seta. Exopod 3-segmented; first segment short, sturdy, somewhat modified, distal inner margin dilated and ornamented with 3 proximally directed spinules, 2 rows of spinules on outer margin, and 1 such row on distal margin; armed with strong, bipinnate spine. Second segment almost as long as third, unarmed but ornamented with spinules on outer and inner distal corners. Third segment ornamented with row of spinules on outer distal corner and hyaline fringe at inner distal corner; armed with 2 bipinnate apical setae, inner one 2.3 times as long as outer one, 2.4 times as long as third exopodal segment, and 0.8 times as long as entire exopod. Endopod reduced to short, membranous, unornamented, plate-like structure ending in tiny papilla fused to the basis.

Leg 5 (Fig. 7A, C, D): trapezoidal plate in ventral view, rectangular in latero-ventral view; fused to the somite at base, ornamented with cuticular pore proximally, no spiniform process at inner distal corner, armed with only 2 setae, outermost seta basally articulate and inserted at outer distal corner (Fig. 7A); a small seta at inner distal corner (perhaps ancestral endopod), 0.6 times as long as outermost seta.

Leg 6 (Fig. 7A, E): asymmetrical, smooth, unarmed and unornamented, forming simple operculum covering gonopore, fused to sixth pediger, triangular in lateral view (Fig. 7E).

Description of Adult Female (Allotype).—Body length excluding caudal setae 521  $\mu$ m. Habitus (Fig. 6A): ornamentation of prosomites, colour, and nauplius eye similar to those of male, except genital and first abdominal somites fused into double-somite.

Genital field (Fig. 7F): located in anterior half of genital double-somite; medial copulatory pore slit-like; gonopores covered by vestigial sixth legs. Seminal receptacles small, copulatory duct inflated proximally and narrowing laterally, as illustrated. Preanal and anal urosomites very similar to those of male.

Caudal rami (Figs. 6A, B, 7B, F): divergent, about 4.6 times as long as wide in ventral view, 1.5 times as long as anal somite, gradually tapering, with armature and ornamentation as in male.

Antennule (Fig. 3I): 7-segmented, 13.3% longer than cephalothorax; ornamented on first segment with solitary spinule on ventral surface; fourth segment with short, slender aesthetasc only slightly overreaching sixth segment; apical aesthetasc on seventh segment fused basally to 2 apical

setae; setal formula: 0.4.4.4 + aes.1.1.9 + aes. All setae smooth except for most proximal one on second segment; seta on ultimate segment articulated basally. Length ratios of antennular segments, from proximal to distal and along caudal margin, 1.0:3.1:1.7:1.9:1.1:1.3:1.8.

Antenna, labrum, mandible, maxillule, maxilla, maxilliped and legs 1 and 5 similar to male.

Leg 2 (Fig. 8B-D): same as in male except for spinules near proximal inner corner of basis being shorter; spinules on endopod varying in size and shape in paratypes (Fig. 8C, D).

Leg 3 (Fig. 8E): coxa with 1 row of spinules medially on posterior surface. Basis ornamented with row of spinules near outer seta and 1 pore on posterior surface; armed with 1 long, smooth outer seta about 0.8 times as long as entire exopod and articulated at base. Exopod 2-segmented, ornamented with large spinules along outer margin, both segments with hyaline frill at inner distal corner; first segment armed with 1 outer spine; second segment with outer spine and strong apical seta 1.7 times as long as spine; all elements bipinnate. Endopod 1-segmented, cylindrical, 5.2 times as long as wide, distinctly shorter than first exopodal segment, armed with greatly reduced apical seta and tiny inner subapical spinule.

Leg 4 (Fig. 8F): coxa trapezoidal, ornamented with 1 row of spinules at outer distal corner; basis subtriangular, armed with moderately long seta on outer margin and ornamented with spinules medially and 1 pore distally. Exopod 3-segmented, ornamented with row of spinules along outer margins of all segments, additional row at inner distal corner of second segment, and hyaline frill at inner distal corner of first and third segments; first segment as long as second segment, armed with bipinnate spine on outer margin subdistally, this being 0.8 times as long as segment; second segment unarmed; third segment with 2 unequal elements. Endopod 1-segmented, straight, with fused apical seta ('spine'), both segment and armature element smooth, together reaching distal end of first exopodal segment (Fig. 8G-I).

Leg 6 (Fig. 7F): unarmed, unornamented, plate-like operculum covering the genital slit.

Variation.—Caudal rami swollen in lateral view of some specimens (Fig. 8K); female leg 4 endopod varying in shape (Fig. 8F-I).

Distribution.—The new species is only known from its type locality.

Etymology.—The specific epithet, alluding to the type locality, the Alaknanda River, is proposed here as noun in apposition to the generic name.

## DISCUSSION

The new genus *Himalayacaris* has three signal autapomorphies on the male leg 4: 1) the enormous, conical, plate-like spiniform structure at the proximal inner of the coxa; 2) the endopod modified into a rather small plate-like, unornamented structure ending in a tiny papilla fused to the basis; and 3) the short and somewhat modified first exopodal segment, ornamented with an additional row of obliquely directed spinules on its dilated inner distal margin. Another

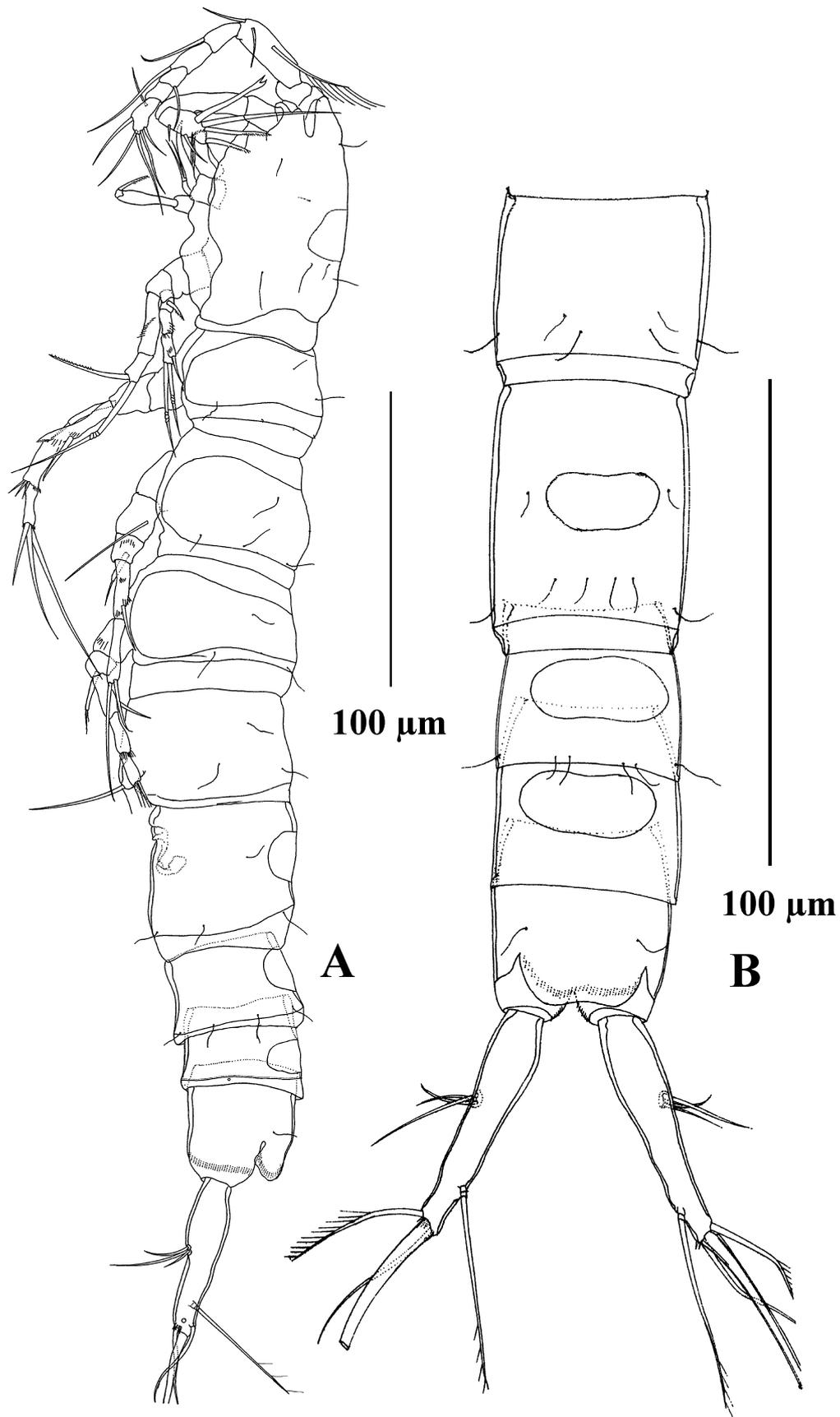


Fig. 6. *Himalayacaris alaknanda* n. gen., n. sp. A, paratype female habitus, lateral; B, allotype female urosome, dorsal.

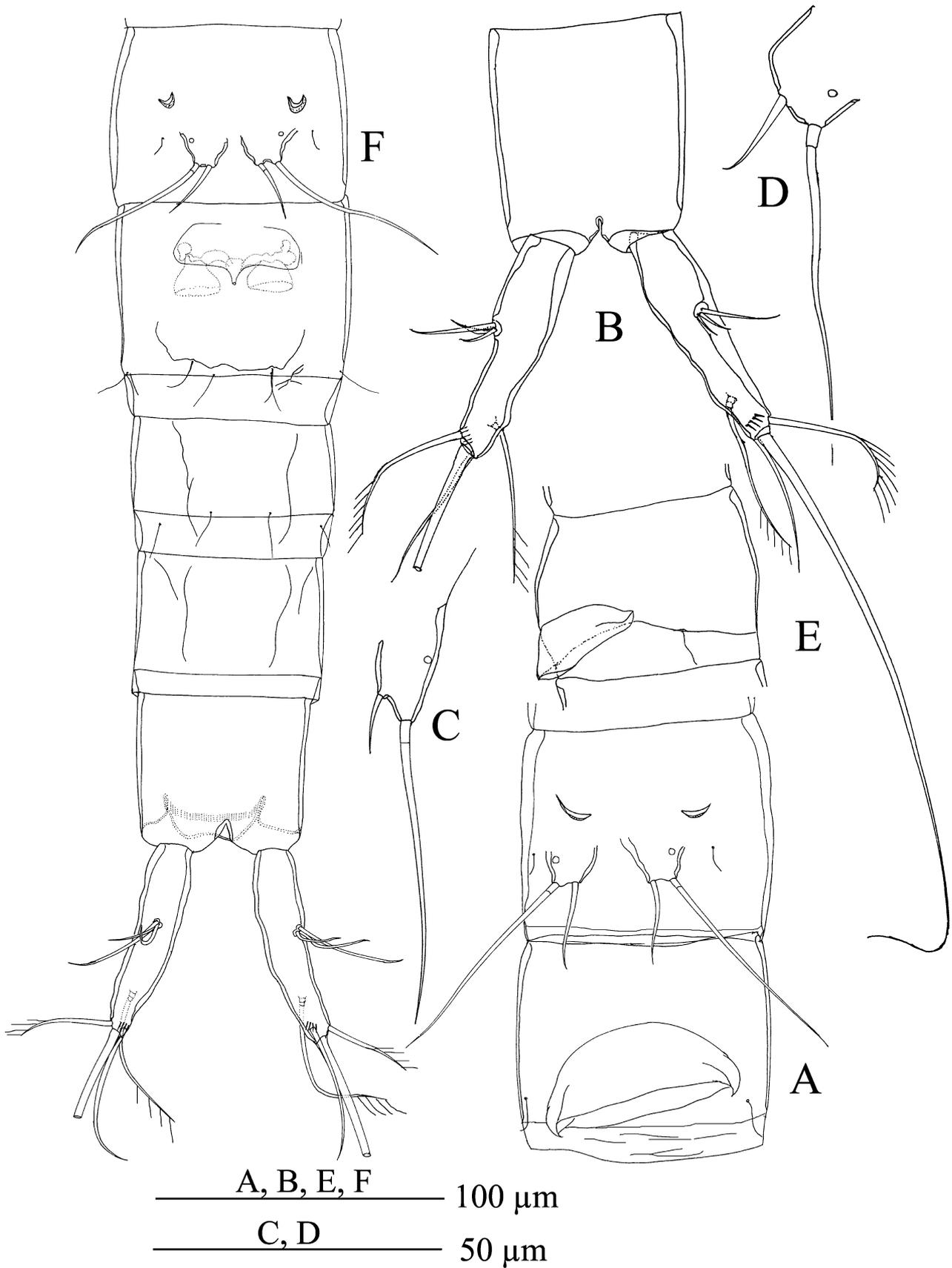


Fig. 7. *Himalayacaris alaknanda* n. gen., n. sp. A-E, paratype male; A, urosomites 1-2, ventral; B, anal somite and caudal rami, ventral; C, leg 5, lateral; D, same, ventro-lateral; E, leg 6, lateral. F, allotype female urosome, ventral.

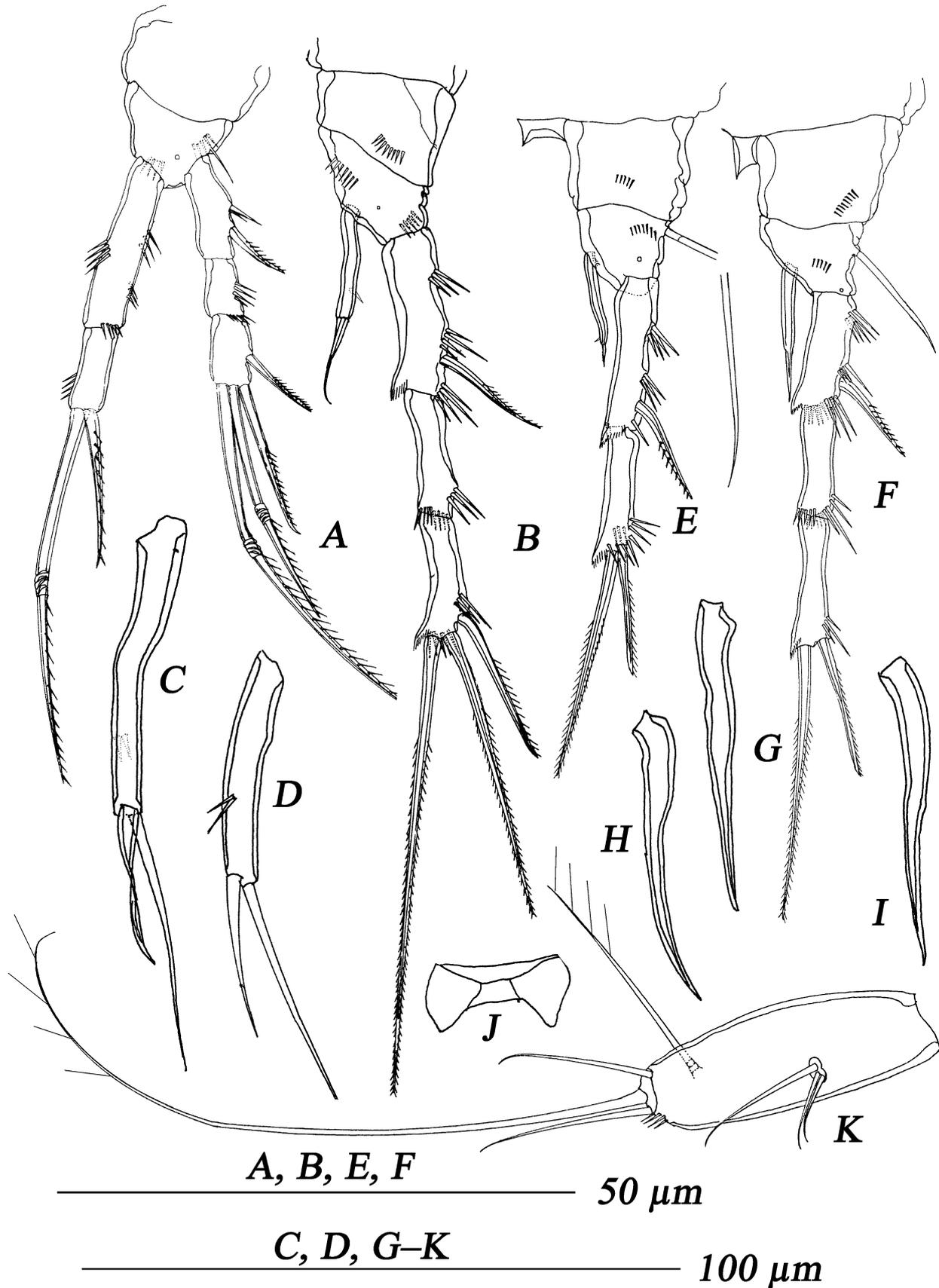


Fig. 8. *Himalayacaris alaknanda* n. gen., n. sp. A, B, E, F, allotype female; C, D, G-K, paratype female; A, leg 1, posterior; B, leg 2, anterior. C-D, leg 2 endopods; E, leg 3, anterior; F, leg 4, anterior; G-I, leg 4, endopods; J, inter-coxal plates of legs 1-4; K, caudal ramus, lateral.

unique feature seems to be the sexually dimorphic leg 2, which has a longitudinal row of large spinules along the proximal inner margin of the basis in the male whereas this spinular row is reduced in the female. Furthermore, the new taxon has a diagnostic combination of other characters as listed in the generic diagnosis.

Within Parastenocarididae, Schminke (2010) recognised two subfamilies, Parastenocaridinae Chappuis, 1940 and Fontinalicaridinae Schminke, 2010, and placed within them all the then known 258 nominal species after thoroughly checking their original accounts and also making use of the unpublished data from Ahnert (1994) and Corgosinho (2007). However, for want of adequate details, several of the species were listed as *incertae sedis* by Schminke himself. This led some authors such as Karanovic and Cooper (2011: 297) to openly criticise Schminke's ideas. Clearly, the phylogenetic importance of the criteria chosen by Schminke (2010) for separating the above-mentioned two subfamilies requires further scrutiny (see below).

#### Phylogenetic Discussion

Figures 9 and 10 show the phylogenetic position of *Himalacaris* within Parastenocarididae. The phylogenetic treatment done here has given rise to two equally parsimonious trees, each with a length of 51 steps,  $C_i = 85$  and  $R_i = 80$ . In both phylogenetic hypotheses, we see the *P. tirupatiensis*-group, *Himalacaris* n. g. and *Remaneicaris* Jakobi, 1972 constituting a monophyletic unity supported by the characters 27-30. However, the striking difference between them concerns the monophyletic condition of the subfamily Parastenocaridinae as proposed by Schminke (2010), who included in it *Remaneicaris* and all the species with modified penultimate segment of the male antennule, broader-than-long female genital field, among other characters. In the first cladogram (Fig. 9), the subfamily Parastenocaridinae is supported by characters 23-26 and includes the *P. tirupatiensis*-group, *Himalacaris* n. g. n. g., and *Remaneicaris*. The second cladogram (Fig. 10) supports a clade formed by the subfamilies Parastenocaridinae and Fontinalicaridinae, whereas the *P. tirupatiensis*-group, *Himalacaris* n. g. and *Remaneicaris* form a distinct monophyletic unit. The bootstrap analysis revealed better values supporting each of the monophyletic units of the cladogram 1 (Fig. 9).

List of Characters.—The characters are listed below and their polarity is given in parentheses. When we mention Parastenocaridinae, we are not using it sensu Schminke (2010). Instead, we consider Parastenocaridinae and all the species included in it by Schminke (2010), except those of *Remaneicaris*. We, therefore, allow the analysis to indicate the phylogenetic position of *Remaneicaris*, *Himalayacaris* and the new species-group, now named *tirupatiensis*-group consisting of *Parastenocaris tirupatiensis* Ranga Reddy, 2011 (cf., Ranga Reddy, 2011b) and two new species (Ranga Reddy and Totakura, in prep.), all these three species from India fall within Parastenocarididae.

1. No. of armature elements on praecoxal arthrite of maxillule: >5 (0); 5 (1);
2. Inner spine on the basis of leg 1: sexually monomorphic (0); sexually dimorphic (1);
3. Leg 5 exopod and baseoendopod: separate (0); fused (1);
4. No. of segments of male antennule: 10 (0); 9 (1); 8 (2);
5. No. of armature elements on triangular antennary exopod: 3 spines/setae, at least 1 modified (0); 1 seta (1);
6. No. of segments on mandibular palp: 2 (0); 1 (1);
7. No. of setae on first endite of maxilla: 2 (0); 1 (1); 0 (2);
8. Accessory setae on the first endopod/claw of maxilla: present (0); absent (1);
9. Syncoxal seta of maxilliped: present (0); absent (1);
10. No. endopodal segments of leg 1: 3 (0); 2 (1);
11. Inner seta on first endopodal segment of leg 1: present (0); absent (1);
12. No. of endopodal segments of leg 2: 2 (0); 1 (0);
13. No. of endopodal segments of leg 3: 2 (0); 1 (1);
14. No. of endopodal segments of leg 4: 2 (0); 1 (1);
15. Endopod of male leg 3: present (0); absent or reduced to a seta (1);
16. Leg 3 exopod of male: not prehensile (0); prehensile (1);
17. Leg 4 endopod: sexually monomorphic (0); sexually dimorphic (1);
18. Integumental windows on all urosomites: present (0); absent (1);
19. No. of segments of female antennule: 8 (0); 7 (1);
20. Female leg 3 endopod: long, with fused distal spiniform structure/seta (0); short, with rounded and unarmed tip (1);
21. Length of leg 5: short (0); long (1);
22. Female genital field: as broad as high (0); broader than high (1);
23. Penultimate segment of male antennule: unmodified (0); modified (1);
24. Position of lateral setae vs. dorsal seta on caudal ramus: not at the same level (0); at the same level (1);
25. Apophysis of male leg 3: with 1 distal spine (0); spine lost or reduced to a hyaline structure (1);
26. Long spinules near insertion of endopod of male leg 4: absent (0); present (1);
27. No. of armature elements on second endite of maxilla: 2 setae and 1 spine (0); 3 setae (1); 2 setae (2);
28. Ornamentation at midlength of inner margin of third exopodal segment of leg 2: absent (0); present (1);
29. Ornamentation at midlength of inner margin of third exopodal segment of leg 4: absent (0); present (1);
30. Leg 5 intercoxal sclerite: present (0); absent (1);
31. Ornamentation at midlength of inner margin of second exopodal segment of leg 2: absent (0); present (1);
32. Ornamentation at midlength of inner margin of second exopodal segment of leg 4: absent (0); present (1);
33. Ornamentation at base of endopod of male leg 4: absent (0); present (1);
34. Position of outer setae on third exopodal segment of leg 4: distal (0); subdistal (1);
35. Spinules near the insertion of the endopod of male leg 4: slender (0); stout (1);
36. Shape and build of basis of leg 3: quadrangular and, if rectangular, sturdy (0); rectangular, slender (1);
37. Strong spinules at anterior margin of coxa of male leg 4: none (0); at least 1 (1);
38. No. of setae on leg 5: >2 (0); 2 (1);

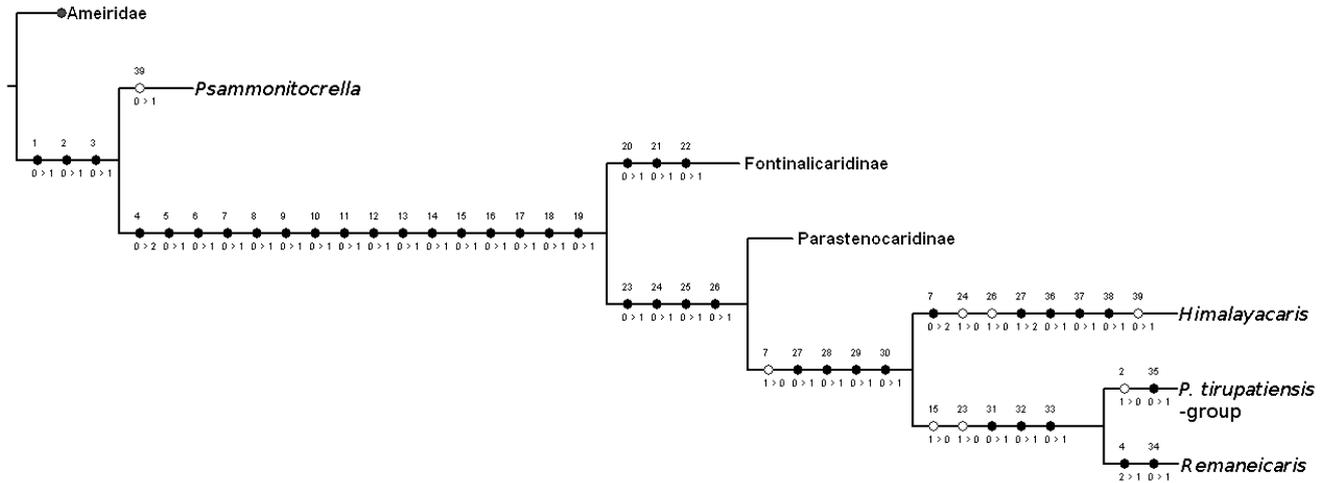


Fig. 9. Phylogenetic hypothesis I for the position of *Himalayacaris* within Parastenocarididae. Closed circles represent autapomorphies, open circles represent autapomorphies by reversion of character state.

39. Development of endopod of male leg 4: normal (0); reduced to small bud or lost, fused to the basis and appearing as a small papilla (1).

**Character Discussion.**—Much has been said about the monophyletic condition of the family Parastenocarididae (Martínez Arbizu and Moura, 1994; Corgosinho and Martínez Arbizu, 2005; Corgosinho et al., 2007). Hence, with exception of Characters 4, 7 and 15, we do not feel the need to discuss most other characters supporting the monophyly of the family (Characters 4-19), which are only some of the many characters used to define the family (see Martínez Arbizu and Moura, 1994). Similarly, we will not discuss also the Characters 1-3 and 39, some of which have already been discussed by Martínez Arbizu and Moura (1994); they are used here only to polarize and root the cladogram.

A critical study of the overall morphology of *Himalayacaris alaknanda* suggests that it is a Parastenocaridinae as borne out by the following four characters: 1) the male antennule is of the ‘pocket-knife type’; 2) the female genital field is ‘rectangular and much broader than high’; 3) the endopod of the female leg 3 is long and spiniform; 4) the coxa of male leg 4 lacks an inner row of spinules, but has only a single enormous, conical, plate-like, modified, anteriorly inserted spiniform structure, as already described; 5) the basis of male leg 4 has no hyaline spinule between the exopod and endopod; and 6) the leg 5 is reduced in size in both sexes, not extending beyond the posterior border of its own somite and without intercoxal sclerite. Two similarities with Fontinalicaridinae, which we consider the result of convergent evolution, are: 1) the gap that distinctly separates the lateral group of setae (I-III) and the dorsal seta (VII) on the

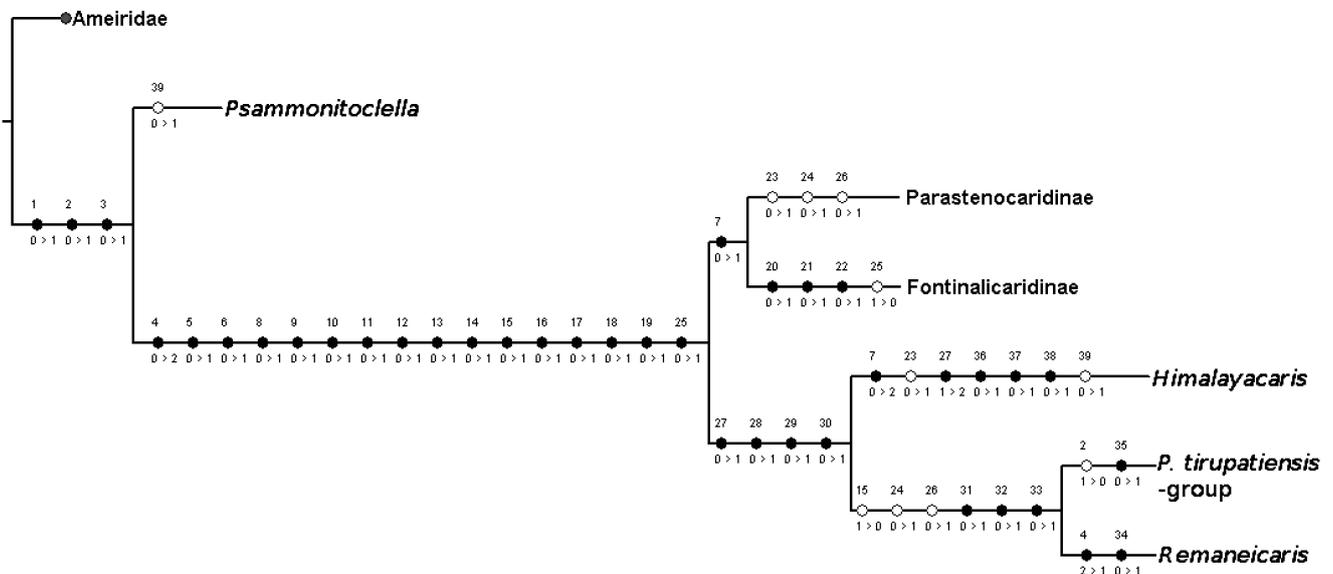


Fig. 10. Phylogenetic hypothesis II for the position of *Himalayacaris* within Parastenocarididae. Closed represent autapomorphies, open circles represent autapomorphies by reversion of character state.

caudal rami; and 2) the separate terminal seta, albeit modified, on the apophysis of male leg 3.

The putative synapomorphies that the new species shares with *Remaneicaris* and the *P. tirupatiensis*-group (Ranga Reddy and Totakura, in prep.) are: Characters 7 (1 → 0) and 27-30 (0 → 1), and some superficial similarities with *Brasilibathynellocaris* Jakobi, 1972 of Fontinalicaridinae (see below).

While recently revising *Brasilibathynellocaris*, Corgosinho et al. (2010) recognised that two of its main synapomorphic features are associated with the all-important male leg 4, viz. the presence of two strong, blunt spinules on the anterior margin of coxa, with a hyaline region around them, and the short and transformed first exopodal segment having proximal invagination on the inner corner. The third synapomorphy concerns the male leg 3 in which the exopod is curved inwardly, ending in a long forceps formed by apophysis and thumb.

On the other hand, in *Himalayacaris*, the coxa of the male leg 4 has but a single huge plate-like structure instead of two strong, blunt spinules, and the first exopodal segment of the same leg is short but has no invagination, and the apophysis and thumb of the exopod of the male leg 3 are short instead being distinctly long. The affinities between the two genera include: the arrangement of lateral and dorsal caudal setae; the relatively long and sturdy male leg 3 basis, with blunt chitinous structure on distal border at least as in *Brasilibathynellocaris brasilibathynellae* (Jakobi and Loyola e Silva, 1962); and the presence of spinules on outer margin of male leg 4 basis between outer seta and first exopodal segment. Outside these two genera, the first exopodal segment of the male leg 4 is short only in *Horstkurtae delamarei* (Chappuis, 1958; in Chappuis and Delamare Deboutteville, 1958), which is obviously a case of convergence (Corgosinho et al., 2010).

Interestingly, the essential morphology of *Himalayacaris* corresponds but superficially with all the basic synapomorphic characters of *Brasilibathynellocaris*, but the degree as well as the orientation of their morphologic differentiation, which fits well two distinct monophyletic subfamilies within the Parastenocarididae, leaves no doubt that the above-mentioned similarities between them are only the result of evolutionary convergence.

In accordance with Schminke (2010), Parastenocaridinae and Fontinalicaridinae can be generally characterized by the following features:

1. Male antennule (Characters 4 and 23): in Parastenocaridinae, the segments 5 and 7 form a functional unit for clasping the female (Character 23; 0 → 1). The segment 7 is sickle-shaped, with an apophysis developed at the distal inner corner, and can fold back onto the fifth segment during copula whereas the segment 8 points medially. It is noteworthy that the genus *Remaneicaris*, which Schminke (2010) includes within the Parastenocaridinae, despite the fact that it has the coiled type of antennule, a character typical of Fontinalicaridinae. This latter condition must be considered plesiomorphic because it also appears in the out-group Ameiridae. Schminke (2010), however, concludes that the sickle-shaped male antennule is an autapomorphy of Parastenocaridinae. In clado-

gram 1 (Fig. 9), we see this character supporting a monophyletic group comprising all the members of Parastenocarididae barring those of Fontinalicaridinae. This no doubt endorses Schminke's (2010) criterion, but calls into question the unpublished data of Corgosinho (2007), who supported a basal position of *Remaneicaris* within the family in view of the presence of some putative plesiomorphic characters shared by this genus. For example, the male antennule of *Remaneicaris* is 9-segmented (Character 4). Corgosinho et al. (2007) mention that the same number of segments occurs also in other parastenocaridid genera such as *Potamocaris* and *Forficatocaris*. Now it is clear that the 8-segmented condition should be interpreted as a derived condition, being the result of the non-formation of segment 6. The 10-segmented condition described for the male of *Potamocaris estevesi* Reid, 1991 (see Rocha et al., 1998) is probably wrong or the result of the *de novo* expression of a plesiomorphic condition, which is found only in the outgroup of the family Parastenocarididae. Thus, this condition would be autapomorphic for *P. estevesi*. Both phylogenetic hypotheses proposed here leave no scope for a 9-segmented male antennule being in the ground pattern of Parastenocarididae. Therefore, this character must be seen as derived, appearing independently in a subgroup of the South American fontinalicaridids and the genus *Remaneicaris*.

Character 23 shows a different optimization in Hypothesis 2 (Fig. 10), appearing there as convergent between the Parastenocaridinae and the genus *Himalayacaris*. We consider this a complex character, an 8-segmented male antennule with the penultimate segment modified, thus providing a unique mode of clasping. And we do not believe that this character appeared independently. Rather, although Hypothesis 1 is less parsimonious than Hypothesis 2, we prefer to consider this kind of male antennule at the base of the cladogram, which would imply the independent loss of this condition in the Fontinalicaridinae, *Remaneicaris* and the *P. tirupatiensis*-group. In fact, in Hypothesis 1 the reversion of the character 23 from 1 to 0, from a Parastenocaridinae to a Fontinalicaridinae condition, is considered a synapomorphy for *Remaneicaris* and the *P. tirupatiensis*-group.

2. Shape of the endopod of female leg 3 (Character 20): this ramus is long and spiniform in Parastenocaridinae, representing a plesiomorphic condition where a terminal seta is fused to it. Thus, it attains a relatively long size in relation to the first segment of the corresponding exopod (almost as long as or longer than the first exopodal segment). The apomorphic condition appears only in the Fontinalicaridinae. In this group, the said ramus is a relatively short, with a rounded apex, carrying spinules terminally and subterminally but no seta.
3. Armature of the apophysis of male leg 3 (character 25): the apomorphic condition appears in Parastenocaridinae in which the apophysis and its terminal seta are fused together in most species, whereas the terminal seta is separate from the apophysis in the Fontinalicaridinae. Exceptions to this rule have been reported in the literature. According to Schminke (2010), "as in *Parastenocaris brevipes*, the terminal seta and the apophysis of the exopod

of male leg 3 are fused in 144 species. They are separate in 11 species, 8 of which belong to the *Parastenocaris*-group as defined by Reid (1995). Among these there are 5 species from Sri Lanka where there appears to be a tiny separate seta accompanied by an inner membrane. The remaining species with a separate seta are *Parastenocaris crenobia* Galassi, 1997, *Parastenocaris grassei* Soyer, 1965, and *Parastenocaris pauliani* Chappuis, 1952. Nothing can be said about 15 species either for lack of known males (12 species), or for insufficient information (3 species).” In *Himalayacaris* n. g. the spine is a modified hyaline structure, similar to what appears in the genus *Parastenocaris* s. str.

In Fig. 9, this character supports the monophyletic condition of the Parastenocaridinae as composed of all the known Parastenocarididae but the Fontinalicaridinae. On the other hand, in Fig. 10, this character supports the monophyletic condition of the Parastenocarididae or, in alternative optimization, can be seen as appearing independently in the Parastenocaridinae and in the monophyletic group including *Remaneicaris*, *Himalayacaris* and the *P. tirupatiensis*-group. However, we have strong orthogenetic evidence supporting the presence of a distal spine on the apophysis of male leg 3, instead of a hyaline tip or its loss as the plesiomorphic condition for Parastenocarididae (Glatzel, 1991; Corgosinho et al., 2010). In our view, this is another character which lends even greater support to the first hypothesis over the second one.

4. Coxa and basis ornamentation (Characters 33, 35 and 37): most Parastenocaridinae lack inner row of spinules on the coxa of male leg 4, but a row of spinules may be present near the insertion of endopod or medially of the basis. In Fontinalicaridinae, we may find an inner row of spinules on the coxa of male leg 4 and a hyaline spinule on the basis between exopod and endopod.

Two strong spinules occur on the anterior margin of the coxa of the male leg 4 in the species of *Brasilibathynellocaris*, *Siolicaris jakobi* (Noodt, 1963), *Siolicaris sioli* (Noodt, 1963), *Murunducaris dactyloides* (Kiefer, 1967), and perhaps also in *Parastenocaris psammica* Songeur, 1961 (Corgosinho et al., 2010). All these species and genera are Fontinalicaridinae. The only known species of Parastenocaridinae with such character is the new species described herein. We cannot ascertain whether the presence of long spinules on the anterior margin of the coxa of male leg 4 is an autapomorphy for a larger group within Fontinalicaridinae or if it appears as a homoplasy within different evolutionary lineages more related to the *Parastenocaris fontinalis*-group. Nevertheless, we can confirm that this character cannot be used to include *Himalayacaris* within Fontinalicaridinae and, therefore, is considered homoplastic.

Many *Remaneicaris* have a row of spinules at or near the insertion of endopod (Characters 33 and 35). A strong ornamentation is also observed at the same region in the *P. tirupatiensis*-group of species. We consider the presence of such ornamentation as synapomorphic for *Remaneicaris* and the *P. tirupatiensis*-group. No such spinular row can be seen in *Parastenocaris brevipes*. A character-

istic feature of the *P. brevipes*-group, however, is the presence of three claws medially of the endopod (Schminke, 2010). The same character appears also in *Cottarelllicaris* Schminke, 2013, and *Stammericaris* Jakobi, 1972. According to Schminke (2010), in the Parastenocaridinae “the spinules are either located medially of the endopod (81 species) or at its base (25 species). In some cases it certainly is a matter of perspective that spinules appear to be at the base rather than medially of the endopod. Nothing can be said about 63 species for lack of known males (12 species), for lack of sufficient information (2 species), for lack of endopod and spinules (9 species), for lack of spinules, not of the endopod (33 species), and for lack of the endopod, not of spinules (7 species).” The synapomorphic condition of this character for Parastenocaridinae cannot be accessed accordingly, but there is no convincing evidence to support any closer relationship of *Remaneicaris* and the *P. tirupatiensis*-group with the above mentioned genera. In *Himalayacaris*, this character is not present, possibly because of the extreme reduction and fusion of the endopod to the basis. The enlarged and flattened spinules of the *P. tirupatiensis*-group (Character 26) is considered autapomorphic and homoplastic with the *Parastenocaris brevipes*-group.

5. Size of leg 5 (Character 21): Parastenocaridinae, *Remaneicaris*, *Himalayacaris* and the *P. tirupatiensis*-group all share a small leg 5 in both sexes, not reaching far beyond its own somite. In the Fontinalicaridinae the same appendage is much larger and triangular in both sexes, extending back well beyond its own somite. It is to be noted that leg 5 is also small in most groundwater Ameiridae, which are a reasonable sister-group of Parastenocarididae. Therefore, here we consider the short leg 5 as plesiomorphic for Parastenocarididae.

According to Schminke (2010), the vast majority (131) of the 158 species of Parastenocaridinae known till then have small fifth legs. Schminke (2008, 2009) underscores large fifth legs for all the known species of *Kinnecaris* Jakobi, 1972 (18 species) and *Monodicaris* Schminke, 2009 (4 species). Here, we consider this character homoplastic, appearing independently in Fontinalicaridinae and defining this subfamily as a synapomorphy, but it is clearly autapomorphic for a few genera and species of Parastenocaridinae.

In addition to its small size, the leg 5 has certain other phylogenetically informative characters such as the presence/absence of the intercoxal sclerite and the total number of setae borne by it (Characters 30 and 38). Character 30 supports the monophyletic condition of the clade formed by *Remaneicaris*, *Himalayacaris* n. g. and the *P. tirupatiensis*-group in both the hypotheses proposed here. According to Corgosinho et al. (2007a, b): “The absence of the intercoxal sclerite on leg 5 is a character present in the ground pattern of *Remaneicaris*. Associated with the lack of the inter-coxal sclerite, there normally occurs a migration of both appendices to a ventro-lateral position. In *R. ignotus* both legs 5 are located more ventrally, a character that we consider plesiomorphic within the genus. No sexual dimorphism should be expected in the ground pattern of *Remaneicaris*”. This assertion seems

to be true since no dimorphism occurs in *Himalayacaris* and the *P. tirupatiensis*-group, and with the fifth legs occurring ventrally, a plesiomorphic condition as described for *P. ignotus*.

6. Shape of the female genital field (Character 22): Parastenocaridinae, *Remaneicaris*, *Himalayacaris*, and the *P. tirupatiensis*-group share the same morphology of the female genital field, which is rectangular and much broader than high. In Fontinalicaridinae, it is roundish and as broad as high. Parastenocaridinae-like genital field also appears in Ameiridae. Therefore, we consider this character plesiomorphic and the condition in Fontinalicaridinae the apomorphic one.
7. Position of the setae on the caudal ramus (Character 24): in most of Parastenocaridinae, *Remaneicaris*, and the *P. tirupatiensis*-group, the lateral group of three setae (I-III) occurs at the same level as, and almost opposite to, the dorsal seta (VII). On the other hand in the fontinalicaridines and *Himalayacaris*, the lateral group of three setae and the dorsal seta are inserted at a distance from each other, the dorsal seta being located distally and the lateral group of setae proximally.

We consider the presence of the dorsal seta and the lateral group of caudal rami setae at the same level, and not away from each other as an apomorphic condition within Parastenocarididae. This character supports Parastenocaridinae comprising all the species proposed by Schminke (2010) plus *Himalayacaris* and the *P. tirupatiensis*-group, as in the first cladogram (Fig. 9), but it is considered homoplastic in the second cladogram (Fig. 10). In fact, this is a weak character and even in the first phylogeny, and the condition displayed by *Himalayacaris* is considered a reversion to what was observed in the ground pattern of the family, and also shared by the fontinalicaridines. Our conclusion is endorsed by what is observed in the outgroup. In most Ameiridae the lateral setae are distally inserted, more or less at the same level of the dorsal seta (probably due to the quadractic or shorter condition of the caudal ramus). In *Psammonitocrella* and other ground-water Ameiridae, one of the lateral setae is distal whereas the other two are displaced proximally. In *Stenocopia* Sars, 1907, Fontinalicaridinae and *Himalayacaris*, the lateral setae are proximal, but the dorsal seta is distal. We are of the opinion that these transitions from the general Ameiridae pattern to Fontinalicaridinae-kind are a feasible series of transformation.

#### Other Phylogenetically Important Characters

Corgosinho and Martínez Arbizu (2005) mention the presence of Characters 28, 29, 31 and 32 as autapomorphic for *Remaneicaris*. In this work, Characters 28 and 29 support the monophyletic condition of the clade formed by *Himalayacaris*, *Remaneicaris*, and the *P. tirupatiensis*-group, whereas Characters 31 and 32 support *Remaneicaris* and the *P. tirupatiensis*-group. Hence we now hypothesize that these characters are not only exclusive to *Remaneicaris*, but synapomorphic at a different level of taxonomic inclusiveness.

Two characters are extremely important in the present context. Characters 7 and 27 for the maxilla and Character 15 for the male leg 3 have their polarity radically changed

from what was reported in the previous contributions to the present one. In the previous works, Corgosinho et al. (2007a, b) regarded the presence of a distinct endopod in the male leg 3 and also the presence of two setae on the first endite of the maxilla as constituting plesiomorphies within the family, thereby supporting the basal placement of *Remaneicaris* in the family. However, in view of the present data, the apomorphic condition of these characters is supported, although they are apparently the *de novo* expression of the plesiomorphic conditions which can be acquired during the evolution by the suppression of a homeobox gene, which is the regulator of the expression/suppression of these characters. The presence of three setae on the second endite of the maxilla, instead of two setae and a spine as in other many Parastenocaridinae, Fontinalicaridinae and Ameiridae, is considered a synapomorphy for *Remaneicaris* and the *P. tirupatiensis*-group.

#### Phylogenetic Implications of the Contrasting Hypotheses

*Himalayacaris* shares with the parastenocaridines most of the characters proposed by Schminke (2010), and there is no doubt that this species belongs in that subfamily. This view is also supported by the phylogenetic Hypothesis 1 (Fig. 9) which, although equally parsimonious as the second one, has better bootstrap values and sound supporting characters. And yet, it is intriguing because of the reversion of characters towards their plesiomorphic condition within Parastenocaridinae.

The discovery of the genus *Himalayacaris* and of the *P. tirupatiensis*-group (Ranga Reddy and Totakura, in prep.), which share many characters in common with *Remaneicaris* and the Parastenocaridinae, raises some reasonable questions:

1. How really close to *Remaneicaris* is *Himalayacaris*?
2. Do *Himalayacaris*, *P. tirupatiensis*-group, and *Remaneicaris* really constitute a monophyletic unit? Are they Parastenocaridinae?
3. Is the subfamily Parastenocaridinae monophyletic after the relocation of *Remaneicaris* and at least the *P. tirupatiensis*-group to the base of the phylogeny of the Parastenocarididae?

The above questions cannot be answered satisfactorily at this juncture without proper phylogenetic analysis of Parastenocaridinae based on additional morphological data on the adults and the postembryonic naupliar and copepodid instars, and, even more important, the molecular data at multi-gene levels.

#### Ecology

*Himalayacaris alaknanda* was found in coarse sand and pebbles beneath boulders, co-occurring with an unidentified non-parastenocaridid copepod species, a few oligochaetes, and insect larvae. It is the second hyporheic species of Parastenocarididae from the Himalayan region, but at a relatively high altitude of 1451 m; the first one, *Parastenocaris sutlej* Ranga Reddy, 2011 (cf., Ranga Reddy, 2011a), was from the Western Himalaya at an altitude of 656 m. The new species was found in just one out of 40 interstitial samples collected in various headstreams of the Ganges River system from Badarinath to Haridwar. On the whole, the samples showed

either an exceptional poverty or a complete absence of interstitial fauna. Perhaps this is attributable to the nature of the alluvial deposits, which were dominated by very fine sand (grain size not determined), thus offering no suitable interstitial niches for the existence of meiofauna.

Another noteworthy feature of the new species is its highly skewed sex ratio – three males vs. ca. 180 females in the sampled population. Although this one-time observation of spanandry of the new species cannot be assumed to imply a parthenogenetic mode of reproduction, parthenogenesis has already been established in certain canthocamptid harpacticoids (Sarvala, 1979). As for the parastenocaridids, Enckell (1969) reported on a remarkable case of spanandry in *Parastenocaris glacilis* Noodt, 1954, in which no males were found in as many as 190 samples even when the total number of specimens had surpassed 1000; he suggested that this species is ‘at least temporarily parthenogenetic.’ According to T. Karanovic (personal communication), the observed spanandry in *H. alaknanda* could be a case of sexual habitat partitioning, whereby the two sexes exploit different parts of the habitat, thus lowering competition and maximizing survival potential.

#### Biogeography

The peninsular part of India is actually ‘the primary and principal biogeographical region’ whereas the Himalaya and other extra-peninsular parts constitute merely ‘biogeographical appendages of secondary importance’ (Mani, 1974c: 700); compared to the peninsular part, ‘the Himalaya is extremely rich in relatively very young and phylogenetically highly plastic forms of more recent and more highly evolved Asiatic groups, with a corresponding poverty of the ancient Gondwana elements’ (Mani, 1974b: 666). Of the 16 parastenocaridid species hitherto known from India and Sri Lanka, ‘a detached portion of the Peninsula’ (Mani, 1974a: 21), the Himalayan *P. sutlej* Ranga Reddy, 2011, belongs to the *brevipes*-group as do several of its Indian and Sri Lankan congeners. According to Reid (1995), the possible origin of this group of species is in ‘tropical Asia.’ So, *P. sutlej*, though occurring in a somewhat subtropical belt, could possibly be an Asiatic derivate of the Himalayan fauna. On the other hand, *Himalayacaris alaknanda* displaying a somewhat close relationship with the Neotropical *Remaneicaris* Jakobi, 1972, is consistent with the already known Gondwanan heritage of the groundwater micro-crustaceans of peninsular India (Ranga Reddy, 2011c). As for the parastenocaridids, one species each of the Gondwanan *Kinnecaris* Jakobi, 1972 and *Siolicaris* Jakobi, 1972 (Ranga Reddy and Schminke, 2009; Corgosinho et al., 2012) has already been reported from peninsular India. Yet another Indian species, *Parastenocaris tirupatiensis* Ranga Reddy, 2011 (cf., Ranga Reddy, 2011b), also has certain interesting morphological affinities with the neotropical *Remaneicaris*, although these affinities are yet to be investigated in detail (Corgosinho et al., 2012). On the whole, the phylogenetic and biogeographic relationships within Parastenocarididae as a whole needs critical analysis.

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