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**Article** *in* Journal of Natural History · June 2016

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**To cite this article:** Yenumula Ranga Reddy, Venkateswara Rao Totakura & Shabuddin Shaik (2016): A new genus and two new species of Parastenocarididae (Copepoda: Harpacticoida) from southeastern India, Journal of Natural History

**To link to this article:** http://dx.doi.org/10.1080/00222933.2015.1130870

Published online: 01 Feb 2016.

JOURNAL OF NATURAL HISTORY, 2016
http://dx.doi.org/10.1080/00222933.2015.1130870

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# A new genus and two new species of Parastenocarididae (Copepoda: Harpacticoida) from southeastern India

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**ABSTRACT**

*Indocaris* gen. nov. with two new species, *Indocaris imbricata* sp. nov. and *Indocaris inopinata* sp. nov., and also for the already known *Indocaris tirupatiensis* (Ranga Reddy 2011a) comb. nov. – all from the groundwaters in peninsular India. The highly diagnostic synapomorphy of the new genus is a composite character associated with the male leg 4 basis: five or six prominent, imbricate, enlarged, petal-like spinules, arranged as a semi-whorl at the insertion of the endopod and increasing in size from internal to external. Another distinctive feature of the same appendage is that its one-segmented endopod is dilated or bulbous in the proximal half, produced distally into an incurved spiniform or horn-like structure about as long as the corresponding first exopodal segment, and ornamented with three or four fine spinules on the subproximal outer margin. The three species also share a unique constellation of other salient morphologic features, which along with the phylogenetic position of *Indocaris* gen. nov. within the family Parastenocarididae are discussed. *Indocaris* gen. nov. has closest phylogenetic affinity with the Neotropical *Remaneicari* Jakobi, 1972. A short note on the ecology and biogeography of the parastenocaridid species of the Indian subcontinent is provided besides a key for their identification.

**ARTICLE HISTORY**
Received 7 June 2014
Accepted 6 November 2015

**KEYWORDS**
Crustacea; *Indocaris* gen. nov.; stygofauna; taxonomy



## Introduction

The harpacticoid family Parastenocarididae Chappuis, 1940, is a highly diversified group of freshwater interstitial microcrustaceans, distributed on all of the continents except Antarctica and New Zealand (Noodt 1968). To date, about 300 nominal species and subspecies in 31 genera are known in the world (Gaviria-Melo and Walter 2015), with nine of Jakobi's (1972) 24 genera yet to be redefined or synonymised (Schminke 2013). It is now well known that generic delineation within this family is 'a real nightmare' because of the conservative nature of a great multitude of its morphological features (Reid 1995; Galassi and De Laurentiis 2004; Karanovic 2005; Schminke 2010). A synoptic view of the recent advancements in the

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systematics of this family by way of the establishment of new genera, revalidation, revision, synonymisation of certain existing genera, etc. can be had from Galassi and De Laurentiis (2004), Corgosinho and Martínez Arbizu (2005), Schminke (2008, 2009, 2010), Corgosinho et al. (2010), Cottarelli et al. (2010), Karanovic and Cooper (2011a, 2011b), Corgosinho, Martínez Arbizu, et al. (2012), Corgosinho, Ranga Reddy, et al. (2012), Karanovic et al. (2012) and others. The Parastenocarididae as a whole is in urgent need of a thorough phylogenetic revision based on additional morphological data and also molecular data at multi-gene levels.

As for the vast tectonic plate of the Indian subcontinent, which includes the whole of India, Bangladesh, Bhutan, Pakistan and Sri Lanka, the parastenocaridid taxonomy started with Enckell (1970) describing six new species under the nominotypical genus *Parastenocaris* Kessler, 1913, from Ceylon (now Sri Lanka): *Parastenocaris irenae* Enckell, 1970, *P. noodti* Enckell, 1970, *P. brincki* Enckell, 1970, *P. singhalensis* Enckell, 1970, *P. lanceolata* Enckell, 1970 and *P. curvispinus* Enckell, 1970. It was only three decades later that the regular taxonomic and stygofaunistic surveys of crustaceans began in India, especially in the coastal deltaic belt of the Rivers Krishna and Godavari in Andhra Pradesh state of the southeastern peninsular zone (see Karanovic and Pesce 2001; Ranga Reddy 2001, 2004a, 2004b, 2014; Totakura and Ranga Reddy 2014, 2015; Totakura et al. 2014; and others). Of about 80 new stygobiotic crustacean species so far collected, 54 species have been described formally (see Ranga Reddy et al. 2015; Totakura and Ranga Reddy 2015). As for the Parastenocarididae, 16 species including the widespread Indo-Sri Lankan *P. curvispinus* are known from India (Totakura and Ranga Reddy 2014). Together with the two new species described herein, the total number of the described species of this group on the Indian subcontinent goes up to 22. Of these, all but *Kinnecaris godavari* Ranga Reddy and Schminke, 2009, *Siolicaris sandhya* (Ranga Reddy 2001), *Proserpinicaris corgosinhoi* Totakura et al., 2014 and *Proserpinicaris karanovici* Totakura et al., 2014, *Himalayacaris alaknanda* Ranga Reddy, Totakura and Corgosinho, 2014 and the three *Indocaris* species remain in the genus *Parastenocaris* Kessler, 1913 – a 'taxonomic repository'. Nevertheless, except for the Indo-Sri Lankan *P. curvispinus* and the Indian *P. mahanadi* Ranga Reddy and Defaye, 2007, which are placed under incertae sedis by Schminke (2010, p. 351), the remaining five Sri Lankan species (see above) and seven Indian species, viz. *Parastenocaris gayatri* Ranga Reddy, 2001, *P. savita* Ranga Reddy, 2001, *P. muvattupuzha* Ranga Reddy and Defaye, 2009, *P. kotumsarensis* Ranga Reddy and Defaye, 2009, *P. sutlej* Ranga Reddy, 2011c, *P. gundlakamma* Ranga Reddy, 2011c and *P. edakkal* Totakura et al., 2014, belong to the *brevipes* group, as revised by Reid (1995) or *Parastenocaris* s. str. of Galassi and De Laurentiis (2004) (see also Karanovic 2005; Ranga Reddy 2011c; Totakura et al. 2014). According to Reid (1995), the *brevipes* group possibly originated 'in tropical Asia', but this hypothesis is at variance with the outcome of the recent cladistic analysis done on this 'highly disjunct' group by Karanovic and Lee (2012) (see Discussion).

In this paper, a new genus, *Indocaris*, is established for two new species, *Indocaris imbricata* sp. nov. and *Indocaris inopinata* sp. nov., and also for the already known *Indocaris tirupatiensis* (Ranga Reddy, 2011a) comb. nov. How *Indocaris* gen. nov. can be justified as a monophyletic entity within the subfamily Parastenocaridinae is explained.

It must also be duly mentioned here that Ranga Reddy et al. (2014), while erecting the genus *Himalayacaris* Ranga Reddy, Totakura and Corgosinho, 2014, from India, carried out a detailed Hennigian phylogenetic analysis of *Himalayacaris* together with *Indocaris* gen. nov. and the Neotropical *Remaneicaris* Jakobi, 1972. However, to be in conformity with the provisions of ICZN (1999), *Indocaris* gen. nov. was then treated as a species group called 'the south Indian *Parastenocaris tirupatiensis*-group consisting of *Indocaris tirupatiensis* Ranga Reddy 2011a and two new species'. In all, 39 characters and their states were considered, with the genus *Psammonitocrella* Rouch, 1992, and other basal genera within the out-group Ameiridae. Hence, we do not repeat the phylogenetic treatment all over again, but limit ourselves to discussing the significant results of the earlier analysis. In addition, a brief note on the ecology and biogeography of the parastenocaridid species of the Indian subcontinent is given together with an updated key for their identification.

## Material and methods

We collected the specimens we studied by filtering of the groundwater when it was pumped out of farm bores (depth c. 10 m). Filtering was done manually by holding a bolting-silk plankton net (mesh size 70 µm) against the water current for 20–30 minutes at each time of sampling (see Totakura and Ranga Reddy 2014, figure 1b). The filtrate was fixed in 5% formaldehyde. Back in the laboratory, 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× . Drawings were made with the aid of a drawing tube mounted on a Leica DM 2500 Trinocular Research Microscope equipped with Universal Condenser for Adaptation, Interference Contrast objective prism and 1–2× magnification changer. Permanent preparations were mounted in glycerol and sealed with wax and Araldite. The type material was deposited in the Muséum national d'Histoire naturelle (MNHN), Paris. The description of both new species is based on the type series.

The phylogenetic conclusions drawn are based on the Hennigian (1966) methods, as already detailed in Ranga Reddy et al. (2014).

## Systematic account

Subphylum **CRUSTACEA** Brünnich, 1772
Class **MAXILLOPODA** Dahl, 1956
Subclass **COPEPODA** H. Milne Edwards, 1840
Order **HARPACTICOIDA** G. O. Sars, 1903
Family **PARASTENOCARIDIDAE** Chappuis, 1940
Subfamily **PARASTENOCARIDINAE** Chappuis, 1940
***Indocaris*** gen. nov.

### *Generic diagnosis*

Small-sized Parastenocaridinae (260–350 µm); body cylindrical habitus, integument weakly sclerotised, somites ornamented with large sensilla; cephalothorax with one

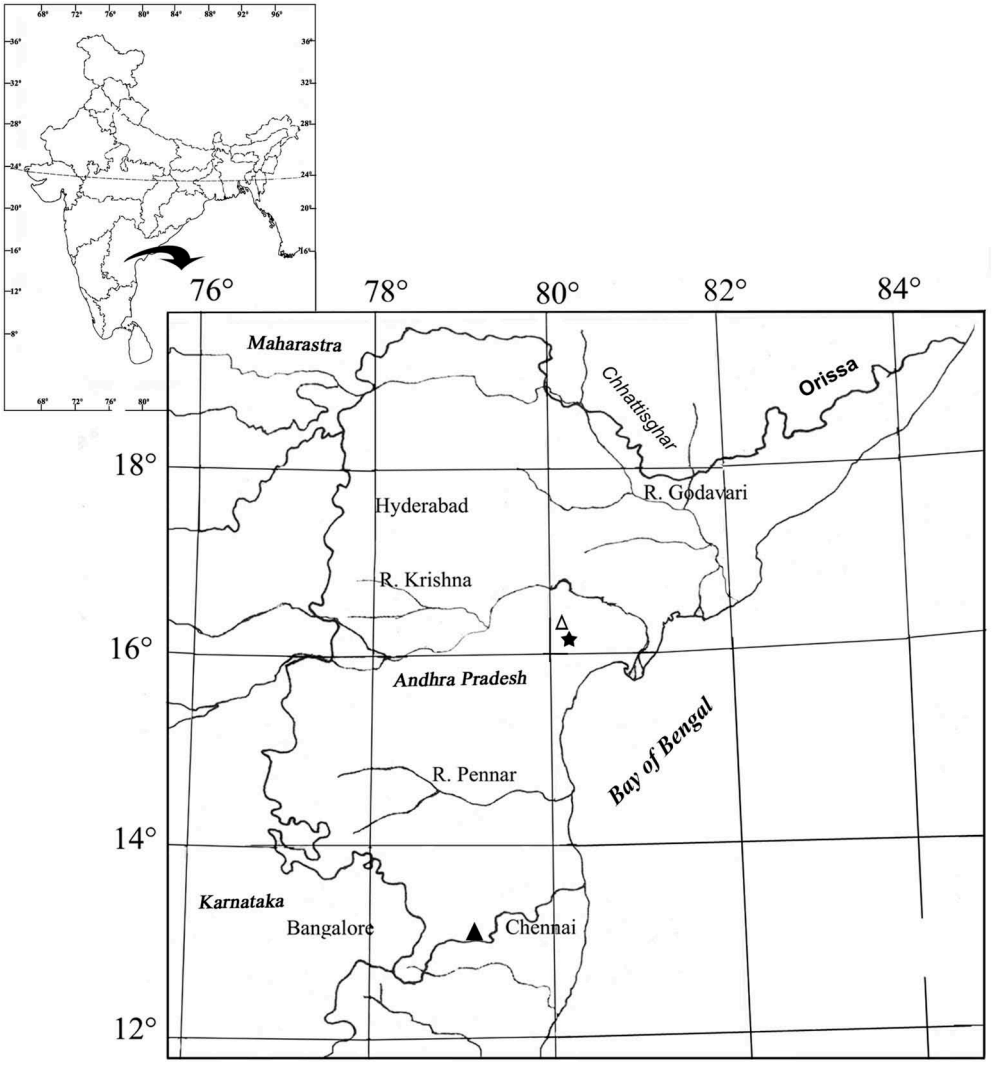


**Figure 1.** Map showing the type localities of *Indocaris imbricata* gen. nov., sp. nov. (★), *I. inopinata* gen. nov., sp. nov. (Δ) and *I. tirupatiensis* comb. nov. (▲).

dorsal integumental window, and urosomites 2 – or 3–5 in males, and 2–4 in females with one dorsal window each. Podoplean boundary between prosome and urosome inconspicuous. Genital complex in female rectangular, occupying anterior ventral half of genital double-somite; single genital aperture and median copulatory pore covered by fused vestigial sixth legs. Caudal rami somewhat cylindrical, armed with seven setae (three lateral, one dorsal, two apical and two subapical), with lateral group of setae and dorsal seta occurring at the same level, all located in distal third of ramus. Male antennule eight-segmented, haplocer and 'coiled type'; distal two segments in line with each other; geniculation between segments 3 and 4, and 6 and 7; segment 5 barely dilated, but with massive aesthetasc overreaching ultimate segment; female antennule seven-segmented. Maxilla with one or two setae on proximal endite. Leg 1

basis with inner armature element in males; exopod shorter than endopod and sharply curved inwards; first endopodal segment with elongate spinules on both margins. Leg 2 in both sexes with one-segmented and short endopod, bearing one apical seta. Female leg 3 endopod of moderate length, or reduced, with or without fused apical seta. Male leg 3 composed of praecoxa, coxa, basis and exopod; intercoxal sclerite moderate in size; both exopodal segments fused to each other almost completely, slender, elongate and bent inwards; ancestral proximal segment ornamented with longitudinal row of spinules along outer distal margin; apophysis short, conical with generally fused apical seta; thumb spiniform, longer than apophysis, and acutely pointed; endopod represented by either slender segment tipped with a small seta or by a simple seta itself. Male leg 4 coxa without spinules on inner margin; basis with five or six prominent, imbricate, enlarged (petaloid) spinules at the insertion of endopod, the spinules increasing in size from internal to external; endopod somewhat dilated or bulbous proximally and drawn out distally into incurved spiniform or horn-like structure, about as long as first exopodal segment, and ornamented with three or four small spinules at subproximal outer margin. Female leg 4 endopod one-segmented, gradually tapering to a point, with serrulate disto-lateral margins. Leg 5 small, trapezoidal, without intercoxal sclerite, armed with three or four setae and only slightly extending beyond its own somite; sexually dimorphic with inner margin being spinulose in male but smooth in female, and the spiniform process at the inner distal corner somewhat shorter in male. Anal somite with or without ventral spinules.

### *Type species*

*Indocaris imbricata* sp. nov.

### *Other species*

*Indocaris inopinata* sp. nov.
*Indocaris tirupatiensis* (Ranga Reddy, 2011a) comb. nov.

### *Etymology*

The prefix of the generic name, 'Indo', alludes to India, where the new genus is found, and the suffix 'karis' is most common in the family Parastenocarididae; gender feminine.

## ***Indocaris imbricata*** gen. nov., sp. nov.
(Figures 1–7)

### *Type locality*

Farm bore (water temperature 26°C, pH 7.0) at Chintalapudi village, ~5 km from Nidubrolu town (16°02′23.8″N, 80°32′35.4″E; elevation 36.5 m) in Guntur District, Andhra Pradesh, southeastern India (Figure 1).

### *Type material examined*

Holotype male (MNHN-IU-2013–11941) and allotype female (MNHN-IU-2013–11942), dissected on four slides each; five paratypes: one male (MNHN-IU-2013–11943) dissected

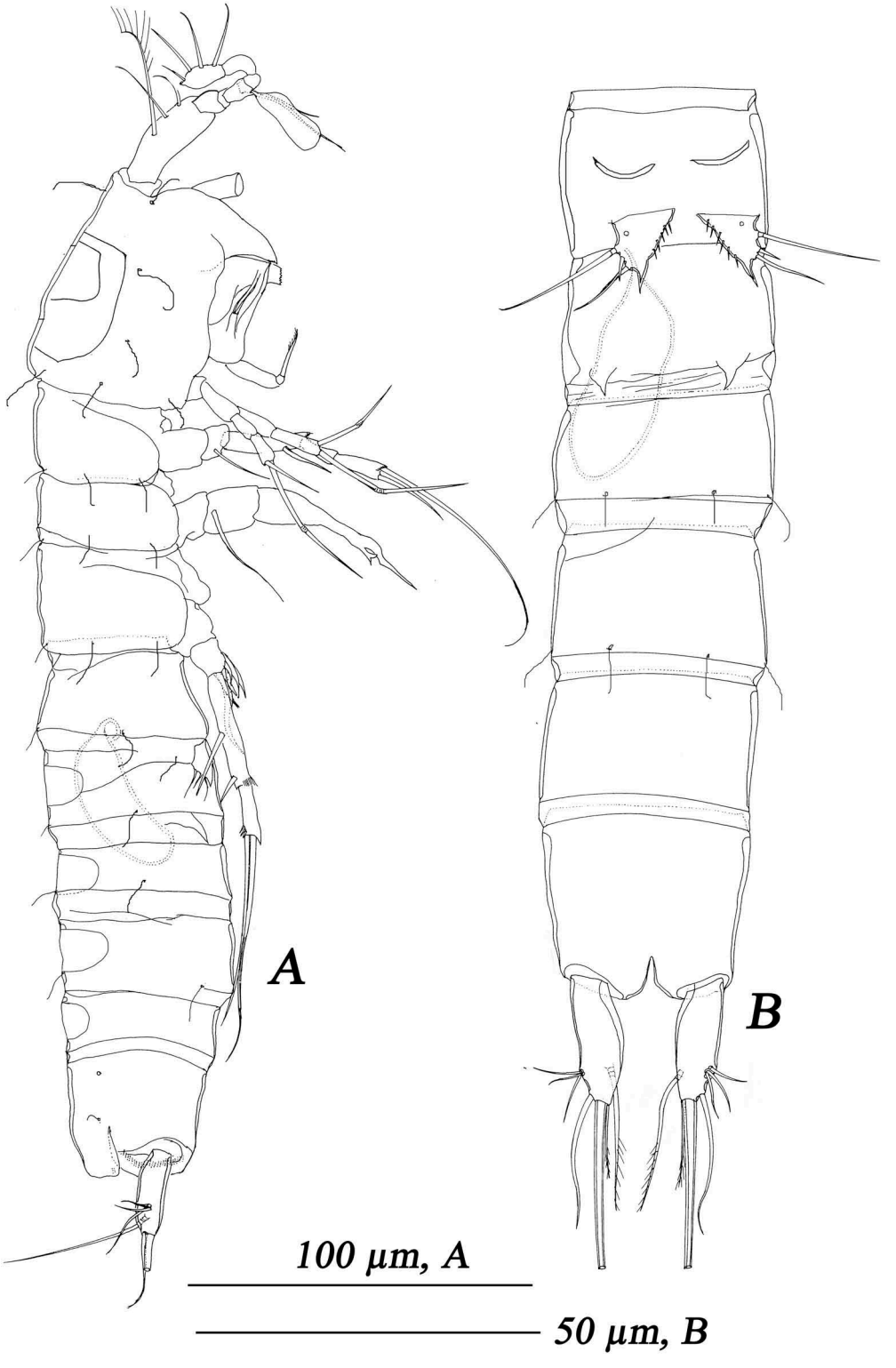


**Figure 2.** *Indocaris imbricata* gen. nov., sp. nov. Male: (A) habitus, lateral view; (B) urosome, ventral view.

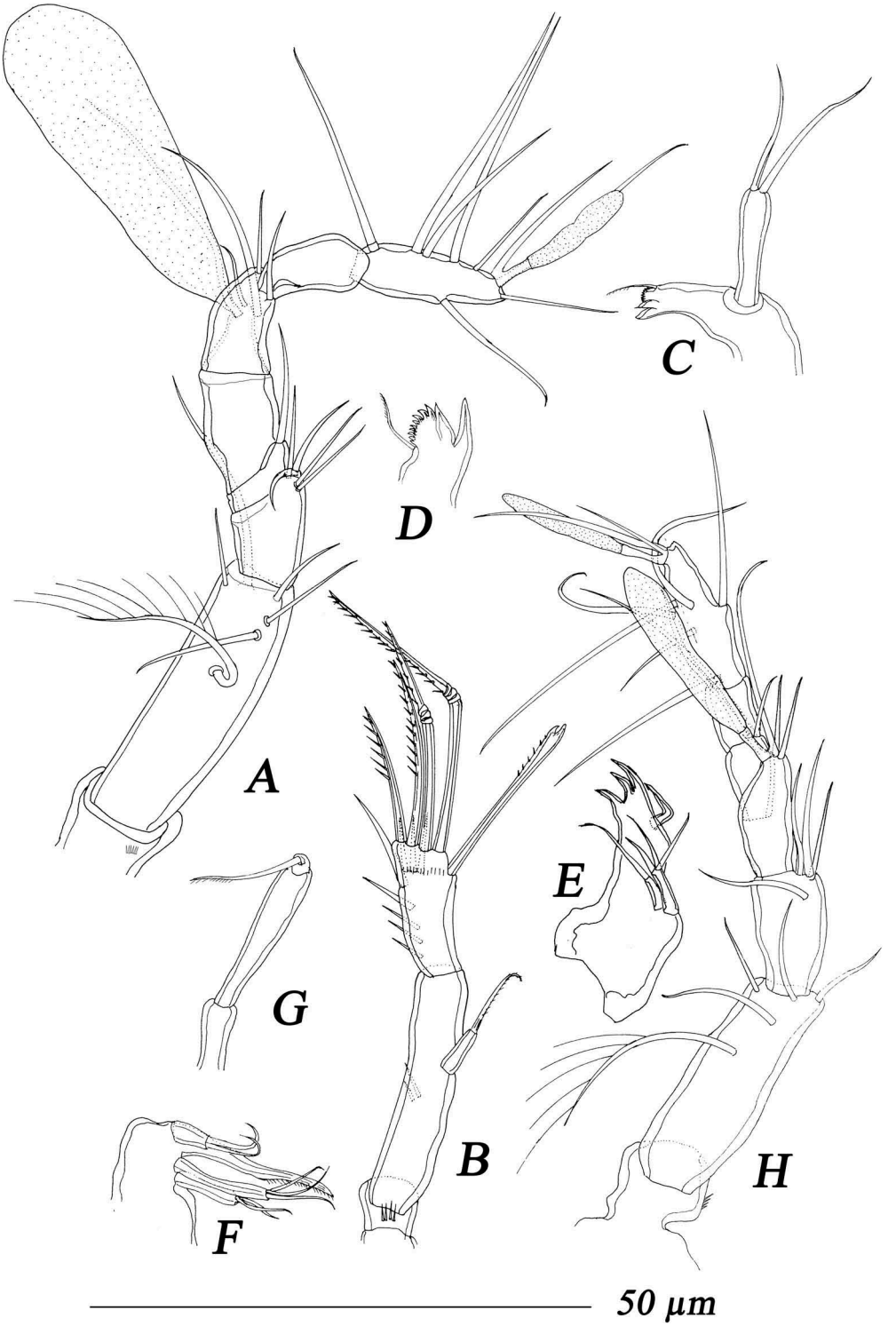


**Figure 3.** *Indocaris imbricata* gen. nov., sp. nov. Male (A–G); female (I): (A) antennule, dorsal view; (B) antenna, antero-lateral view; (C) mandible, ventral view; (D) mandibular gnathobase, posterior view; (E) maxillule, anterior view; (F) maxilla, lateral view; (G) maxilliped, lateral view; (H) antennule, dorsal view.

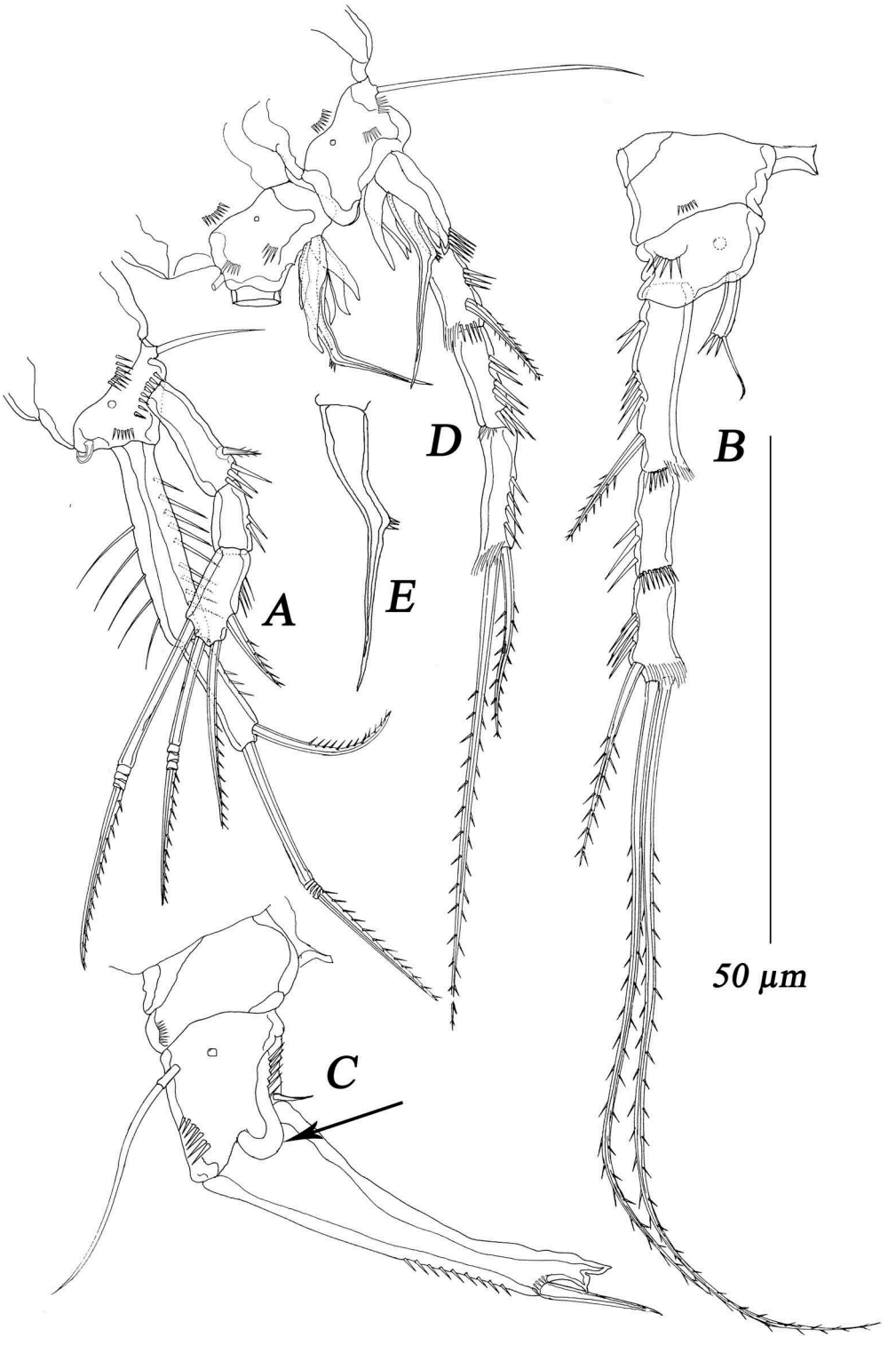


**Figure 4.** *Indocaris imbricata* gen. nov., sp. nov. Male: (A) leg 1, anterior view; (B) leg 2, posterior view; (C) leg 3, anterior view (arrow pointing to knob-like protuberance); (D) leg 4, posterior view; (E) same, endopod, posterior view.

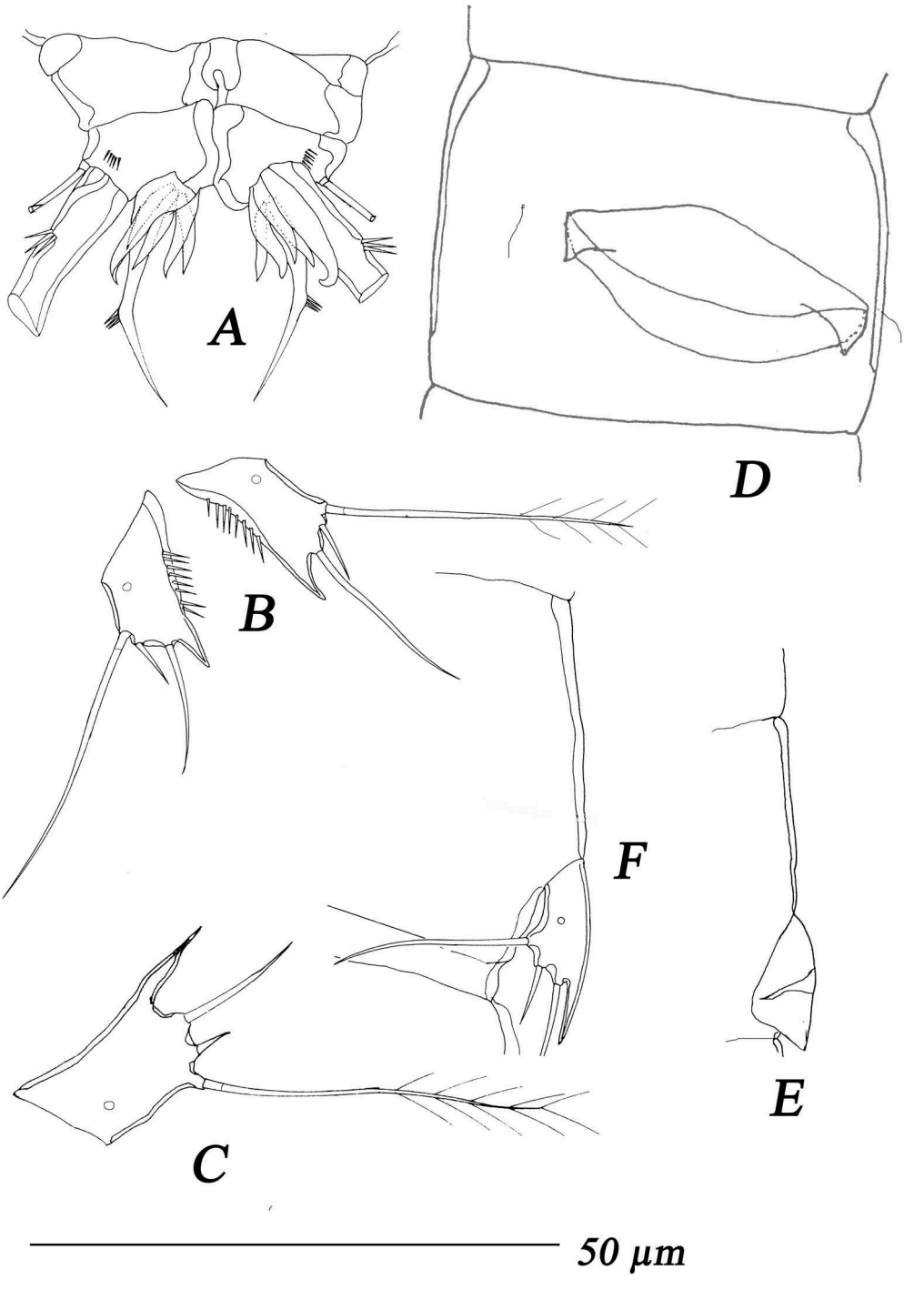


**Figure 5.** *Indocaris imbricata* gen. nov., sp. nov. Male (A, B, D, E); female (C, F): (A) leg 4 (in part), posterior view; (B) leg 5, anterior view; (C) same, anterior view; (D) leg 6, ventral view; (E) same, lateral view; (F) leg 5, lateral view.

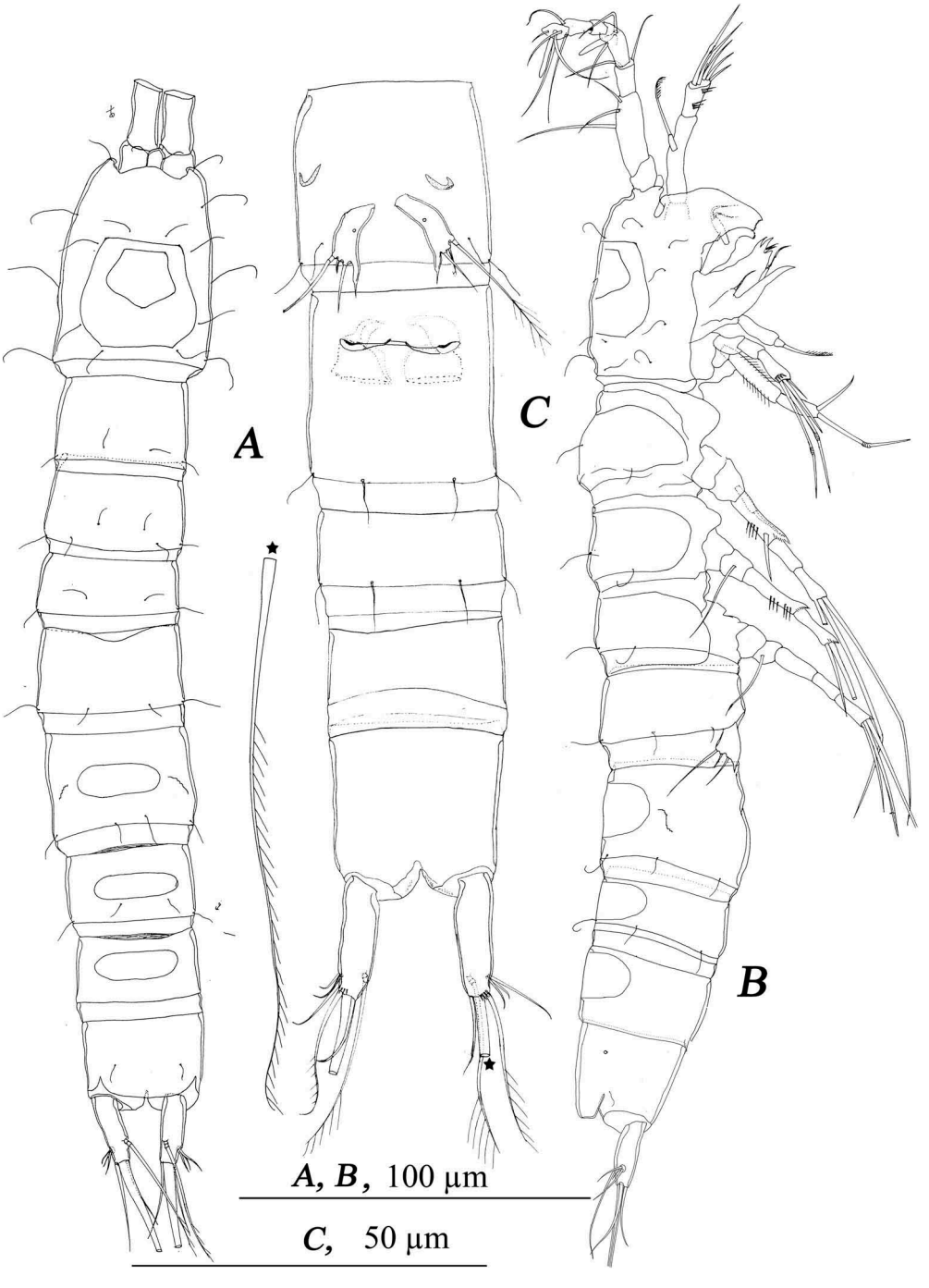


**Figure 6.** *Indocaris imbricata* gen. nov., sp. nov. Female: (A) habitus, dorsal view; (B) habitus, lateral view; (C) urosome, ventral view.

on two slides and one female (MNHN-IU-2013–11944) dissected on four slides, two males (MNHN-IU-2013–11945-11946) and one female (MNHN-IU-2013–11947) whole-mounted on one slide each; 5 February 2010, Coll. V.R. Totakura.

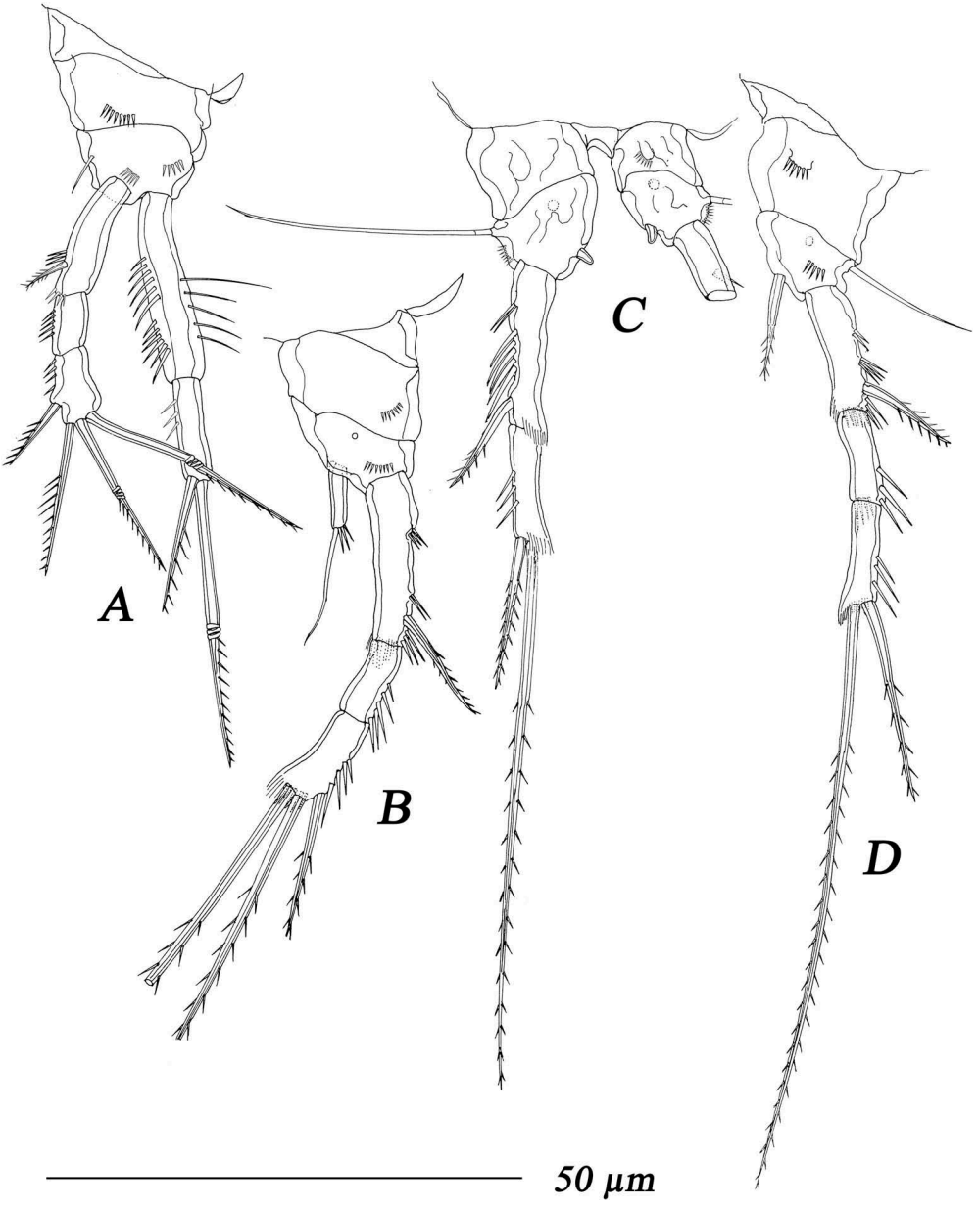


**Figure 7.** *Indocaris imbricata* gen. nov., sp. nov. Female: (A) leg 1, anterior view; (B) leg 2, anterior view; (C) leg 3, posterior view; (D) leg 4, posterior view.

### *Other material examined*

Farm bore (water temperature 26°C, pH 7.0) at Kunchanapalli village (16°23′42.1″N, 80° 32′28.2″E; elevation 26 m) near Vijayawada city, in Guntur District, Andhra Pradesh, southeastern India; two males and 20 females in alcohol in one vial (MNHN-IU-2013–11948), 5 February 2012, Coll. V.R. Totakura.

### Etymology

The new species is named *imbricata* (Latin adjective), meaning overlapping, alluding to the characteristic arrangement of the modified spinules at the base of the male leg 4 endopod.

### Description of adult male

Total body length, measured from tip of rostrum to posterior margin of caudal rami, 250–330 µm (285 µm in holotype). Preserved specimens colourless. Nauplius eye absent. Habitus (Figure 2A) cylindrical and slender, without any demarcation between prosome and urosome; prosome/urosome ratio about 0.8 in lateral view; greatest width in dorsal view at cephalothorax. Body length/width ratio about 5.8. Free pedigerous somites without any lateral or dorsal expansions, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and hard to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented only with sensilla and pores (no spinules), with dorsal cuticular double-window on cephalothorax, and elliptical dorsal, simple cuticular window each on genital somite and next three somites. Pleural areas of cephalothorax and free pedigerous somites moderately developed; cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum (not drawn) small, linguiform, membranous, as long as wide, not demarcated at base, ornamented with two dorsal sensilla. Cephalothorax (Figure 2A) about as wide as genital somite and somewhat dilated distally, 1.3 times as long as wide in lateral view, representing 21.5% of total body length. Surface of cephalic shield ornamented with eight pairs of large sensilla (no cuticular pores or any other ornamentation); posterior half of cephalothorax widest in dorsal view; free pedigerous somites 2–4 gradually widening and with narrow, smooth hyaline fringes. Second pedigerous somite with one pair of mid-dorsal and one pair of lateral sensilla. Third somite as long as second one but slightly wider and ornamented with three pairs of distal sensilla. Fourth pedigerous somite widest of all prosomites in dorsal view, slightly shorter than third prosomite, with three pairs of sensilla. First urosomite about as wide as, but longer than, fourth pediger, and also with only three pairs of sensilla. Genital somite widest of all urosomites and with two pairs of posterior sensilla. Third urosomite narrower and shorter than first urosomite and with three pairs of large posterior sensilla; fourth urosomite longer than third one, with three pairs of sensilla; preanal somite as long as fourth urosomite and without any surface ornamentation. Anal somite about 0.7 times as long as preanal somite and ornamented with one pair of large dorsal sensilla at base of anal operculum and one proximo-lateral cuticular pore, but without any spinules. A single large, longitudinally placed spermatophore (Figure 2A, B) discernible through cuticle of genital somite and next two somites; spermatophore about 2.9 times as long as wide, kidney-shaped, with curved, narrow neck. Anal operculum (Figure 2A) well developed, with smooth and almost straight distal margin, reaching posterior end of anal somite. Anal sinus wide open and ornamented with fine spinules.

Caudal rami (Figure 2A, B) subcylindrical, parallel to body somites, inner margin convex, outer margin nearly straight; about 2.7 times as long as greatest width in ventral view; three times as long in lateral view and about 0.6 times as long as anal somite, with space between them about 1.7 times as long as maximum width of ramus; with full

complement of seven setae (three lateral, one dorsal, two apical and one subapical); spinules occurring at inner distal corner ventrally and one pore proximo-laterally. Dorsal seta (VII) slender, plumose, inserted close to inner margin at distal third and opposite to lateral group of setae, but 1.2 times as long as caudal ramus, biarticulate basally. Inner apical seta (VI) smooth, inserted close to ventral margin, about 0.7 times as long as ramus. Middle apical seta (V) somewhat swollen at base, without breaking plane, unipinnate, about five times as long as ramus, pointing distally. Outer subapical seta (IV) without breaking plane, 1.2 times as long as ramus, inserted close to dorsal surface caudally.

Antennule (Figure 3A) slightly longer than cephalothorax, slender, eight-segmented, prehensile, coiled type, digeniculate, geniculation between third and fourth, and sixth and seventh segments. First segment short, ornamented with one row of fine spinules; segments 3–5 only slightly dilated, aesthetasc on segment 5 large, balloon-like, with rounded tip, overreaching ultimate segment, and fused basally to simple seta; apical aesthetasc on eighth segment shorter and slenderer, about as long as segment, slightly constricted at midlength, fused basally with two setae (acrotheck). Setal formula: 0.6.4.1.0.5+aes.0.9+aes. All setae smooth except proximalmost seta on second segment unipinnate. Length ratios of segments from proximal to distal end and along caudal margin 1.0:3.5:1.4:0.7:1.5:1.4:1.4:1.9.

Antenna (Figure 3B) composed of coxa, allobasis, one-segmented endopod and one-segmented exopod. Coxa very short, unarmed and ornamented with one row of short spinules. Allobasis about five times as long as maximum width, unarmed but ornamented with one ventral row of spinules near inner margin. Exopod small, cylindrical, about 2.6 times as long as wide, unornamented and armed with unipinnate apical seta, which is 1.8 times as long as segment. Endopod 0.5 times as long as allobasis and about 2.3 times as long as wide, with surface frill distally, ornamented with three large ventral spinules on inner margin, armed with two short unequal spines laterally and with five strong apical elements (two spines, two geniculate setae and one unipinnate transformed seta).

Labrum (Figure 2A) triangular in lateral view.

Mandible (Figure 3C, D) coxa with narrow cutting edge, elongate, armed with two complex teeth ventrally, one unipinnate seta dorsally, and several small teeth. Palp one-segmented, cylindrical, somewhat dilated distally, about 3.1 times as long as wide, unornamented and armed apically with two smooth, subequal apical setae.

Maxillule (Figure 3E) praecoxal arthrite rectangular, about 2.3 times as long as wide in lateral view, armed with strong lateral seta and three claw-like apical elements. Coxal endite armed with one smooth apical seta. Basis slightly longer than coxal endite, armed with three smooth apical setae. Exopod and endopod absent.

Maxilla (Figure 3F) composed of syncoxa, basis and one-segmented endopod. Syncoxa with two endites, basal one shorter than distal endite, armed with two smooth apical setae, distal endite armed with three smooth apical setae. Allobasis prolonged into strong unipinnate claw and without seta at base. Endopod represented by small segment, 1.2 times as long as wide, armed with two smooth apical setae.

Maxilliped (Figure 3G) syncoxa short and relatively strong, unarmed and unornamented; basis slender, 4.7 times as long as wide, unornamented and unarmed; endopod smallest with unipinnate claw, 0.7 times as long as basis.

Leg 1 (Figure 4A) coxa ornamented with one arched row of fine spinules near distal margin. Basis shorter than coxa, trapezoidal; ornamented with one row of spinules at base of exopod and another but shorter spinular row at base of endopod; armed with small, smooth seta on outer margin and one strong, small, hook-like spine at inner distal angle. Exopod three-segmented, bent inwards, with each segment bearing one row of spinules along outer margin; armed with one small, outer bipinnate spine on first segment; first segment 0.7 times as long as next two segments combined; second segment unarmed and four elements on third segment (one outer spine, one apical seta and two apical geniculate setae). Endopod two-segmented, longer than exopod; first segment about 1.2 times as long as proximal two exopodal segments combined, 4.7 times as long as wide, unarmed, ornamented with one row of elongate, widely spaced spinules along outer and inner margins; second segment thin, ornamented with one row of spinules on outer margin, armed with one spine subapically and one long, geniculate seta apically; endopodal geniculate seta about as long as entire endopod, twice as long as outer spine on endopod, 0.9 times as long as inner geniculate seta on exopod. All exopodal and endopodal armature elements unipinnate along outer margin except bipinnate spine on first exopodal segment.

Leg 2 (Figure 4B) coxa ornamented with one arched row of small spinules medially. Basis slightly smaller than coxa, unarmed, ornamented with one arched row of spinules near outer margin and one proximal pore. Exopod three-segmented, each segment ornamented with spinules along outer margin, as illustrated; hyaline frill at inner distal corner of first and third exopodal segments, but second segment with one row of spinules at inner distal corner. First segment 0.9 times as long as next two segments combined, armed with moderately large outer spine; second segment unarmed; third segment armed with three long setae: two apical and one subapical; innermost apical seta 1.9 times as long as exopod. Endopod one-segmented, subcylindrical (distal part only slightly dilated), 3.5 times as long as wide, 0.3 times as long as first exopodal segment; apical margin armed with smooth seta, which is 0.9 times as long as segment, and ornamented with three spinules.

Leg 3 (Figure 4C) coxa trapezoidal, smaller than basis, ornamented with one arched row of spinules at distal outer angle. Basis robust and produced at inner distal corner into knob-like protuberance; ornamented with anteriorly directed row of spinules along inner margin, one oblique row of spinules at outer distal angle and one pore on anterior surface; and armed with basally articulate, long, slender seta on outer margin. Endopod represented by a small seta, inserted on inner margin at two thirds of basis length. Exopod one-segmented; ancestral proximal segment moderately stout, gradually tapering, outer margin straight, inner margin only slightly curved, 2.9 times as long as wide in ventral view; ornamented with one row of fine spinules on outer distal margin and one transverse row of fine spinules at base of thumb. Apophysis bilobed (one of the lobes probably representing a remnant of fused apical seta); thumb stout, spiniform, with distinct base, longer than apophysis.

Leg 4 (Figures 4D, E, 5A) coxa rhomboidal, ornamented with one row of small spinules near distal margin. Basis shorter than coxa and subquadratic, ornamented with one arched row of small spinules on posterior surface and one oblique row of spinules on outer margin; armed with long seta on outer margin; six large, imbricate, petaloid spinules lying at insertion of endopod and increasing in size from internal to

external. Exopod three-segmented, slightly bent inwards, with each segment bearing spinules along outer margin, and hyaline frill at inner distal corner of first and third exopodal segments but second segment with one row of spinules at inner distal corner; first segment 0.8 times as long as next two segments combined, armed with moderately strong bipinnate outer spine subdistally, 0.6 times as long as segment; second segment unarmed; third segment slightly longer than preceding segment, armed with two apical, bipinnate setae; inner apical seta 2.3 times as long as smaller outer seta, 3.3 times as long as third exopodal segment, about 1.2 times as long as entire exopod. Endopod one-segmented, proximal half dilated, distal part tapering off into an incurved spiniform process, exceeding the posterior border of first exopodal segment and ornamented with three or four tiny spinules at midlength of outer margin.

Leg 5 (Figures 2B, 5B) without intercoxal sclerite; elongate trapezoidal plate, ornamented with longitudinal row of eight small, almost equal spinules along inner margin and one small cuticular pore proximally; inner spiniform process acuminate, reaching almost proximal third of next somite, distal margin oblique, armed with three setae. Outermost seta long, articulate at base, and arising from small lobe; one small seta (probably ancestral exopodal seta) on lobe; another long seta on inner lobe.

Leg 6 (Figures 2B, 5D, E) smooth, unarmed, forming simple operculum covering gonopore, fused with somite; spiniform, triangular plate-like structure.

### *Description of adult female*

Body length, excluding caudal setae, 260–350 µm (260 µm in allotype). Habitus (Figure 6A, B): ornamentation of prosomites, colour, etc., similar to male, except genital and first abdominal somites fused into double-somite, and habitus slightly stronger.

Genital complex (Figure 6C) occupying anterior ventral half and distinctly broader than high; single genital aperture and median copulatory pore covered by fused, vestigial sixth legs; seminal receptacles small, hard to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Preanal and anal somites almost as in male.

Caudal rami (Figure 6A–C) similar to those of male in relative proportions and arrangement and size of setae.

Antennule (Figure 3H) seven-segmented, ornamented on first segment with few minute spinules on ventral surface, aesthetasc on fourth segment large, somewhat constricted at midlength, reaching end of ultimate segment, aesthetasc on seventh segment much slenderer and shorter than that on segment 4 and fused basally to two apical setae; setal formula: 0.5.4.4+aes.1.0.9+aes. All setae smooth except unipinnate proximalmost one on second segment. Length ratios of segments, from proximal to distal end and along caudal margin 1.0:2.8:1.4:1.3:0.9:0.8:1.8.

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

Leg 1 (Figure 7A) coxa rhomboidal, ornamented with one arched row of spinules near distal margin; basis trapezoidal, armed with one slender outer seta, ornamented with one row of spinules at base of exopod and one row near inner margin; armature and ornamentation of exo- and endopod similar to those of male.

Leg 2 (Figure 7B) exopod similar to that of male. Endopod cylindrical, 3.8 times as long as wide, 0.4 times as long as first exopodal segment, other details same as in male but apical seta longer.

Leg 3 (Figure 7C) coxa with arched row of spinules near distal margin. Basis ornamented with one row of spinules on outer margin and armed with long and smooth outer seta. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frill each at inner distal corner; first segment armed with outer spine and long spinules on outer distal margin; second segment with subapical outer spine and apical strong seta, and three spinules on outer margin; seta 3.4 times as long as spine; all elements bipinnate. Endopod greatly reduced to small, simple stub-like structure with blunt end.

Leg 4 (Figure 7D) exopod similar to that of male; endopod slender, straight, 1.7 times as long as first exopodal segment, tapering into acuminate point, lateral margins of distal half fringed with spinules.

Leg 5 (Figures 5C, 6C) as in male, but large in size with longer distal inner spinous process and ornamented with one small pore; inner margin smooth.

Leg 6 (Figure 6C) unarmed, unornamented plate-like operculum covering gonopores and fused with its somite.

### *Variation*

The number of the petaloid spinules on the male leg 4 basis is either five or six (Figure 5A).

### *Distribution*

This species is known only from two farm bores, about 50 km apart, in Guntur District, Andhra Pradesh state.

### *Ecology*

At Kunchanapalli, *Indocaris imbricata* sp. nov. was found co-existing with *Atopobathynella* sp., *Habrobathynella* sp., *Serbanibathynella* sp., *Rybocyclops* sp., *Nitocrella* sp., *Dussartstenocaris* sp., unidentified harpacticoids, mites, nematodes, oligochaetes and insect larvae, and at Chintalapudi (05 February 2010) with *Serbanibathynella* sp. and *Rybocyclops* sp.

## ***Indocaris inopinata*** gen. nov., sp. nov.
(Figures 1, 8–13)

### *Type locality*

Bore-well (water temperature 27°C; pH 7.0) at Block II on Acharya Nagarjuna University campus, Nagarjunanagar, ~12 km ENE of Guntur city (16°22′41.0″N, 80°31′39.4″E; elevation 19.8 m) in Guntur District, Andhra Pradesh, South India (Figure 1). The well, which is approximately 55 m deep, accesses a groundwater aquifer developed in garnet-sillimanite gneiss ('khondalite') bedrock, belonging to the Eastern Ghats group, which is approximately 3000 million years old. There is ample evidence that the Acharya Nagarjuna University campus area sustained marine transgressions during the Cenozoic (see Holsinger et al. 2006).

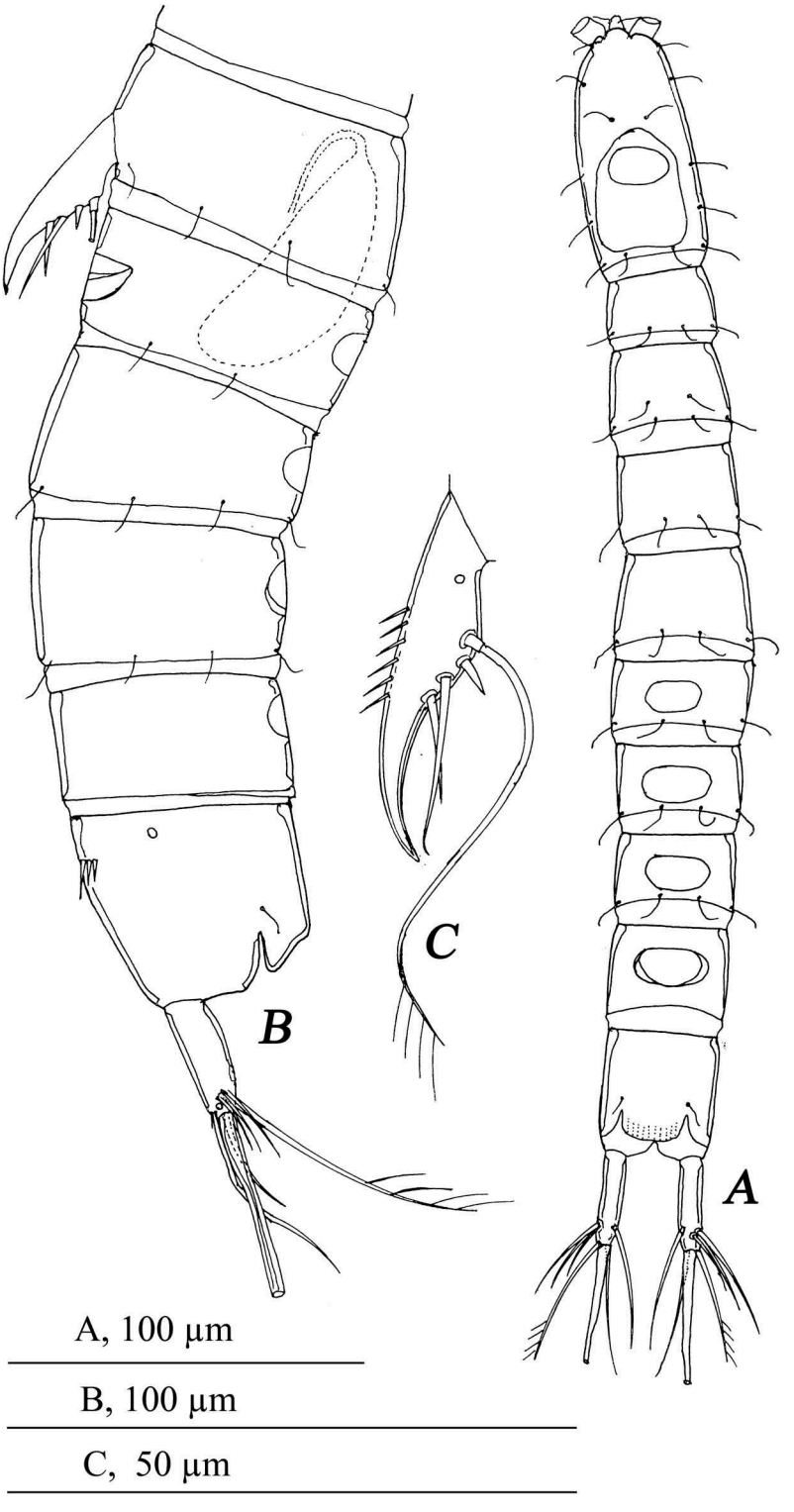


**Figure 8.** *Indocaris inopinata* gen. nov., sp. nov. Male: (A–B); holotype male (C): (A) habitus, dorsal view; (B) urosome, lateral view; (C) leg 5, lateral view.

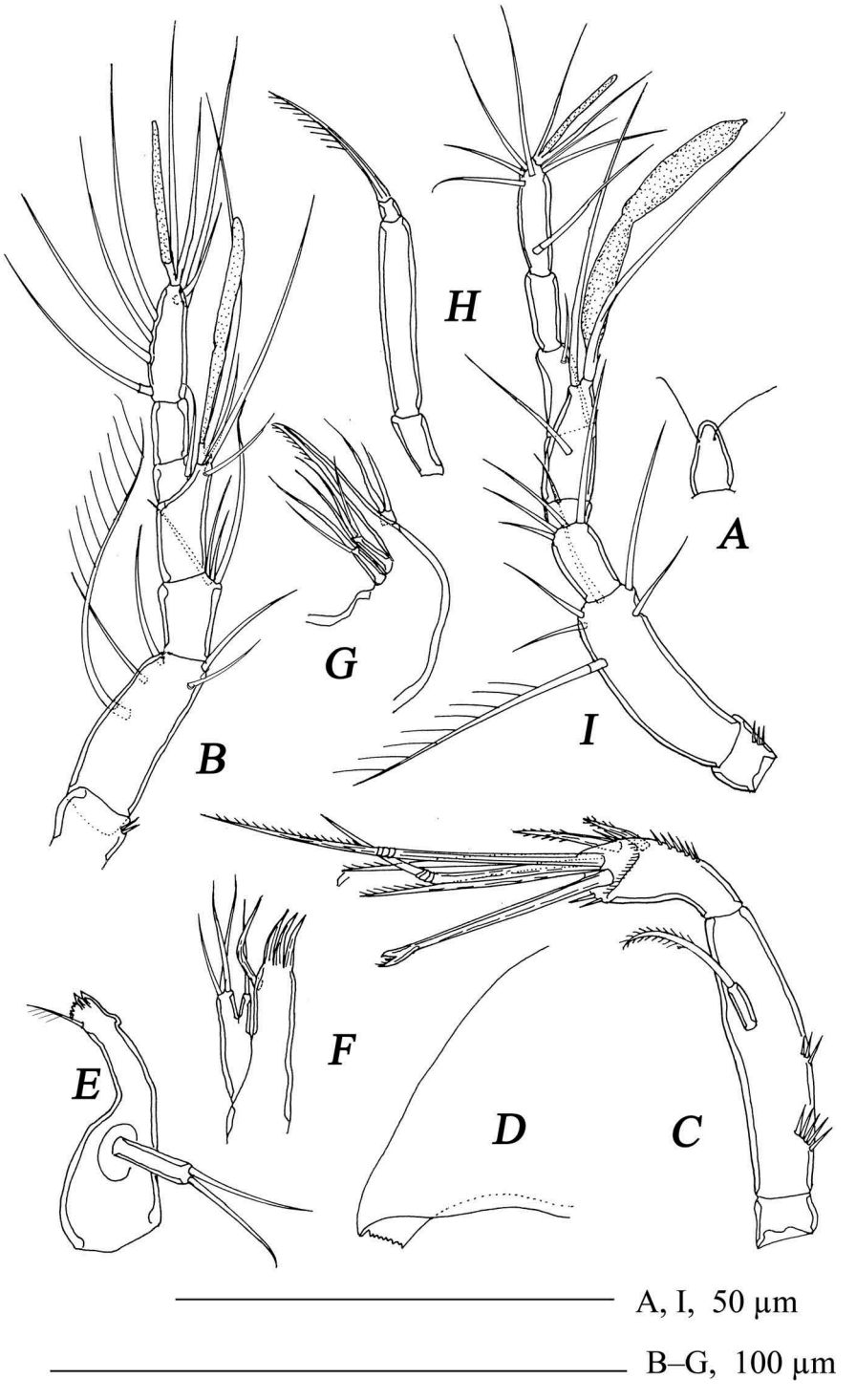


**Figure 9.** *Indocaris inopinata* gen. nov., sp. nov. Female (A–H); male (I): (A) rostrum, dorsal view; (B) antennule, ventral view; (C) antenna, lateral view; (D) labrum, lateral view; (E) mandible, posterior view; (F) maxillule, anterior view; (G) maxilla, lateral view; (H) maxilliped, lateral view; (I) antennule, anterolateral view.

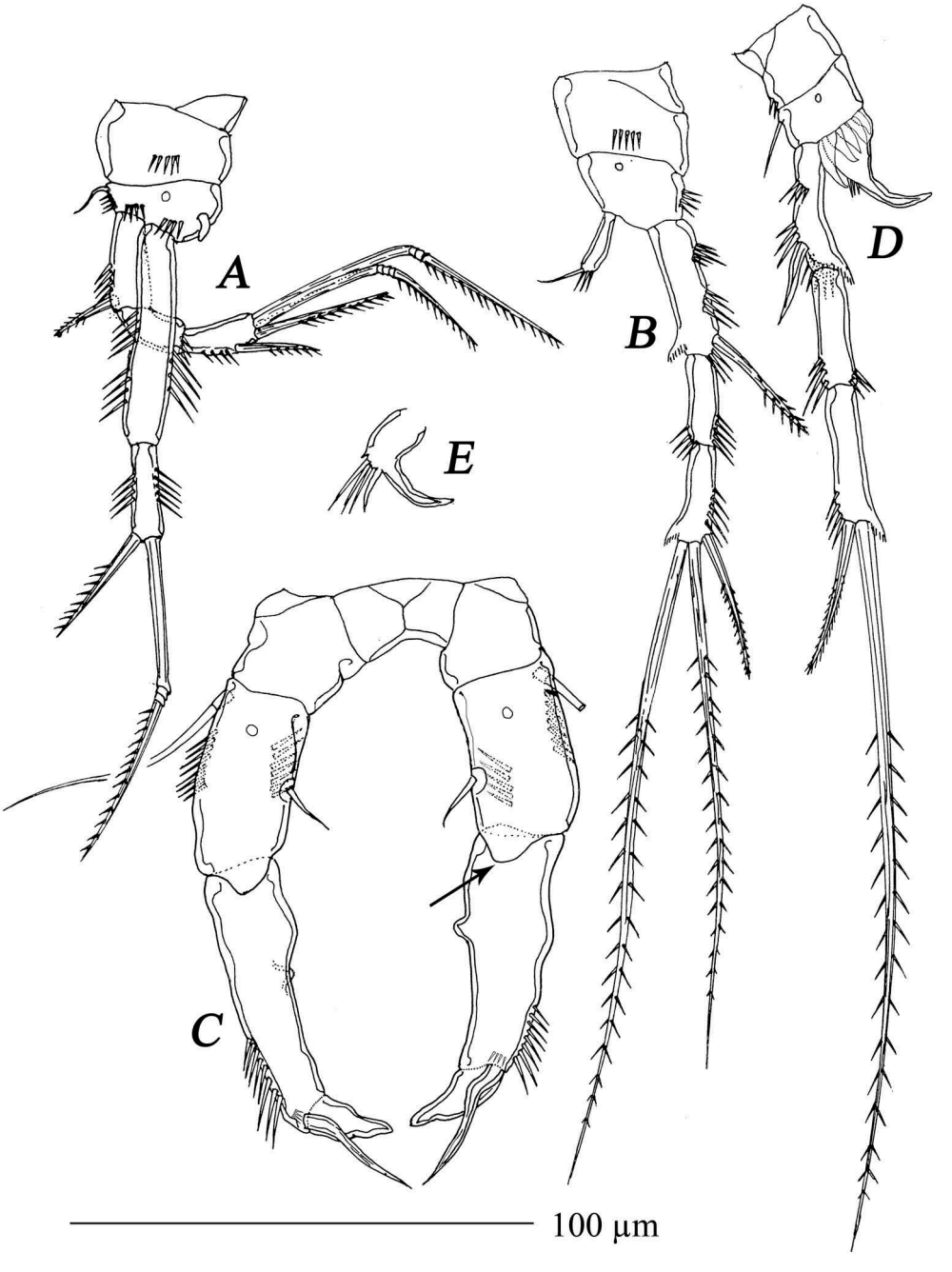


**Figure 10.** *Indocaris inopinata* gen. nov., sp. nov. Male: (A) leg 1, anterior view; (B) leg 2, anterior view; (C) third pair of legs, anterior view (arrow pointing to subtriangular plate-like structure); (D) leg 4, anterior view; (E) endopod of leg 4 (not drawn to scale).

### *Type material examined*

Holotype male (MNHN-IU-2013–11949) and allotype female (MNHN-IU-2013–11950) dissected on two slides each; five paratypes: one male (MNHN-IU-2013–11951) and one

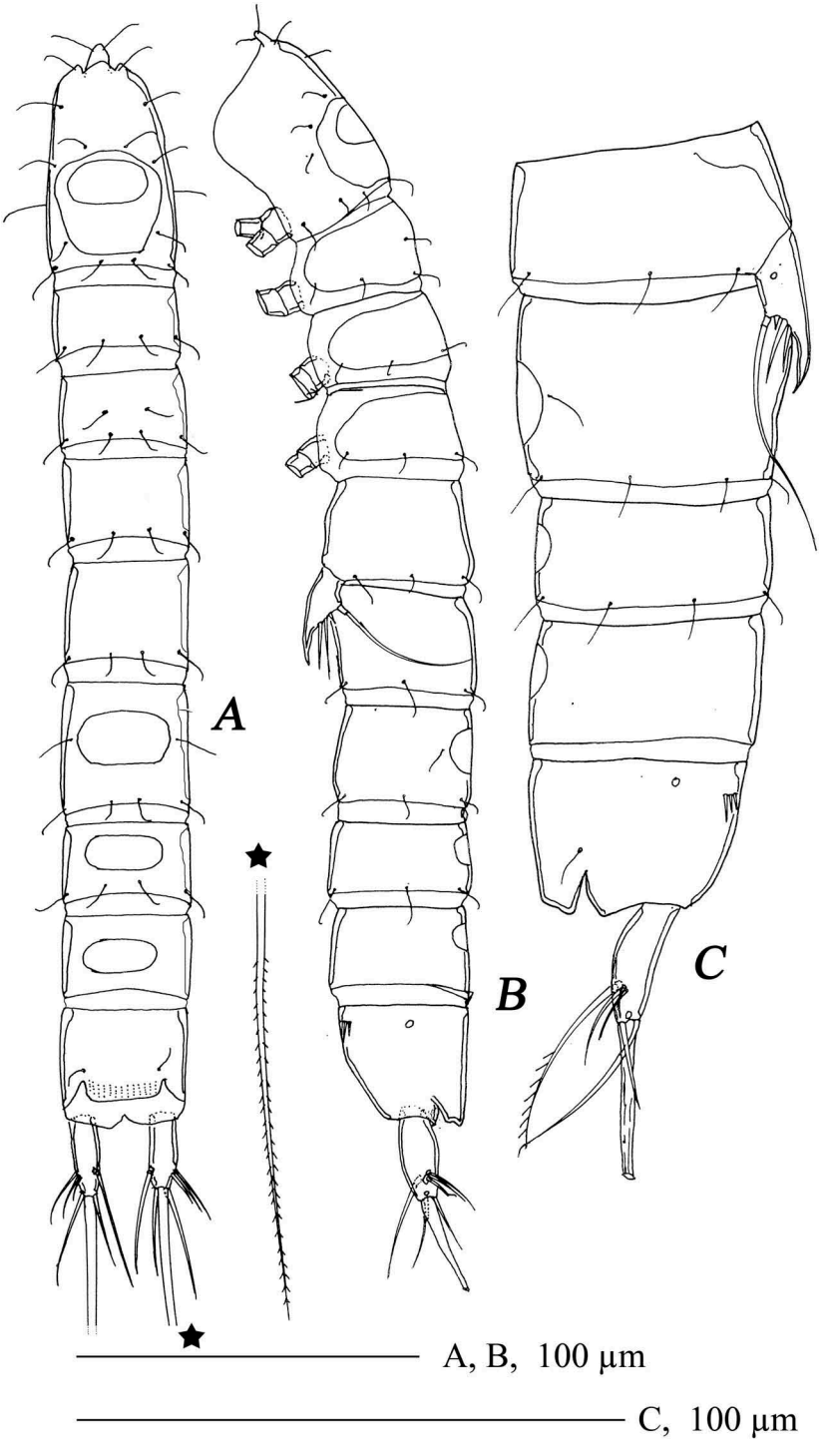


**Figure 11.** *Indocaris inopinata* gen. nov., sp. nov. Female: (A) habitus, dorsal view; (B) habitus, lateral view; (C) urosome, lateral view.

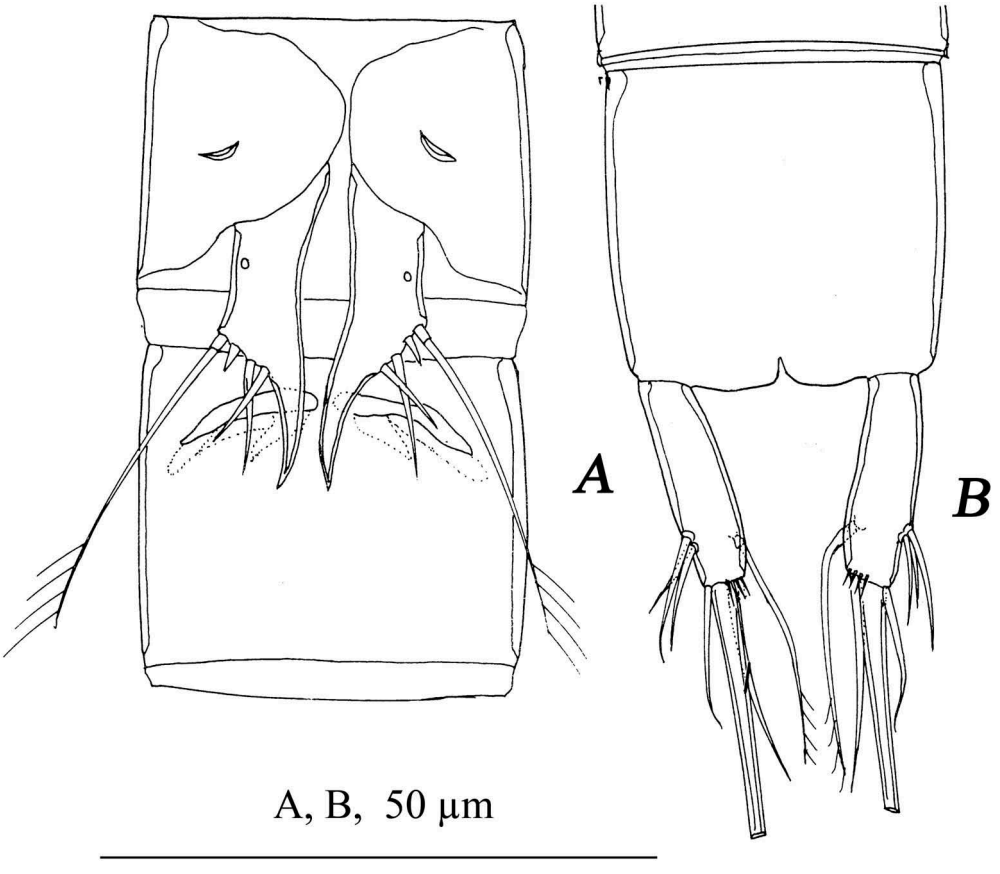


**Figure 12.** *Indocaris inopinata* gen. nov., sp. nov. Female: (A) fifth pedigerous somite and genital double-somite, ventral view; (B) anal somite and caudal rami, ventral view.

female (MNHN-IU-2013–11952), dissected on two slides each, and three females (MNHN-IU-2013–11953-11955), whole-mounted each on one slide; one male dissected on two slides in junior author's personal collections; 19 November 2003, Coll. Y. Ranga Reddy.

### *Etymology*

The specific epithet is derived from the Latin adjective '*inopinatus*', meaning 'unexpected' and alluding to the fortuitous discovery of this interesting taxon. The name agrees in gender with the (feminine) generic name.

### *Description of adult male*

Total body length, measured from tip of rostrum to posterior margin of caudal rami, 201–345 µm (340 µm in holotype). Preserved specimens colourless. Nauplius eye absent. Habitus (Figure 8A) cylindrical and slender, without any demarcation between prosome and urosome; prosome/urosome ratio about 0.7 in dorsal view; pedigers 2–3 slenderer than urosome in dorsal view, greatest width in dorsal view at first urosomite. Body length/width ratio about 8.8. Free pedigerous somites without any lateral or dorsal expansions, all connected by well-developed arthrodial membranes. Hyaline fringes of

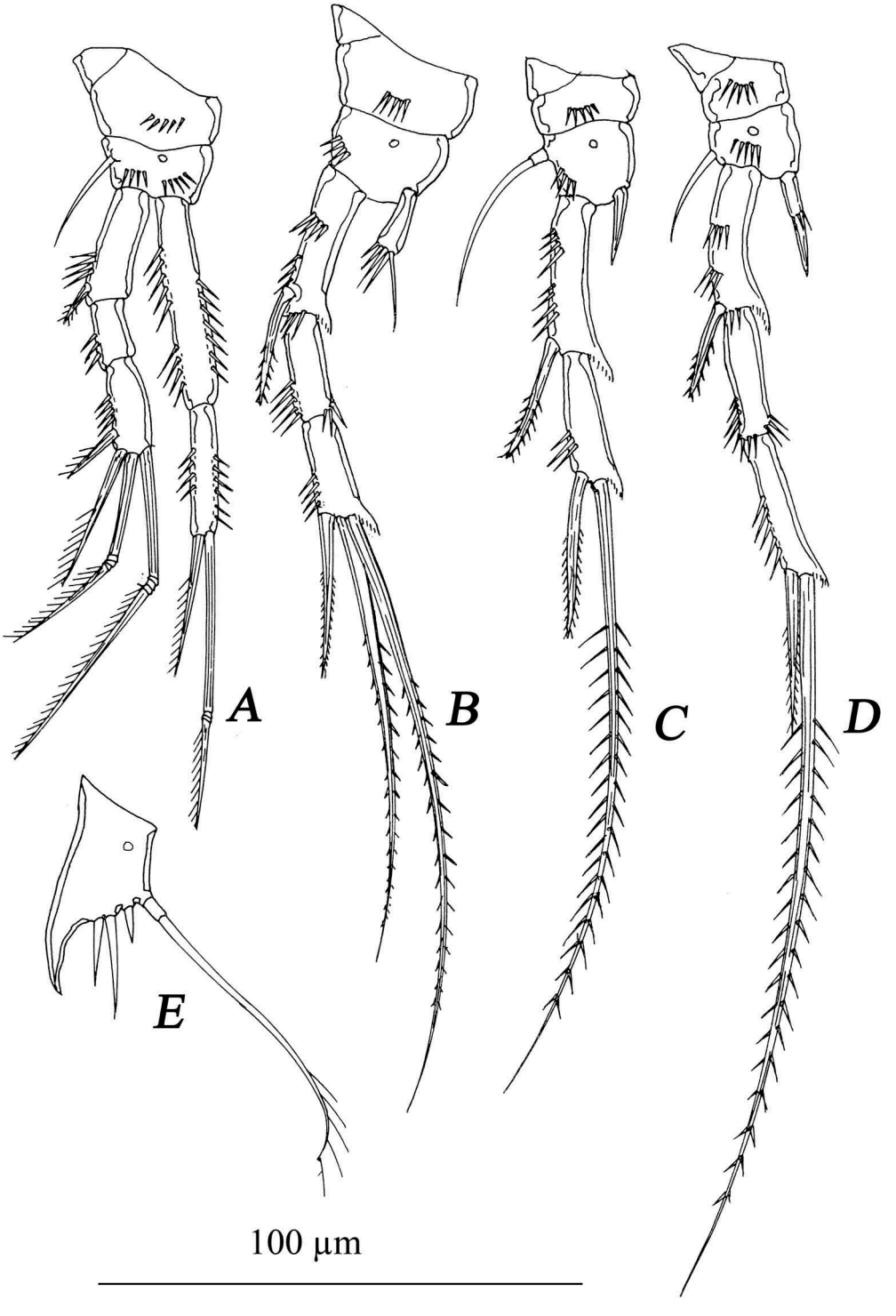


**Figure 13.** *Indocaris inopinata* gen. nov., sp. nov. Allotype female: (A) leg 1, posterior view; (B) leg 2, posterior view; (C) leg 3, anterior view; (D) leg 4, anterior view; (E) leg 5, latero-ventral view.

all somites smooth, very narrow and hard to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented with sensilla, spinules and pores (no cuticular pits), with dorsal cuticular double window on cephalothorax, and somewhat elliptical, dorsal cuticular window each on genital somite and next three somites. Pleural areas of cephalothorax and free pedigerous somites well developed. Rostrum (Figures 8A, 9A) small, linguiform, membranous, 1.2 times as long as wide, demarcated at base, ornamented with two long dorsal sensilla. Cephalothorax (Figure 8A) about 0.9 times as wide as genital somite, about 2.4 times as long as wide in dorsal view and representing 11.5% of total body length. Surface of cephalic shield ornamented with eight pairs of large sensilla; free pedigerous somites 2–4 gradually widening. Second pedigerous somite with one pair of mid-dorsal and one pair of lateral sensilla. Third somite as long as second one but slightly wider and ornamented with three pairs of distal sensilla. Fourth pedigerous somite as wide as prosomites in dorsal view, slightly longer than third prosomite, with two pairs of sensilla. Urosomites gradually narrowing distad. First urosomite widest of all urosomites, longer than fourth prosomite and with only two pairs of sensilla. Genital somite shorter than first urosomite, ornamented with two pairs of posterior sensilla. Third and fourth urosomites about as long as genital somite, with two pairs of large posterior sensilla; preanal somite 0.8 times as long as fourth urosomite and without any surface ornamentation. Anal somite 1.2 times as long as wide, ornamented with one pair of large dorsal sensilla at base of anal operculum, one proximo-lateral cuticular pore and two groups of small spinules ventro-laterally. A single large, longitudinally placed spermatophore (Figure 8B) discernible through cuticle of fifth and genital somite; spermatophore about 2.7 times as long as wide, kidney-shaped, with curved, narrow neck. Anal operculum well developed, unornamented, with slightly serrulate and almost straight distal margin, not reaching posterior end of anal somite, representing 57.6% of somite's width. Anal sinus wide open and ornamented with fine spinules ventrally.

Caudal rami (Figure 8A, B) subcylindrical, straight, inner margin convex, outer margin nearly straight in lateral view; 2.9 times as long as wide in lateral view, about 3.3 times as long as greatest width in dorsal view, and about 0.6 times as long as anal somite, with space between them about 2.9 times as long as that of one maximum width of caudal ramus; with full complement of setae (three lateral, one dorsal, one subapical, two apical); spinules occurring at inner distal corner and one pore disto-laterally. Dorsal seta (VII) inserted close to inner margin at distal third and opposite to lateral group of setae, slightly longer than caudal ramus, biarticulate basally. Inner apical seta (VI) smooth, inserted close to ventral margin, about 1.2 times as long as ramus. Middle apical seta (V) somewhat swollen at base, without breaking plane, bipinnate and about 5.2 times as long as ramus. Outer subapical seta (IV) without breaking plane and unipinnate and inserted close to dorsal surface.

Antennule (Figure 9I) somewhat longer than cephalothorax, slender, eight-segmented, slightly prehensile, coiled type, digeniculate, geniculation between third and fourth, and sixth and seventh segments. First segment short, ornamented with one row of spinules; segments 3–5 barely dilated; aesthetasc on segment 5 elongate, constricted at midlength, with narrow tip, overreaching ultimate segment and fused basally to simple seta; apical aesthetasc on eighth segment staff-like, shorter and slenderer than segment, fused basally with two setae (acrotheck). Setal formula: 0.6.4.1.3+aes.1.0.9+aes. All setae smooth except

proximalmost seta on second segment unipinnate. Length ratios of segments, from proximal to distal end and along caudal margin, 1.0:3.9:1.5:0.5:2.2:1.5:1.4: 2.1.

Antenna (Figure 9C) composed of coxa, allobasis, one-segmented exopod and one-segmented endopod. Coxa short, unornamented and unarmed. Allobasis 3.8 times as long as maximum width, unarmed but ornamented with two arched rows of spinules on anterior margin. Exopod small, cylindrical, about thrice as long as wide, unornamented and tipped with bipinnate seta, which is 2.5 times as long as segment. Endopod about 0.6 times as long as allobasis and about 2.8 times as long as wide, with surface frill distally, ornamented with two rows of spinules on inner margin, armed laterally with two short unequal, bipinnate spines and apically with five strong elements (two spines, two geniculate setae and one transformed unipinnate seta).

Labrum (Figure 9D) subtriangular, with fine denticles on distal margin in lateral view.

Mandible (Figure 9E) narrow cutting edge on elongate coxa bearing two complex teeth ventrally, one unipinnate seta dorsally, and several small teeth. Palp one-segmented, cylindrical, about 3.6 times as long as wide, unornamented and armed with 2 smooth, slightly unequal, apical setae.

Maxillule (Figure 9F) praecoxal arthrite rectangular, about 2.2 times as long as wide in lateral view, armed with strong lateral seta and three apical elements. Coxal endite armed with one smooth apical seta. Basis slightly longer than coxal endite, armed with three smooth apical setae. Exopod and endopod absent.

Maxilla (Figure 9G) composed of syncoxa, basis and one-segmented endopod. Syncoxa with two endites, proximal one short, armed with two smooth setae apically, distal endite armed with three smooth setae apically. Allobasis prolonged into strong, distally unipinnate claw, and without seta at base. Endopod represented by small segment, bearing two smooth apical setae.

Maxilliped (Figure 9H) syncoxa short, unarmed and unornamented; basis slender, 5.3 times as long as wide, unornamented and unarmed; endopod small with unipinnate claw, 0.8 times as long as basis.

Leg 1 (Figure 10A) coxa trapezoidal, ornamented with one row of spinules near mid-distal margin. Basis shorter than coxa, trapezoidal; ornamented with one row of spinules on outer margin, one row near base of exopod and another row at base of endopod, armed with one small, smooth seta on outer margin and one small out-curved, blunt, knob-like, small spine at inner distal angle. Exopod three-segmented, sharply bent inwards, each segment bearing a row of spinules along outer margin; armed with one small, outer bipinnate spine on first segment; first segment about 0.8 times as long as next two segments combined; second segment unarmed and four elements on third segment (one outer spine, one apical seta and two apical geniculate setae). Endopod two-segmented and longer than exopod; first segment about 1.4 times as long as proximal two exopodal segments combined, five times as long as wide, unarmed, ornamented with elongate spinules along outer and inner margins; second segment thin, ornamented with elongate spinules along outer and inner margins, armed with one spine subapically and one long, geniculate seta apically; geniculate seta about as long as entire endopod, 2.6 times as outer spine on endopod, about as long as inner geniculate seta on exopod. All exopodal and endopodal armature elements unipinnate along outer margin except bipinnate spine on first exopodal segment.

Leg 2 (Figure 10B) coxa ornamented with one row of spinules medially near distal margin. Basis slightly smaller than coxa, unarmed, ornamented with one row of small spinules on outer margin and one proximal pore. Exopod three-segmented; first segment with three short rows of spinules on outer margin; second and third segments with one distal row of spinules each on outer margin; hyaline frill at inner distal corner of first and third exopodal segments but second segment with one row of spinules at inner distal corner. First segment 0.7 times as long as next two segments combined, armed with outer spine; second segment unarmed; third segment armed with three long elements (one subapical, two apical setae); innermost one 1.4 times as long as exopod. Endopod one-segmented, subcylindrical, distal part only slightly swollen, thrice as long as wide, 0.4 times as long as first exopodal segment, apical margin with three small spinules and one smooth seta, which is 0.8 times as long as segment and pointing inwards.

Leg 3 (Figure 10C) coxa trapezoidal, much smaller than basis, ornamentation not discernible. Basis robust and produced at inner distal corner into simple subtriangular plate-like structure; ornamented with one row of spinules on outer margin, one anteriorly directed row of spinules near inner margin and one pore on anterior surface, armed with moderately long, basally articulate, slender seta on outer margin. Endopod represented by small seta, inserted on inner margin at two thirds of basis length. Exopod having two partly fused segments; ancestral proximal segment moderately stout, 2.6 times as long as wide in ventral view, inner margin only slightly curved, with small bulbous hyaline structure; ornamented with one row of spinules on outer distal angle and one transverse row of fine spinules at base of thumb. Apophysis with vague septum at base and pyriform in outline and without any seta. Thumb moderately strong, somewhat spiniform with acuminate tip, and longer than apophysis.

Leg 4 (Figure 10D, E) coxa trapezoidal, ornamented with one row of spinules at outer distal angle. Basis shorter than coxa, rectangular and armed with small seta on outer margin; five large, imbricate, petaloid spinules lying at the insertion of endopod and increasing in size from internal to external. Exopod three-segmented and ornamented with rows of spinules along outer margins of all segments, as illustrated; hyaline frill on inner distal corner of first and third exopodal segments but second segment with one row of spinules at inner distal corner; first segment about half as long as next two segments combined, armed with moderately strong bipinnate outer spine subdistally; second segment unarmed; third segment slightly longer than second exopodal segment, armed with two apical, bipinnate setae; inner apical seta 4.4 times as long as outer seta, about five times as long as third exopodal segment, nearly twice as long as entire exopod. Endopod one-segmented, about as long as first exopodal segment, proximal half bulbous, distal part tapering to acuminate point and curved inwards and ornamented with three or four small spinules at about mid-length of outer margin (Figure 10E).

Leg 5 (Figure 8B, C) without inter coxal sclerite; elongate trapezoidal plate, ornamented with longitudinal row of moderately large, almost equal spinules along inner margin and one small cuticular pore proximally; inner spiniform process horn-like, with acuminate tip, reaching almost distal-third of next segment, distal margin oblique, armed with four setae. Outermost seta long, articulate at base and

arising from small outer lobe; one small spiniform seta (probably ancestral exopodal seta) on small lobe; another two unequal setae on inner lobe, outer seta 1.2 times as long as innermost seta.

Leg 6 (Figure 8B) smooth, unarmed, forming simple operculum covering gonopore, fused with somite; elliptical plate-like structure in ventral view.

### *Description of adult female*

Body length, excluding caudal setae, 255–350 µm (260 µm in allotype). Habitus (Figure 11A, B) similar to male in ornamentation of prosomites, colour, etc., but genital somite and first abdominal somites fused into double-somite and habitus slightly stronger. Genital complex rectangular, occupying anterior ventral half (Figure 12A); single genital aperture and median copulatory pore covered by vestigial sixth legs; seminal receptacles small, hard to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Preanal somite and anal somite very similar to male.

Caudal rami (Figures 11A–C, 12B) similar to those of male in relative proportions.

Antennule (Figure 9B) seven-segmented, ornamented on first segment with few minute spinules; aesthetasc on fourth segment slender, constricted at about midlength, overreaching ultimate segment; apical aesthetasc on seventh segment longer than its segment and fused basally to two apical setae; setal formula: 0.6.4.4+aes.1.0.8+aes. All setae smooth except unipinnate proximalmost one on second segment. Length ratios of segments, from proximal to distal end and along caudal margin, 1.0:3.4:1.5:2.1:0.6:1.0:2.1.

Antenna, labrum, mandible, maxillule, maxilla and maxilliped similar to those of male.

Leg 1 (Figure 13A) coxa trapezoidal, unarmed, ornamented with one row of spinules near mid-distal margin; basis trapezoidal, armed with only one outer seta, and ornamented with one row of spinules each at base of exopod and endopod; armature and ornamentation of exopod and endopod similar to those of male.

Leg 2 (Figure 13B) exopod similar to that of male. Endopod spatulate, 3.8 times as long as wide, 0.4 times as long as first exopodal segment; other details same as in male.

Leg 3 (Figure 13C) coxa with arched row of spinules near distal margin. Basis trapezoidal, ornamented with one pore anteriorly and one row of spinules at outer distal angle and armed with long, basally articulate, smooth outer seta. Exopod two-segmented, either segment ornamented with one row of spinules along outer margin, as illustrated, and with hyaline frill at inner distal corner; first segment armed with outer spine; second segment with outer spine and apical strong seta; seta 3.6 times as long as spine; all armature elements bipinnate. Endopod spiniform, 1.9 times as long as first exopodal segment, smooth, and tapering to acuminate point.

Leg 4 (Figure 13D) exopod similar to that of male; endopod straight, somewhat spiniform, 0.7 times as long as first exopodal segment, tapering to acuminate point, with transverse row of spinules at midlength.

Leg 5 (Figure 13E) ornamented with one small pore; inner margin smooth; spiniform process at inner distal corner shorter than in male; armature as in male.

Leg 6 (Figure 12A) vestigial, fused into simple cuticular flap, covering gonopore.

### Distribution

This species is only known from the type locality.

### Ecology

The new species was accompanied on different occasions by *Nitocrella* sp., and *Haplocyclops fiersi* Karanovic and Ranga Reddy 2005 (Copepoda), *Indocandona nagarjuna* Karanovic and Ranga Reddy 2008 (Ostracoda), *Habrobathynella nagarjunai* Ranga Reddy 2002 (Bathynellacea), *Andhracoides* sp. (Isopoda), *Bogidiella indica* Holsinger, Ranga Reddy and Messouli, 2006 (Amphipoda), and unidentified nematodes and mites.

## *Indocaris tirupatiensis* (Ranga Reddy, 2011a) comb. nov.
(Figures 1, 14A–F)

*Synonymy: Parastenocaris tirupatiensis* Ranga Reddy, 2011a: 21–29, figs 1–5; Ranga Reddy, 2014: 5320; Totakura et al., 2014: 535.

### Type locality

Borewell on the Sri Venkateswara University campus (13°37′44″N, 79°23′58″E); elevation 162 m), Tirupati, Andhra Pradesh, South India (Figure 1).

### Diagnosis of adult male

Total body length, measured from base of rostrum to end of caudal rami, 350 µm. Body length/urosome 7.7. Hyaline frills on all somites smooth. Cephalothorax somewhat rectangular, with vague, spherical integumental window. Urosomites 3–5 each with somewhat elliptical, dorsal integumental window. Anal somite (Figure 14A) ornamented with two pairs of crescentic rows of particularly large but unequal spinules on ventral surface. Caudal rami four times as long as wide and 0.8 times as long as anal somite; dorsal seta inserted at four fifths of ramus length opposite to lateral group of setae. Aesthetasc on fifth antennular segment large, club-shaped. Leg 1 basis (Figure 14B) with digitiform chitinous structure near proximal inner corner in addition to usual outer seta; exopod shorter than endopod; second and third exopodal segments sharply bent inwards. Leg 2 endopod (Figure 14C) spatulate, unornamented, bearing an apical bipinnate, inwardly bent claw-like seta. Leg 3 (Figure 14D) arc-like, exopod one-segmented, ornamented with large spinules on outer distal margin and tiny hyaline lobe on inner distal margin; apophysis conical, shorter than spiniform, outcurved thumb and somewhat bulging at proximal outer angle. Endopod short, one-segmented, digitiform and tipped with simple seta. Leg 4 (Figure 14E) basis with a row of five large, imbricate spinules at insertion of endopod; spinules increasing in size from internal to external; endopod one-segmented, flask-shaped, 0.8 times as long as first exopodal segment, with bulbous proximal half and narrow, incurved, horn-like distal region, and ornamented with three slender spinules at about mid-length of outer margin; exopodal segments of legs 2 and 4 ornamented with a row of spinules each outer margin. Leg 5 (Figure 14F) without intercoxal sclerite; large, conical plate-like structure, ending in short spinous process, reaching almost midlength of next somite; armature consisting of uniarticulate outer seta followed by one short spiniform seta and two moderately long setae; inner margin ornamented with five large spinules around the middle. Leg 6 smooth,

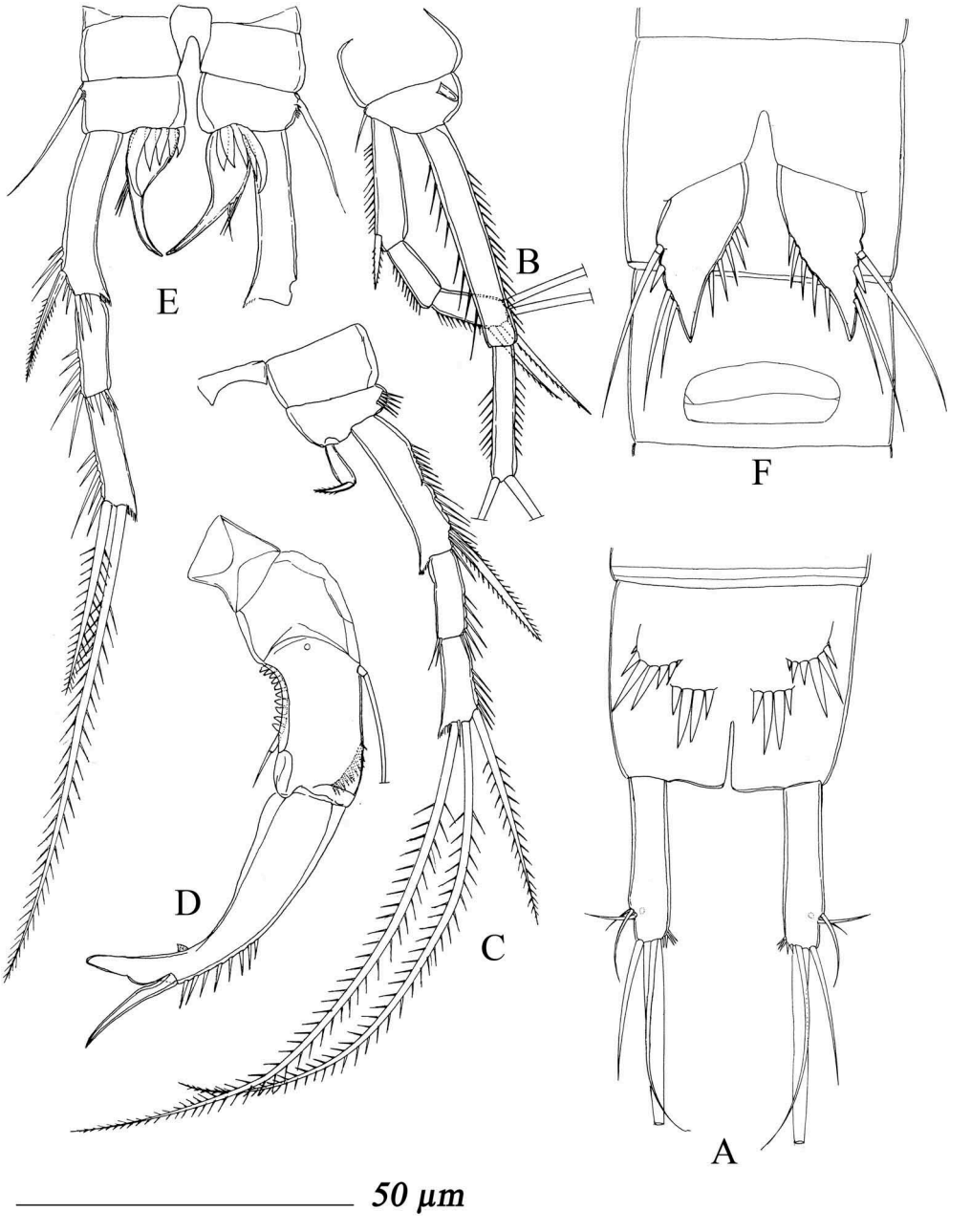


**Figure 14.** *Indocaris tirupatiensis* comb. nov. Male: (A) anal somite and caudal rami, ventral view; (B) leg 1, posterior view; (C) leg 2, posterior view; (D) leg 3, posterior view; E, leg 4, posterior view; (F) fifth and sixth pedigerous somites, ventral view. Redrawn from Ranga Reddy (2011a).

unarmed, forming simple operculum covering gonopore, fused with somite; in lateral view (Figure 14F) appearing a conical protrusion, reaching posterior margin of same somite.

***Female:*** unknown.

## Discussion

The genus *Indocaris* gen. nov. with its three species forms a homogeneous monophyletic entity within the family Parastenocarididae. The most diagnostic synapomorphy of this group concerns the number, form, and arrangement of the spinules on the male leg 4 basis: five or six spinules that are large and petaloid in form, overlapping one another (imbricate), increasing in size from internal to external (outermost spinule the largest), and arranged as a semi-whorl at the insertion of the endopod. Why this composite character is unique within the Parastenocarididae is clarified below.

According to Schminke (2010, p. 354), the spinules on the male leg 4 basis

> 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).

So, the presence of said spinule is almost widespread among the parastenocaridid species. In fact, these spinules were the chief criterion for Lang (1948) to propose the *minuta* group for 11 species within the genus *Parastenocaris*. Subsequently, the genus *Minutacaris* Jakobi, 1972 was established for this species group based mainly on the same criterion. Although the genus is technically available according to ICZN (1999) and listed in the latest World Copepoda database (Gaviria-Melo and Walter 2015), it continues to be a genus inquirendum because of its ambiguous phylogenetic validity. Following Galassi and De Laurentiis (2004), Ranga Reddy and Defaye (2007) listed under the 'polyphyletic' *minuta* group about 50 species and subspecies together with their geographic distribution and the nature of their habitats. Some of these taxa have recently been allocated to the newly revised or erected genera, such as *Stammericaris* Jakobi, 1972, *Kinnecaris* Schminke, 2008, *Monodicaris* Schminke, 2009, and *Cottarellicaris* Schminke, 2013 (see Schminke 2008, 2009, 2013). However, the highly transformed spinules and their arrangement in *Indocaris* gen. nov., as already described, are distinctly different from those of any of the aforementioned taxa, in which the spinules are mostly small and unmodified. One can, however, find some superficial resemblance of this character between *Indocaris* gen. nov. and the West African genus *Monodicaris*. However, a critical comparison of its states between the two genera reveals clear-cut differences. For example, *Indocaris* gen. nov., as opposed to *Monodicaris*, has five or six vs one or four, sturdy and petal-like vs moderately large, curved spinules, which become larger vs smaller from internal to external. The apparent similarity of this feature between the two taxa is possibly the result of evolutionary convergence. That the two genera are distinct from each other is also evident from several other phylogenetically informative characters (Ranga Reddy 2011a). For example, body cuticle in *Indocaris* smooth vs pitted in *Monodicaris*, integumental windows on urosomites dorsal vs lateral/dorso-lateral, caudal rami with the lateral group of setae and dorsal seta inserted distally vs at midlength or even more proximally, male antennule 'coiled type' vs 'pocket-knife' type, and male leg 2 endopod, though short, not stub-like vs stub-like. Even more important, the form, size and ornamentation of the male leg 4 endopod are significantly different between the two genera.

The new genus also has a unique constellation of the following morphologic characters within the family Parastenocarididae: (1) caudal ramus is elongate, with the lateral group of three setae and the dorsal seta inserted opposite to each other in the distal third of the ramus; (2) the male antennule is of 'coiled type', eight-segmented, and has a large aesthetasc on the fifth segment; (3) male leg 1 is sexually dimorphic, having a modified, hook-like spine on basis; exopod is sharply incurved; (4) exopodal segments of legs 2 and 4 in both sexes have spinules on the outer margin; (5) male leg 3 ancestral proximal segment of exopod is elongate, slender and ornamented with a longitudinal row of spinules on outer distal margin, and apophysis unilobed or bilobed, unarmed and shorter than the spiniform thumb; endopod is represented by either a slender segment tipped with a weak seta or a seta itself; (6) the male leg 4 endopod is one-segmented, dilated or bulbous in the proximal half and produced into an incurved spiniform or horn-like structure distally, about as long as the first exopodal segment, and ornamented with three or four fine spinules on the subproximal outer margin; and (7) leg 5 has no inter-coxal sclerite and is sexually dimorphic, the inner margin being spinulose in male vs smooth in female, and the spiniform process at the inner distal corner is short in male vs long in female. The taxonomic significance of all these characters and their states is discussed under Phylogenetic considerations (see below).

That the family Parastenocarididae is a monophyletic group within Harpacticoida is now beyond any doubt (see Martínez Arbizu and Moura 1994; Corgosinho and Martínez Arbizu 2005; Corgosinho et al. 2007; Karanovic and Cooper 2011a, 2011b; and others). Within this family, Schminke (2010) has recognised two subfamilies: Parastenocaridinae Chappuis, 1940 and Fontinalicaridinae Schminke, 2010, though the phylogenetic validity of some of the discriminating criteria proposed by him has come into question (Karanovic and Cooper 2011a, 2011b; Ranga Reddy et al. 2014). Yet the new genus can be assigned to the subfamily Parastenocaridinae at least by the following criteria:

(1) The genital field of the female is rectangular and broader than high.
(2) The lateral group of caudal setae and the dorsal seta are located at the same level on the caudal rami.
(3) The male leg 1 basis has a modified inner armature element.
(4) On the male leg 3, the apophysis of the exopod and terminal seta are fused together.
(5) The female leg 3 endopod has fused terminal seta (exception: *I. imbricata* sp. nov.)
(6) The male leg 4 has imbricate modified spinules at the base of the endopod such that one or two of them lie between exopod and endopod.
(7) Leg 5 is generally small, not extending beyond its own somite (exception: *I. tirupatiensis*).

## *Phylogenetic considerations*

As mentioned in the Introduction, Ranga Reddy et al. (2014) have already done the phylogenetic treatment of the genus *Indocaris* gen. nov. (as the *tirupatiensis* group of species) together with *Himalayacaris* Ranga Reddy, Totakura and Corgosinho (2014) and the Neotropical *Remaneicaris* Jakobi, 1972. The analysis has given rise to two computer-generated and equally parsimonious trees (Ranga Reddy et al. 2014, figures 9 and 10),

both signifying the monophyletic unity of *Indocaris* gen. nov., *Himalayacaris*, and *Remaneicaris* within Parastenocarididae. Amongst the three genera, all belonging to the subfamily Parastenocaridinae, the morphologic affinity between *Indocaris* gen. nov. and *Remaneicaris*, which, according to Corgosinho (2007), is 'the most diverse group of the Neotropical Parastenocarididae', is appreciably overwhelming, as revealed by the following characters:

(1) Female genital field. In *Indocaris* gen. nov., *Remaneicaris* and *Himalayacaris*, the female genital field is 'rectangular and much broader than high', which, according to Schminke (2010, p. 814), is one of the chief criteria of Parastenocaridinae. On the other hand, it is roundish and as broad as high in Fontinalicaridinae. Since a Parastenocaridinae-like genital field also occurs in *Psammonitocrella* and other basal genera of the outgroup Ameiridae, we consider this character plesiomorphic in contrast to its apomorphic state in Fontinalicaridinae (Martínez Arbizu and Moura 1994; Corgosinho 2007; Corgosinho, Ranga Reddy, et al. 2012; Ranga Reddy et al. 2014).

(2) Ornamentation of anal somite. The ventral elaborate ornamentation of the anal somite of *I. tirupatiensis* comb. nov. is unique among the parastenocaridid species of the Indian subcontinent as a whole. However, it has a close resemblance with what obtains in the members of *Remaneicaris*, a basal genus of Parastenocaridinae. Hence we are of the opinion that this character represents a plesiomorphic state of *I. tirupatiensis* comb. nov. On the other hand, the spinular ornamentation of the anal somite is greatly reduced to short ventro-lateral rows in *I. imbricata* sp. nov. and completely absent in *I. inopinata*, possibly representing the derived condition.

(3) Maxilla. The syncoxal proximal endite of *I. imbricata* sp. nov. has two setae as in most members of *Remaneicaris*, but a single seta in *I. inopinata* sp. nov. and *I. tirupatiensis* comb. nov. The presence of two setae, according Corgosinho et al. (2007, p. 25), is a 'a peculiar symplesiomorphy' of the genus *Remaneicaris*.

(4) Position of the setae on the caudal ramus. In both these genera and most taxa of Parastenocaridinae, the lateral group of three setae (I–III) occurs at the same level as, and almost opposite to, the dorsal seta (VII), but they are away from each other in *Himalayacaris* and Fontinalicaridinae. The former character state is no doubt apomorphic within Parastenocarididae, and Schminke (2010) has rightly proposed it as diagnostic of the subfamily Parastenocaridinae. However, the aforementioned phylogenetic analysis has revealed that the condition displayed by *Himalayacaris* as well as Fontinalcaridinae is 'a reversion to what was observed in the ground pattern of the family' (Ranga Reddy et al. 2014, p. 817). This conclusion is based on what is observed in the outgroup taxon, in which setae I–III are distally located, almost at the same level as seta VIII. Also in *Psammonitocrella* and other groundwater Ameiridae, one of the lateral setae is distal whereas the other two are displaced proximally. Hence, 'these transitions from the general Ameiridae pattern to Fontinalicaridinae-kind are a feasible series of transformations' in phylogeny (see Ranga Reddy et al. 2014, p. 817).

(5) Male antennule. Though *Indocaris* and *Remaneicaris* differ from each other by having eight (apomorphy) and nine (plesiomorphy) segments, respectively, both

of them share a coiled type of antennule – a character typical of Fontinalicaridinae. The latter condition must be considered plesiomorphic because it occurs in the out-group Ameiridae (see also Martínez Arbizu 1994). Interestingly, Schminke (2010) includes *Remaneicaris* in Parastenocaridinae. According to Ranga Reddy et al. (2014, figure 10); the 'pocket-knife type' condition of the antennule in *Himalayacaris* and most other taxa of Parastenocaridinae occurs at the base of the cladogram, thus implying 'the independent loss of this condition in the Fontinalicaridinae, *Remaneicaris* and the *P. tirupatiensis*-group' (p. 815). Incidentally, the morphology of the aesthetasc on segment 5 is species specific. It is large and balloon-like in *I. imbricata*, relatively moderate in size and club-shaped in *I. tirupatiensis*, and large and bilobed in *I. inopinata*. According to Galassi and De Laurentiis (2004), the aesthetasc morphology might be an adaptive feature to groundwater life in stygobionts that entered groundwater early in evolution of the family. A close look at the parastenocaridid species of the Indian subcontinent, in which the male antennule description is available, shows that the aforesaid aesthetasc is generally long and slender in the hyporheic species whereas it is large and short in the phreatic species. In the hyporheic *Parastenocaris mahanadi* Ranga Reddy and Defaye, 2007, it is longest in the family as a whole, being 90% of the length of the same appendage (see Ranga Reddy and Defaye 2007).

(6) Male leg 1. Whereas an inner modified armature element is present on the male leg 1 basis of all *Indocaris* species, none such occurs in all *Remaneicaris* species barring *R. ignotus* (Dussart, 1983). While this feature is non-existent in Fontinalicaridinae, it may occur in Parastenocaridinae (see Schminke 2010). This element could be present in males and/or females of certain species belonging to different phylogenetic lineages (Galassi and De Laurentiis 2004), but still within Parastenocaridinae. Cottarelli et al. (2006) discussed this character and its states further, listing relevant examples of the *Parastenocaris* species. According to Corgosinho et al. (2007), the inner element together with a row of spinules on the inner margin of leg 1 endopod is a plesiomorphy of Parastenocarididae.

Generally, the exopod, especially of the males, tends to bend inwards to varying degrees in different lineages of Parastenocarididae. In all three species of *Indocaris* gen. nov., but not in *Remaneicaris* (exception: *Remaneicaris tridactyla* Corgosinho, Martínez Arbizu, and Dos Santos-Silva, 2007, etc.), the spectacular inward bending of the entire ramus, or at least its distal two segments, calls for some reflection on its possible function. Although no involvement of the male leg 1 exopod in the mating behaviour of parastenocaridids (e.g. Glatzel and Schminke 1996) has hitherto been documented in the literature, it would be worthwhile investigating its functional significance in future studies. Also, the leg 1 endopod is longer than the exopod not only in *Indocaris* and *Remaneicaris* but also in different lineages (see Bruno and Cottarelli 2015, p. 21). This character is obviously plesiomorphic, because it occurs in the outgroup Ameiridae.

(7) Male leg 2. It has already been pointed out by Corgosinho, Ranga Reddy, et al. (2012, p. 68), based solely on the original account of the male of *I. tirupatiensis* comb. nov., that the exopodal segments of legs 2 and 4, which are ornamented

with a row of spinules each outer margin, is a point of similarity with *Remaneicaris*. Now, this observation is further supported by what obtains in *I. imbricata* sp. nov. as well as *I. inopinata* sp. nov. Within *Indocaris* gen. nov., the shape of the endopod together with its apical seta is also highly diagnostic of *I. tirupatiensis* comb. nov.

(8) Male leg 3. In *I. tirupatiensis* comb. nov., the endopod, though small, is distinct, bearing a seta, but it is represented only by a seta in both new species. According to Corgosinho et al. (2007), the presence of a distinct endopod on this appendage is one of the plesiomorphies of Parastenocarididae, thus supporting the basal position of *Remaneicaris* in the family. On the contrary, the phylogenetic analysis carried out by Ranga Reddy et al. (2014, p. 817) shows its apomorphic nature. And another phylogenetically informative character, which is common to *I. tirupatiensis* comb. nov., *I. inopinata* sp. nov. and *Remaneicaris* species, is the fusion of the exopodal apophysis with the terminal seta. The fusion of the terminal seta with apophysis is an apomorphy in Parastenocaridinae. (Schminke 2010, p. 347). On the other hand, in *I. imbricata* sp. nov., though the terminal seta is fused to the apophysis, its remnant still exists as a small lobe. A more or less similar condition can be seen in *Himalayacaris* in which the remnant of the terminal seta/spine appears as a modified hyaline structure, which is apparently an autapomorphy of the species.

(9) Female leg 3 endopod. This ramus with its terminal seta fused to it is generally long and spiniform in Parastenocaridinae, representing the plesiomorphic condition as in both *Indocaris* and *Remaneicaris*. In the type and only species of *Himalayacaris*, a remnant of the terminal seta is present. Fontinalicaridinae, on the contrary, shows its apomorphic condition because the ramus becomes short, carrying spinules terminally and subterminally, but no seta. *I. imbricata* sp. nov. displays a unique condition in which the ramus is greatly reduced to a small stub-like structure, having smooth, blunt end.

(10) Male leg 4. The overall morphology of this appendage in *Indocaris* gen. nov. must be said to be to have a sister-group relationship with that of *Remaneicaris*, though the endopod in the latter is distinctly large, 'leaf-shaped' and covered with numerous spinules all over, sometimes along the lateral margins, etc., in accordance with the existence of its several 'phyletic subunits' (see Corgosinho and Martínez Arbizu 2005). On the other hand, the number of spinules in *Indocaris* is reduced to three or four, and they are located at about the midlength of the outer margin of the ramus. The spinules at the base of the endopod are remarkably slender in *Remaneicaris* in comparison to their significant transformation in both their size and number in *Indocaris* (see Discussion).

(11) Leg 5. The absence of an intercoxal sclerite supports the monophyletic condition of the clade formed by *Remaneicaris, Himalayacaris* and *Indocaris* in both cladograms discussed in Ranga Reddy et al. (2014, p. 814), and this character is in the ground pattern of *Remaneicaris* (Corgosinho et al. 2007, p. 26). A close affinity of these taxa can also be seen in the overall form and size of leg 5 and the arrangement of its armature elements. Leg 5 in the Fontinalicaridinae is much larger and triangular in both sexes, extending back well beyond its own somite.

It is interesting to note that leg 5 is small in most groundwater Ameiridae, which is a reasonable sister-group of Parastenocarididae. So, we consider the short leg 5 plesiomorphic for a vast majority of Parastenocarididae. Schminke (2008, 2009) underscores the large fifth legs as diagnostic of all the then-known 18 species of *Kinnecaris* Jakobi, 1972 (three more species have been added to this genus by Bruno and Cottarelli 2015) and four species of *Monodicaris* Schminke, 2009. Hence, Ranga Reddy et al. (2014, p. 816) treat this character as 'homoplasic, appearing independently in Fontinalicaridinae and defining this subfamily as a synapomorphy, but it is clearly autapomorphic for a few genera and species of Parastenocaridinae'. Though no sexual dimorphism is seen in the ground pattern of *Remaneicaris* (Corgosinho et al. 2007), in the two new *Indocaris* species, for which both sexes are known, the sexual dimorphism, though not of a spectacular kind as in certain *brevipes*-group species, is indeed discernible because the inner margin of leg 5 is spinulose in the male but smooth in the female, and the spiniform process at the inner distal corner is longer in the female than in the male. Intriguingly, the male leg 5 in *I. tirupatiensis* comb. nov. is a large, undifferentiated and subconical plate, protruding apically to a point, and extending beyond the limit of its own somite. Now, it is clear from the foregoing phylogenetic considerations that this character state is autapomorphic for this species. In the two new congeners, on the other hand, the inner distal corner is produced into a weak or somewhat strong spiniform process – a typical character state in a majority of parastenocaridids. Similarly, the strongly developed and widely spaced spinules on the inner margin of leg 5 could be another autapomorphic feature of *I. tirupatiensis* comb. nov.; said spinules are generally weak and closely arranged as in the two new species. As for the armature of leg 5, both *Indocaris* and *Remaneicaris* generally have four elements (exception: three elements in *I. imbricata* sp. nov.). However, *Himalayacaris* stands out in the monophyletic entity by having an autapomorphic condition of just two setae.

On the whole, the affinities between *Indocaris* gen. nov. and *Remaneicaris* seem to bear out what has already been asserted by Corgosinho and Martínez Arbizu (2005, p. 161): 'that the sister group of *Remaneicaris* should be found within the former Gondwanaland but outside Neotropis'. *Indocaris* gen. nov. and *Remaneicaris* seem to have derived from a common ancestral group. The morphological interrelationships of *Indocaris* species are briefly outlined in Table 1.

## Ecological and biogeographic remarks

Our observations on the ecological distribution of the Indian parastenocaridid species during the past 15 years or so have confirmed a certain degree of their habitat preference in the groundwater realm. For example, *P. curvispinus, P. gayatri* and *K. godavari* are generally confined to the porous, alluvial aquifers of rivers, but can occasionally appear in the riparian bore wells. *P. curvispinus* and *P. mahanadi* can tolerate brackish conditions as well (Ranga Reddy and Defaye 2007; Totakura and Ranga Reddy 2014). On several occasions, *P. gayatri, P. savita* and *S. sandhya* were found sympatrically in hyporheic habitats where they were heavily preyed

**Table 1.** The principal morphological differences between the males of *Indocaris tirupatiensis* comb. nov., *I. imbricata* gen. nov., sp. nov. and *I. inopinata* gen. nov., sp. nov.

| Characters | *tirupatiensis* | *imbricata* | *inopinata* |
|---|---|---|---|
| **Habitus** | | | |
| Total body length (μm) | 350 | 260–285 | 260–350 |
| Nature of the integument | Smooth | Partially perforated | Smooth |
| Dorsal window on first urosomite | Absent | Present | Present |
| Anal somite ventral ornamentation | 2 pairs of crescentic rows of large spinules | Absent | 1 pair of small ventrolateral spinules |
| **Caudal ramus** | | | |
| Length/width ratio | 4.0 | 2.7–3.0 | 3.3–4.0 |
| **Maxilla** | | | |
| No. of setae on proximal endite | 1 | 2 | 2 |
| **Antennule** | | | |
| Aesthetasc on segment 5 | Relatively moderate in size and club-shaped | Large, balloon-shaped | Large, elongate |
| **Leg 1 basis** | | | |
| Shape of inner armature element | Straight | Incurved | Incurved |
| **Leg 2 endopod** | | | |
| Shape and armature/ ornamentation | Spatulate, only with 1 seta | Rod-like, spinular row and 1 seta | Cylindrical, spinular row and 1 seta |
| **Leg 3** | | | |
| Endopod | 1-segmented | Represented by a seta | Represented by a seta |
| Apophysis + apical seta | Completely fused | Apical seta as lobe | Completely fused |
| **Leg 4** | | | |
| No. of spinules at base of endopod | 5–6 | 5 | 5 |
| Length of endopod vs exopod-1 | 0.8× | 1.1× | ≈ |
| Proximal half of endopod | Bulbous | Moderately dilated | Bulbous |
| Ornamentation of endopod | 3 spinules | 2 or 3 spinules | 3 or 4 spinules |
| **Leg 5** | | | |
| Shape and size | Subconical, large | Trapezoidal, small | Trapezoidal, small |
| No. of armature elements | 4 | 3 | 4 |
| Size of inner spinules | Large | Small | Small |



upon by the juveniles of a commercially important gobioid fish, *Glossogobius giuris* (Hamilton, 1822), as evidenced by gut content analysis of the fish juveniles (see Ranga Reddy 2001). While *P. kotumsarensis*, *P. edakkal* and *Proserpinicaris corgosinhoi* prefer karstic cave pools, *Proserpinicaris karanovici* and all the three *Indocaris* species are restricted to the phreatic waters of bore wells. The remaining nine species including the Sri Lankan species have hitherto been known only from interstitial hyporheic habitats. Not surprisingly, *P. curvispinus* is most common in the hyporheic habitats of both east and west coastal belts of southern India (Ranga Reddy and Defaye 2007).

The overall ecological distribution pattern of the Indian of stygobionts calls into question the general perception of short-range endemism. Certain species such as *P. curvispinus, P. mahanadi* and a parabathynellid, *Habrobathynella schminkei* Ranga Reddy 2004b (see Ranga Reddy and Totakura 2010), have a remarkably wide-range distribution in peninsular India that seems to run counter to the generally accepted concept of short-range endemism of Harvey (2002), Schram (2008), Eberhard et al. (2009), Karanovic and Cooper (2011a), and several other stygobiologists. These and

some bathynellacean taxa exceeding Harvey's (2002) nominal distribution range of less than 10,000 km$^2$ should prompt much deeper morphological as well as molecular studies to determine whether they are sibling species at all.

The hitherto-known parastenocaridid taxa of the Indian subcontinent can be assigned to three biogeographic lineages: Gondwanan, tropical Asian and Palearctic. The Gondwanan heritage is expressed by four genera: *Kinnecaris* Jakobi, 1972, *Siolicaris* Jakobi, 1972 and *Himalayacaris* Ranga Reddy, Totakura and Corgosinho, 2014, with a single species each, and *Indocaris* gen. nov., with three species. The Gondwanan heritage among stygobiotic copepods and bathynellaceans of peninsular India has been briefly dealt with by Ranga Reddy (2011b). Now, some additional remarks are made based on subsequent findings. Clearly, the observed Gondwanan affinity mostly applies to the supraspecific taxa but not to the species, which are endemic, having evolved on the Indian plate following its separation from all the Gondwana land masses. The genus *Kinnecaris* had so far been reported from all along the eastern side of Africa from Ethiopia down to South Africa, and also in West Africa, Madagascar, Western Australia, Papua New Guinea and the Oriental sensu Morrone (2002) (see Schminke 2008; Ranga Reddy and Schminke 2009; Karanovic and Cooper 2011a). Recently, Bruno and Cottarelli (2015) provided a novel dimension to the biogeography of this genus by describing two new *Kinnecaris* species from Turkey – the first record from the Palearctic Region, but, biogeographically, the present-day Anatolia is not completely divorced from the tectonic history of the Gondwana (see Çinku et al. 2011). According to Karanovic and Cooper (2011a) and Bruno and Cottarelli (2015), the Australian and Anatolian *Kinnecaris* species probably represent two phyletic units within the monophyletic *Kinnecaris*. The lone Indian *K. godavari* seems to be a typical Gondwanan derivative, closely fulfilling all the original generic criteria proposed by Schminke (2008). Similarly, *Siolicaris sandhya* also has clear-cut Gondwanan heritage but with certain distinct apomorphic features of its own, and its valid congeners are distributed only in northern South America (Amazonian region) (see Corgosinho, Ranga Reddy, et al. 2012). The monophyletic unity of the Indian *Himalayacaris* and *Indocaris* gen. nov. with the Neotropical *Remaneicaris* within Parastenocarididae has already been discussed. *Himalayacaris* with its apparent Gondwanan affinities is biogeographically interesting in that it is confined to the Garhwal Lesser Himalaya of the Himalayan mountain system, whereas most of the presently known typical Gondwanan derivatives occur in peninsular India, 'which *per se* is biogeographically *India vera*, the largest and the oldest region of the original floras and faunas of India' (Mani 1974, p. 700). According to Mani (1974, p. 666), the Himalaya is known to be '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'. No further discussion is necessary on the obvious Gondwanan affinities of *Indocaris* gen. nov.

According to Karanovic and Lee (2012), the *brevipes* group originated not in 'tropical Asia', as hypothesised by Reid (1995), but 'somewhere in the Gondwanaland in the rift valley between India and Western Australia, just before

the separation of the Indian plate'. The available records show that all these species have endemic distribution within the Indian plate. It is noteworthy that of the seven Indian species of the *brevipes* group, *P. sutlej* alone occurs in a somewhat subtropical belt of Western Himalaya.

The genus *Proserpinicaris* Jakobi 1972, sensu Karanovic, Cho and Lee, 2012, presently containing 20 species, of which four are from Asia (one from Japan and three from South Korea), is Palearctic in distribution, with its centre of diversity lying in southern Europe (Karanovic et al. 2012). *P. corgosinhoi* and *P. karanovici* are the only Palearctic elements so far known from the Indian subcontinent. Incidentally, Ranga Reddy et al. (2015) have reported a typical Palearctic bathynellacean taxon from northeastern India. To understand the biogeographic complexity of this part of Asia in relation to the Palearctic elements, it is pertinent to note that

> the continental blocks of the region [South East Asia] were derived from the margin of eastern Gondwana as three successive continental strips or collages of continental blocks that separated in the Devonian, Early Permian and Triassic-Jurassic and which then assembled during the Late Palaeozoic to Cenozoic to form present day East and SE Asia. (Metcalfe 2011, p. 7)

In this scenario, to trace the migratory route of the Indian Palearctic taxa is not easy. However, the literature shows that certain 'Palearctic forms that differentiated in the Mediterranean sub-region, in southwest Asia, southeast Europe, and North Africa, and in the Turkmenian subregion, Middle Asia, entered India from the northwest and have sparsely colonized the hills of the South India' (Mani 1974, p. 635). All in all, much critical scrutiny is essential for deciphering the phylogenetic and biogeographic relationships within the Parastenocarididae as a whole.

Despite the fact that the Sri Lankan species are incompletely characterised, a simple, undated key to identify all the heretofore-known 22 nominal species of the Indian subcontinent is given below.

## Key to parastenocaridid species of the Indian subcontinent

1. Male leg 4 coxa with massive, conical, plate-like structure at proximal inner corner (genus *Himalayacaris* Ranga Reddy et al. 2014) ..... *H. alaknanda* Ranga Reddy et al. 2014
   None such ..... 2

2. Urosomites 4 and 5 each with a pair of lateroventral integumental windows; leg 5 distinctly projects outwards (genus *Kinnecaris* Jakobi 1972)..... *K. godavari* Ranga Reddy and Schminke, 2009
   Urosomites 2– or 3–5 generally with one dorsal integumental window each; leg 5 adheres to genital somite ..... 3

3. Lateral group of caudal setae (I–III) remarkably proximal in position (genus *Siolicaris* Jakobi 1972)..... *S. sandhya* Ranga Reddy, 2001
   Same setae away from the proximal end of caudal ramus ..... 4

4. Male leg 4 with hyaline structure between exopod and endopod (genus *Proserpinicaris* Jakobi 1972); caudal ramus 1.2 times as long as wide..... ..... *P. corgosinhoi* Totakura et al. 2014
Same; caudal ramus at least 2.5 times as long as wide..... ..... *P. karanovici* Totakura et al. 2014

5. Male leg 4 basis with five or six large, imbricate, petaloid spinules arranged as a semi-whorl at the insertion of endopod (genus *Indocaris* gen. nov.); male anal somite ornamented with two pairs of crescentic rows of large spinules on ventral surface..... *I. tirupatiensis* (Ranga Reddy, 2011a) comb. nov.
Same genus: male anal somite without such ventral ornamentation..... 6

6. Male leg 5 inner spiniform structure strong and long..... *I. inopinata* sp. nov.
The same slender and short..... *I. imbricata* sp. nov.

7. Male leg 4 with characteristic endopodal complex, i.e. basis with 1–3 claws medially of endopod, and also sometimes with large sclerotised plate (*brevipes* group; *Parastenocaris* s. str.)..... 8
Male leg 4 without endopodal complex (*Parastenocaris* s. l.)..... 15

8. Male leg 5 produced into spiniform process at inner distal corner..... 9
Male leg 5 without spiniform process at distal corner..... 12

9. Caudal ramus with unguiform process at inner distal corner in both sexes; male leg 3 exopod without any bulge on outer margin..... ..... *P. muvattupuzha* Ranga Reddy and Defaye, 2009
Caudal ramus without such process; male leg 3 exopod with triangular bulge at about midlength of outer margin ..... *P. brincki* Enckell, 1970

10. Male leg 3 exopod with distinct tubercular bulge at proximal outer corner; antennular segment 7 without any apophysis..... *P. sutlej* Ranga Reddy, 2011c
Same ramus without such bulge; antennular segment 7 with short, blunt apophysis ..... *P. kotumsarensis* Ranga Reddy and Defaye, 2009

11. Male leg 5 with three setae; inner distal margin expanded, blunt, triangular ..... ..... *P. edakkal* Totakura et al. 2014
Same with four setae; inner distal margin narrow, acuminate spinous process. ..... *P. irenae* Enckell, 1970

12. Male leg 4 endopod with a distal row of four long spinules – *P. singhalensis* Enckell, 1970
Male leg 4 endopod without any distal spinular row..... *P. lanceolata* Enckell, 1970

13. Anal somite with a pair of dorso-lateral rows of spinules; male leg 3 first exopodal segment without dentate process on inner margin ..... ..... *P. noodti* Enckell, 1970
Anal somite without such spinules; male leg 3 first exopodal segment has large dentate process on inner margin..... *P. gayatri* Ranga Reddy, 2001

14. Body integument heavily chitinised and perforated; male leg 3 apophysis longer than thumb ..... *P. gundlakamma* Ranga Reddy, 2011c
Body integument poorly chitinised; male leg 3 apophysis shorter than thumb. ..... *P. savita* Ranga Reddy, 2001

15. Caudal ramus 1.6–2.6 times as long as wide; male leg 4 endopod slender, long, hook-like with distal third sharply bending inwards *P. curvispinus* Enckell, 1970
Caudal ramus 4.0–4.6 times as long as wide; male leg 4 endopod short, thick, leaf-like or so with proximal and distal spinules..... ..... *P. mahanadi* Ranga Reddy and Defaye, 2007



## Acknowledgements

We thank Mr. K. Yesubabu for providing some field assistance. This manuscript greatly benefitted from the constructive comments offered by two anonymous reviewers.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This study was supported by the Ministry of Environment, Forests and Climate Change, and the Department of Science and Technology, Ministry of Science and Technology, Government of India, New Delhi, under the Major Research Projects 22018/08/2010-CS (Tax) and SR/SO/AS-21/2011, respectively.

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