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A NEW GENUS AND SPECIES OF THE FAMILY DIOSACCIDAE (COPEPODA: HARPACTICOIDA) FROM THE GROUNDWATERS OF INDIA

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ABSTRACT

The recent renewed interest in the Indian stygofauna has led to the discovery of another interesting copepod representative, from the almost exclusively marine family Diosaccidae Sars, 1906. *Neomiscegenus* n. gen. and *Neomiscegenus indicus* n. sp., from the subterranean freshwaters of the Krishna River at Vijayawada, Andhra Pradesh, are described. The new genus belongs to that evolutionary line of Diosaccidae that encompasses the genera *Amphiascoides* Nicholls, 1941; *Paramphiascella* Lang, 1948; *Paramphiascoides* Wells, 1967; and *Miscegenus* Wells, Hicks, and Coull, 1982. The genus *Miscegenus* has the highest number of synapomorphies with *Neomiscegenus*, including the shape of the caudal rami and the armature formula of the swimming legs. A peculiar shape of the genital field in the female and the armature of the antennal exopod in both sexes are the most important autapomorphies of the new genus, while the fine structure of the sexually dimorphic second leg in the male is probably plesiomorphic. The phylogenetic position of the new genus is briefly discussed.

In a global context, the stygofauna of the Indian subcontinent is very poorly known (Marmonier *et al.*, 1993; Ranga Reddy, 2002b, in press b), with only a few records until the mid-1980's (Botosaneanu, 1986). As far as the freshwater subterranean copepods are concerned (Lescher-Moutoué, 1986; Rouch, 1986), by that time only six species of the genus *Parastenocaris* Kessler, 1913, from Sri Lanka (Enckell, 1970) and one species of the genus *Elaphoidella* Chappuis, 1928, from the mainland (Chappuis, 1954) had been described. Four cyclopoids, reported by Pesce and Pace (1984) from several Indian freshwater wells, are actually all stygophiles (or even stygoxenes), not stygobites. The recent renewed interest in the Indian stygofauna has revealed a number of very interesting subterranean copepods (Ranga Reddy, 2001; Karanovic and Pesce, 2001; Karanovic and Ranga Reddy, in press), as well as some ancient bathynellids (Ranga Reddy, 2002a; in press a). The latter probably emerged from their marine ancestors as far back as the Permian (Schminke, 1981; Pandourski and Ognjanova, 2001), i.e., just after the Permo-Carboniferous glaciation, which occurred when India formed part of the Gondwana supercontinent (Frakes, 1999; Playford, 2003). In this paper, another freshwater stygobiont with clear marine ancestry is described as a new genus in the harpacticoid family Diosaccidae Sars, 1906.

The family Diosaccidae presently encompasses about 388 species and subspecies, classified into 43 valid genera (Lang, 1948; Bodin, 1997; Mu and Gee, 2000). They are predominantly marine free-living forms, with only a few species reported as commensals or semiparasites on lobsters (Humes, 1953). Two large genera, *Schizopera* Sars, 1905, and *Stenhelia* Boeck, 1864, represent almost 35% of the whole family, while even 22 genera (more than 50%) have three or fewer species, and 12 genera (28%) are monospecific. Obviously, this is not a young and aggressive family, but rather just a remnant of the former, and probably very distant, flourishing. That may be one of the reasons for their relatively unsuccessful colonization of the freshwater habitats, although the genus *Schizopera* does have a number of freshwater forms, with a small species flock of about 10 species in the ancient Lake Tanganyika (Boxshall and Jaume, 2000). But even those representatives found in inland continental habitats prefer waters of increased salinity (Karanovic, 2004). However, because the stygal component of the freshwater copepod fauna is practically unknown in many parts of the world, and especially in the former parts of

Gondwana, it is very hard to make even the most general assumption about the freshwater colonizations. The new genus described here, as well as another one described earlier (Karanovic and Pesce, 2001) from the almost exclusively marine family Ectinosomatidae Sars, 1904, makes one just wonder what the Indian copepod stygofauna looks like. One of the implications of this finding is the beginning of our realization that the colonization of the subterranean freshwater habitats may have a very different history in parts of the former Gondwana from that in the Northern Hemisphere.

Materials and Methods

The sample was collected from the subterranean passages flowing into the River Krishna near Vijayawada from the adjacent, soaked, agricultural land. About a week before sampling, an abnormal flood occurred in the river, inundating the low-lying areas of southern bank. The study area and the recorded microfauna were described by Ranga Reddy (2001). A plankton net (mesh size 70 μm) was held against the groundwater runoff for about 30 minutes. The material was preserved in 10% formaldehyde solution, and the copepods were later separated with a dissecting microscope and transfered to 70% ethanol. Specimens were dissected in Fauré's medium, which was prepared following the procedure discussed by Stock and von Vaupel Klein (1996). Dissected appendages were covered with a coverslip. For the urosome or the whole animal, two human hairs were mounted between the slide and coverslip, so the parts could not be compressed. By moving the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making possible the observation of morphological details. During the examination, water slowly evaporated, and appendages or the whole urosome eventually remained in completely dry Fauré's medium. All drawings were prepared using a drawing attachment (tube) on a Leica DMLS brightfield compound microscope, with C-PLAN achromatic objectives (40×/0.65; 63×/0.75 and 100×/1.25 oil). Morphological terminology follows Huys and Boxshall (1991), except for the swimming legs armature formula, where a simplified version is used. The material is deposited in the Western Australian Museum, Perth (WAM). The new species was never found in the core samples collected during 1998–2001 in the riverbed.

Results

Order: Harpacticoida Sars, 1903
Family: Diosaccidae Sars, 1906
Neomiscegenus, n. gen.

Diagnosis.—Small Diosaccidae with fusiform habitus. Female genital double-somite with rigid internal sclerotized ridge; genital complex with single large copulatory pore and without epicopulatory bulb, with short copulatory duct and 2 small, reniform, seminal receptacles. Caudal rami cylindrical, more than 1.5 times as long as wide, with posterior margins terminating ventrally in acuminate lappets; ancestral proximal lateral seta inserted ventrally at midlength of ramus; dorsal seta inserted medially, close to inner margin. Female antennula about 1.5 times as long as rostrum and clearly 8-segmented. Antenna with allobasis and 3-segmented exopod; second exopodal segment unarmed, third one armed with 1 apical and 1 lateral seta. Mandibula with 1-segmented endopod and exopod; exopod with 2 lateral and 2 apical setae. Maxillula also with 1-segmented endopod and exopod; endopod armed with 1 lateral and 3 apical setae. Maxilla with 2, 2, and 3 setae on syncoxal proximal, middle, and distal endites respectively. Maxilliped with only 2 setae at distal inner corner of basis. All swimming legs with 3-segmented exopods and endopods; first swimming leg with first endopodal segment half as long as exopod; female swimming leg armature formula same as in the genera *Amphiascoides*, *Paramphiascella*, *Paramphiascoides*, and *Miscegenus*. Female fifth leg with 5 strong armature elements on baseoendopod and 5 elements on exopod: middle one slender, setiform, and apically inserted, others spiniform. Female sixth leg with 2 setae; outer one stouter and plumose. Male with sexually dimorphic pore on third exopodal segment of third leg and with transformed second and third segments on second leg: ancestral outer apical seta on third segment transformed into serpentine, smooth and strong element, with swollen distal end and 2 characteristic tips on it.

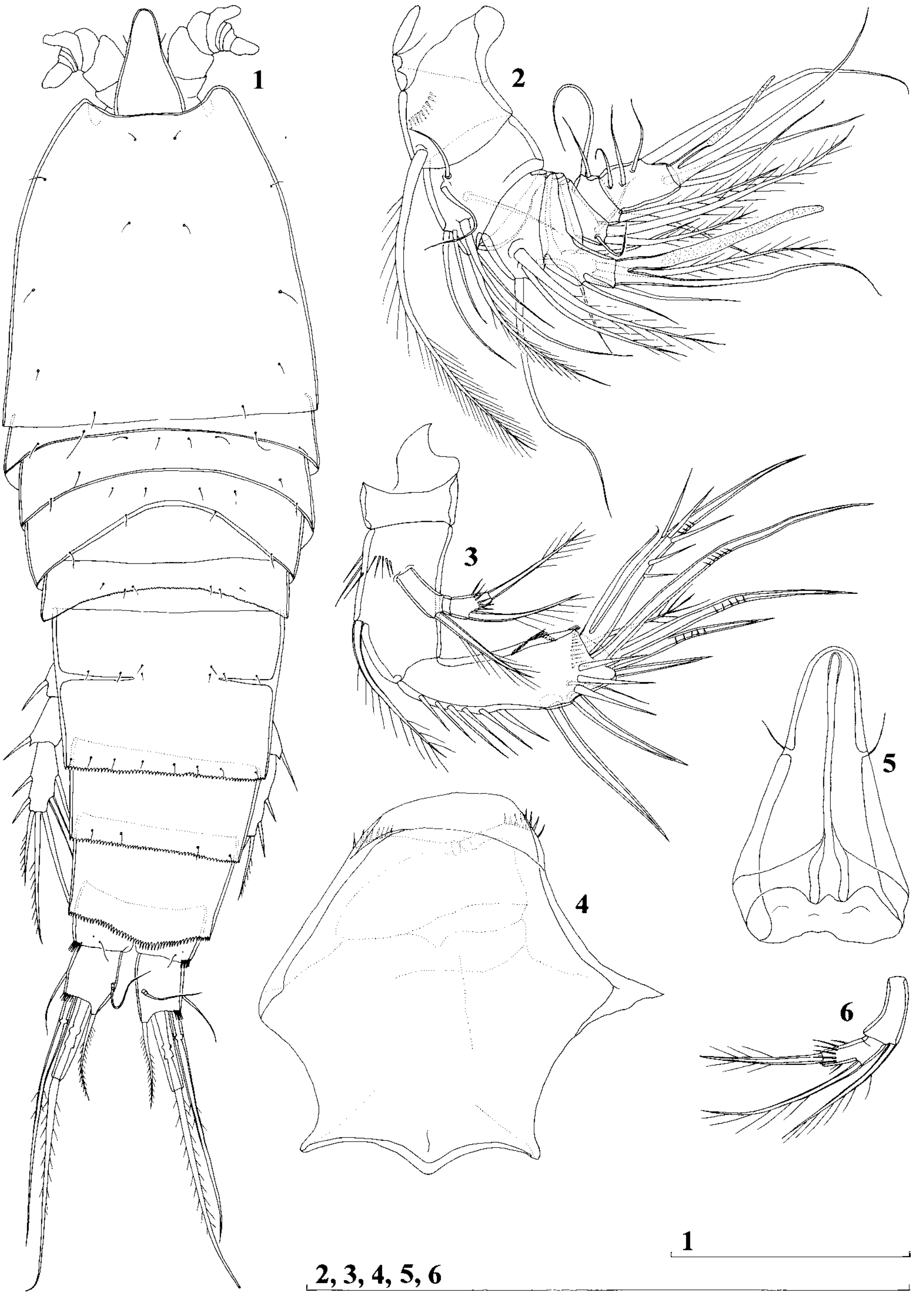
Type and Only Species.—*Neomiscegenus indicus*, n. sp.

Etymology.—The generic name is composed of the genus name *Miscegenus*, which is morphologically closest to the new genus, and the Greek prefix "neo" (meaning: new). Gender masculine.

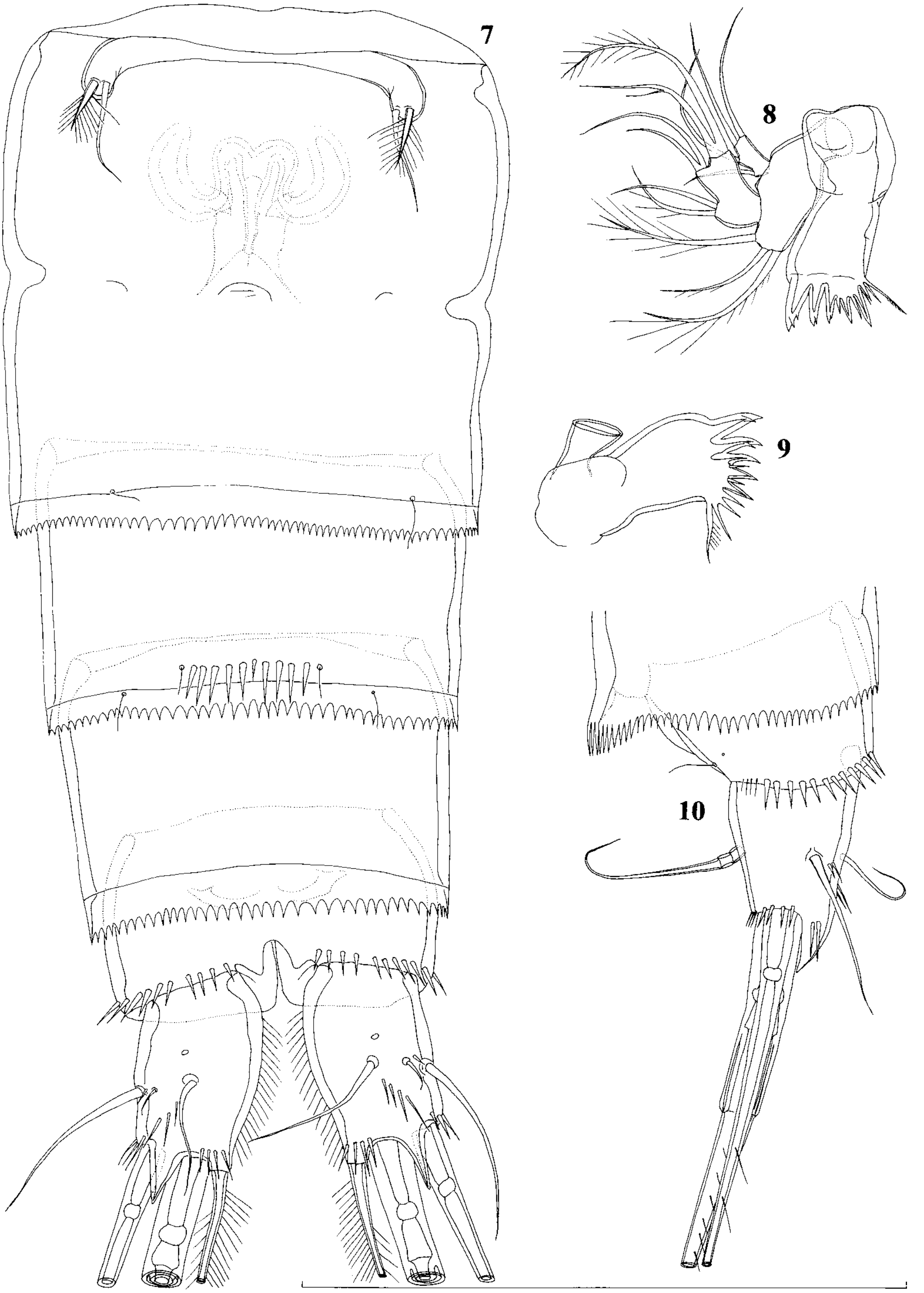
Neomiscegenus indicus, n. sp.
Figs. 1–29

Material Examined.—Holotype: Female (WAM C28608) - India, Andhra Pradesh, Krishna River at Vijayawada, groundwater runoff on the southern bank, 24 October 1998, *leg*. Y. Ranga Reddy, 16°31′N 80°40′E: dissected on 2 slides.

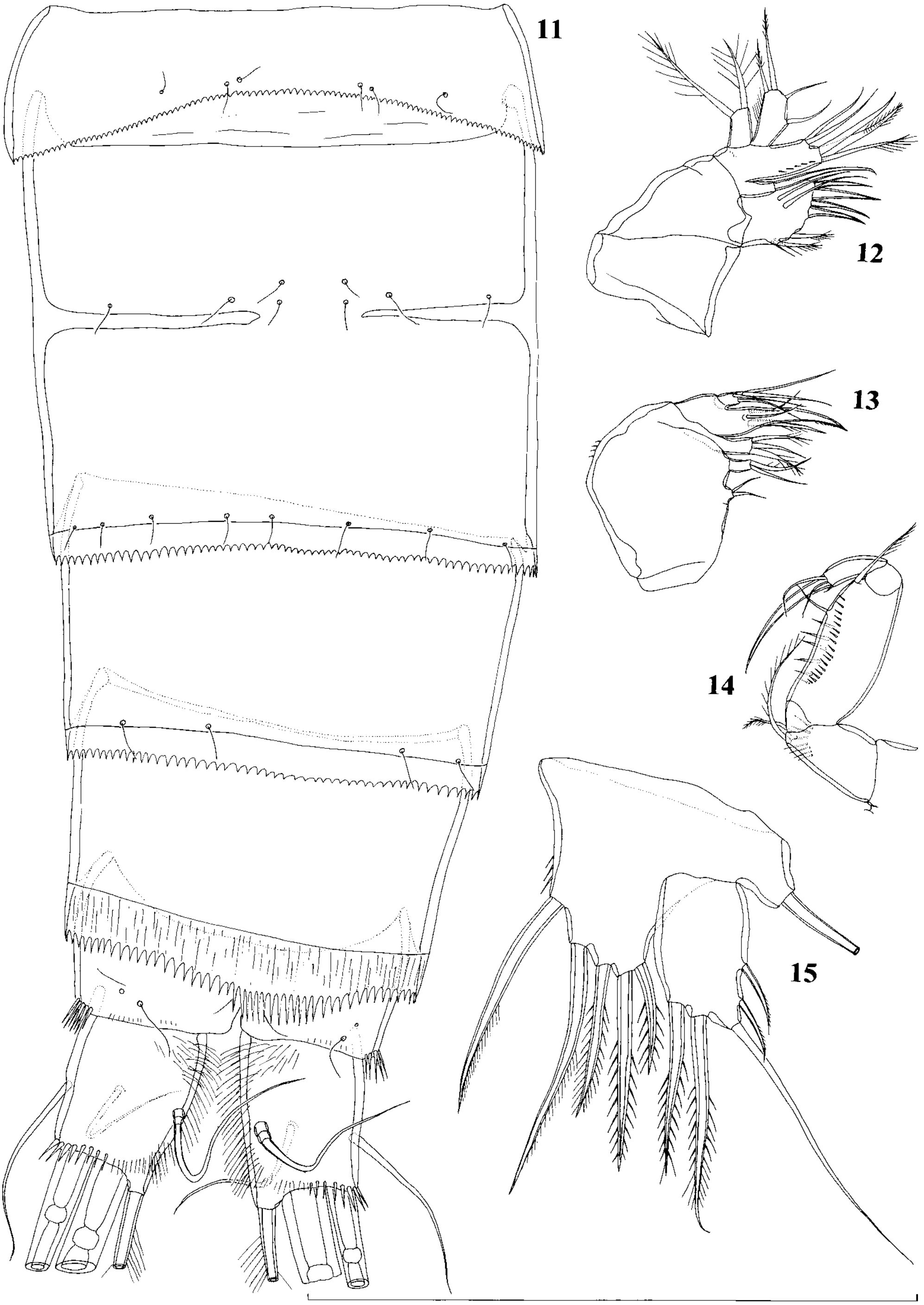
Allotype: Male (WAM C28609) - India, Andhra Pradesh, Krishna River at Vijayawada, groundwater runoff on the southern bank, 24 October 1998, leg. Y. Ranga Reddy, 16°31′N 80°40′E: dissected on 1 slide.



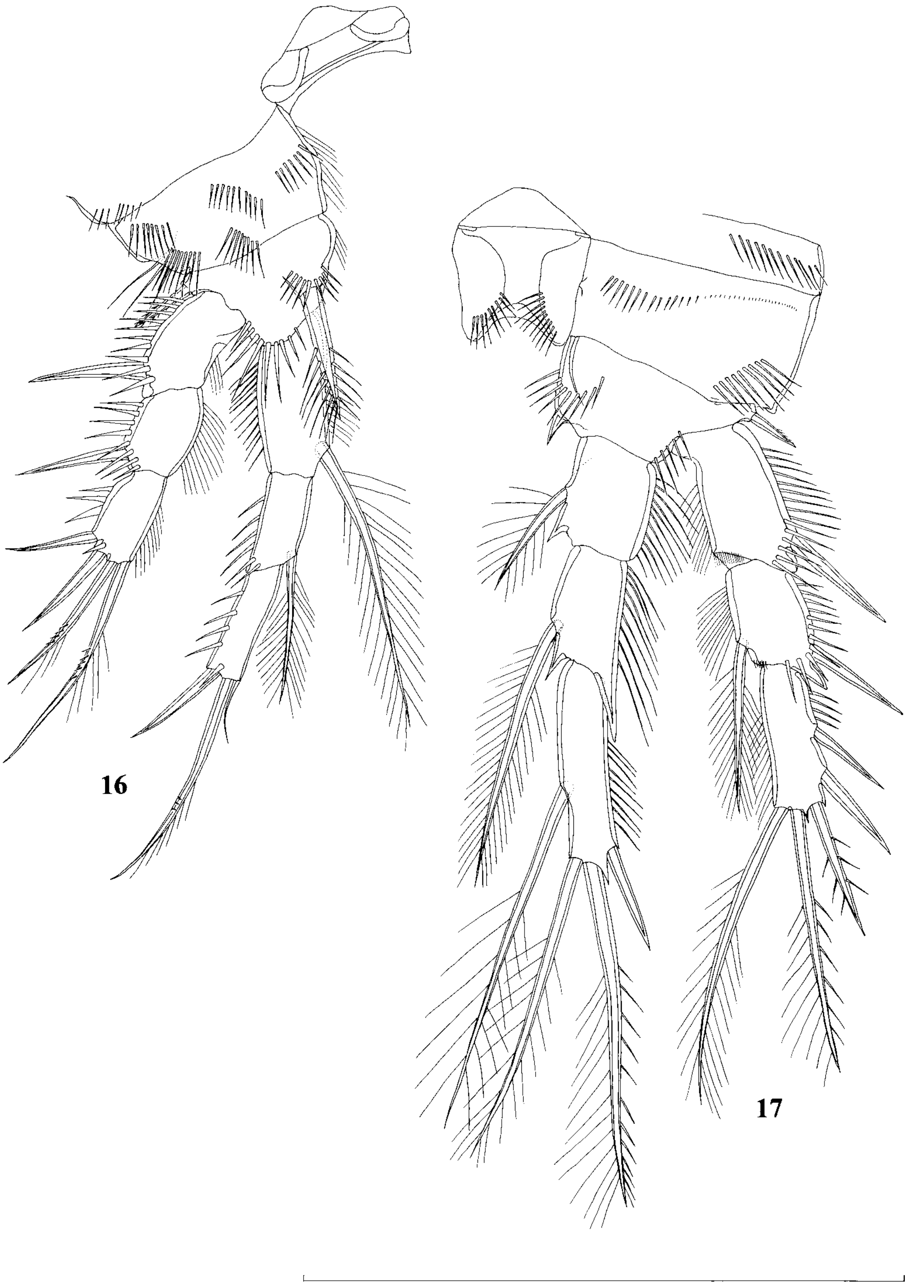
Figs. 1–6. *Neomiscegenus indicus*, n. gen., n. sp., holotype (female): 1 - habitus, dorsal view; 2 - antennula; 3 - left antenna; 4 - labrum; 5 - rostrum; 6 - exopod of right antenna. Scales = 0.1 mm.



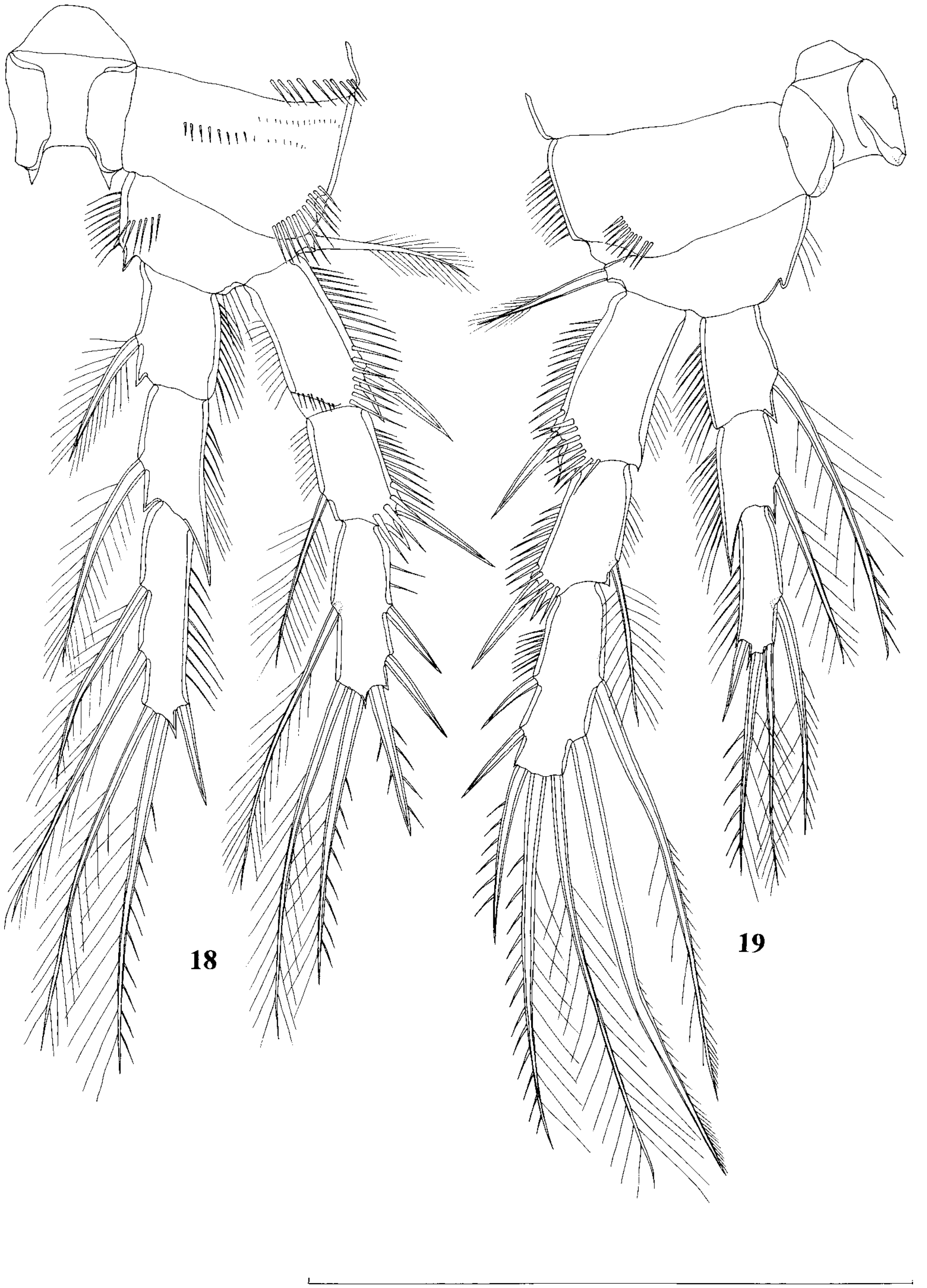
Figs. 7–10. *Neomiscegenus indicus*, n. gen., n. sp., holotype (female): 7 - abdomen, ventral view; 8 - mandibula; 9 - coxa of mandibula; 10 - anal somite and right caudal ramus, lateral view. Scale = 0.1 mm.



Figs. 11–15. *Neomiscegenus indicus*, n. gen., n. sp., holotype (female): 11 - urosome, dorsal view; 12 - maxillula; 13 - maxilla; 14 - maxilliped; 15 - fifth leg. Scale = 0.1 mm.

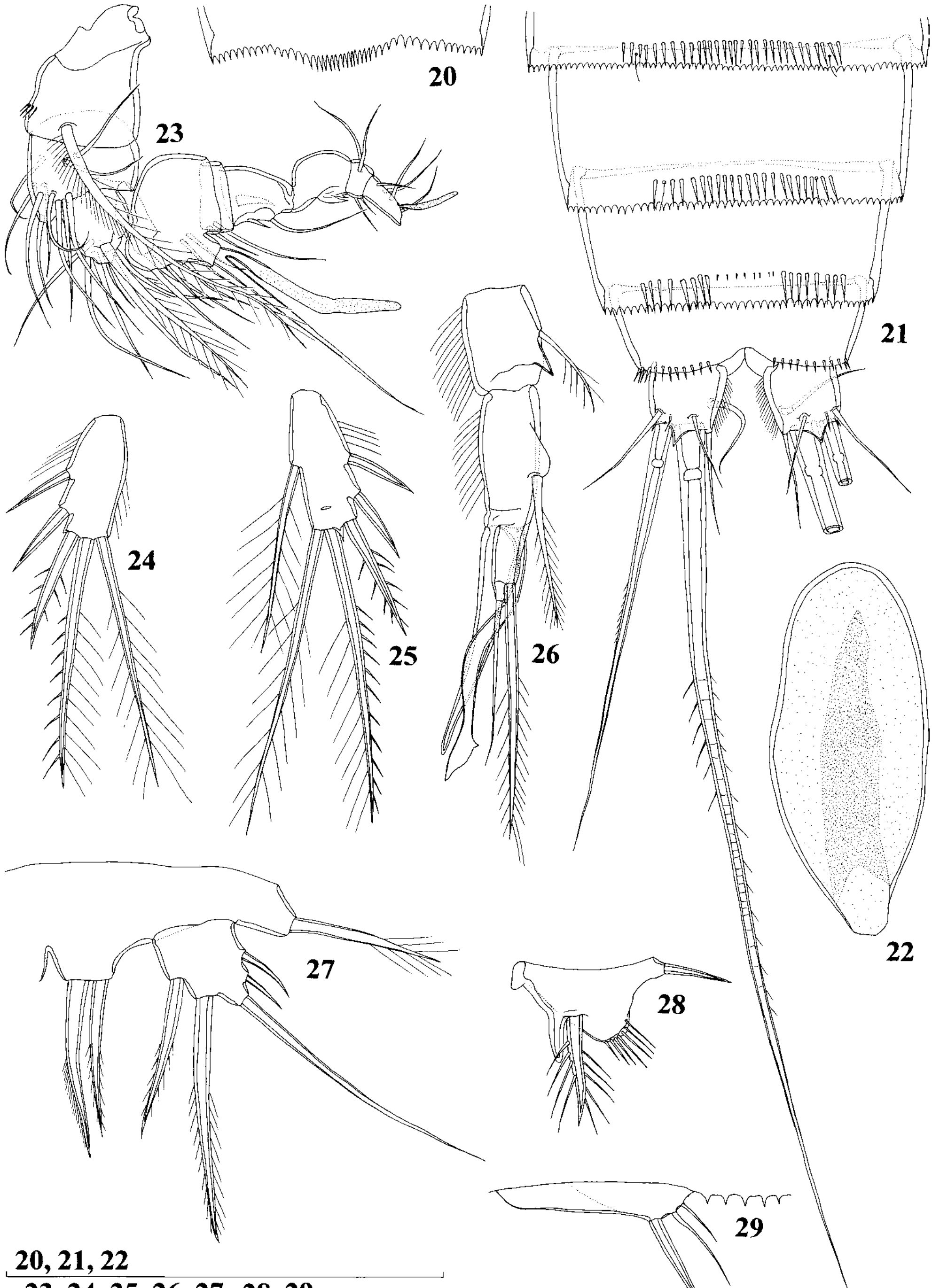


Figs. 16–17. *Neomiscegenus indicus*, n. gen., n. sp., holotype (female): 16 - first swimming leg; 17 - second swimming leg. Scale = 0.1 mm.



Figs. 18–19. *Neomiscegenus indicus*, n. gen., n. sp., holotype (female): 18 - third swimming leg; 19 - fourth swimming leg. Scale = 0.1 mm.

Description.—Female (holotype): Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 0.417 mm. Preserved specimen yellowish. Nauplius eye not visible. Habitus (Fig. 1) fusiform but relatively slender, compressed dorsoventrally, without distinct demarcation between prosome and urosome; prosome/urosome ratio



Figs. 20–29. *Neomiscegenus indicus*, n. gen., n. sp., allotype (male): 20 - pseudoperculum, dorsal view; 21 - abdomen, ventral view; 22 - spermatophore; 23 - antennula; 24 - third exopodal segment of second swimming leg; 25 - third exopodal segment of third swimming leg; 26 - endopod of second swimming leg; 27 - fifth leg; 28 - basis of first swimming leg; 29 - sixth leg. Scales = 0.1 mm.

1.2 and greatest width at second pedigerous (first free) somite. Body length/width ratio about 3.3; cephalothorax 1.36 times as wide as genital double-somite. Free pedigerous somites without particular expansions laterally or dorsally. Integument strongly chitinized, but with smooth surface. Rostrum (Figs. 1, 5) long, reaching distal margin of third antennular segment, linguiform, with blunt tip, about 1.7 times as long as wide and clearly demarcated at base; ornamented with 2 sensilla laterally. Cephalothorax (without rostrum) slightly longer than wide, representing 33% of total body length. Surface of dorsal shield covering cephalothorax with many large sensilla, as well as tergites of 3 free pedigerous somites. Hyaline fringes of all prosomites narrow, smooth. Fifth pedigerous somite (first urosomal) ornamented with 6 dorsal sensilla and with hyaline fringe finely serrated. Genital double-somite (Figs. 7, 11) about as long as wide (ventral view), without subdivision line visible dorsolaterally but with rigid internal sclerotized ridge instead, furnished with 8 large sensilla dorsally (Fig. 11); additionally ornamented with 6 dorsal, 2 ventral, and 2 lateral sensilla near posterior margin; hyaline fringe sharply serrated both ventrally and dorsally. Female genital complex with single large copulatory pore and without epicopulatory bulb; copulatory duct short, cylindrical, rigidly sclerotized; 2 small seminal receptacles reniform, placed inside single large genital aperture; aperture covered by fused and reduced sixth legs (Fig. 7). Third urosomal somite ornamented with 4 dorsal, 4 ventral, and 2 lateral sensilla and with short ventral row of large spinules near posterior margin; fringe sharply serrated both dorsally and ventrally, although ventral teeth larger. Preanal somite without any sensilla or spinules; hind margin clearly bulging posteriorly in dorsal region, forming very sharply serrated pseudoperculum (Fig. 11); hyaline fringe frilled dorsally and serrated both dorsally and ventrally. Anal somite without anal operculum; ornamented with 2 large sensilla and 2 cuticular pores dorsally, as well as with transverse row of large spinules on posterior margin ventrally and laterally (Figs. 7, 11). Anal sinus smooth.

Caudal rami (Figs. 7, 10, 11) cylindrical in dorsal or ventral view, but slightly conical in lateral view, with posterior margins terminating ventrally in narrow acuminate lappets (between middle and outer apical seta), divergent, with space between them being about third of ramus width, and about 1.7 times as long as greatest width (without lappets); ornamented with many hairs along inner margins, 1 ventral cuticular pore each, and 1 setula at base of lateral seta, as well as with posterior row of large spinules and transverse row of several spinules ventrally, between ventral seta and posterior outer corner; armed with 6 setae, 1 ventrally, 1 laterally, 1 dorsally, and 3 apically. Dorsal seta about 1.5 times as long as ramus from dorsal view, inserted at midlength of ramus close to inner margin, biarticulate at base and smooth. Ventral seta (in fact ancestral lateral proximal seta, which moved strongly ventrally) smooth, inserted at middle of ramus and about 0.7 times as long as ramus. Lateral seta (ancestral distal lateral one) also smooth and slightly shorter than ramus, inserted at 3/5 of ramus length. Inner apical seta bipinnate, 1.3 times as long as ramus, arising from small protuberance. Middle apical seta strongest, bipinnate at distal end, with breaking plane, but obviously abnormal (probably damaged during postembryonic development). Outer apical seta without deformities, also with breaking plane, about 2.8 times as long as inner apical seta, smooth or pinnate along very short section (Fig. 1).

Antennula (Fig. 2) 8-segmented, very short, approximately 1.5 times as long as rostrum, with slender aesthetasc on eighth segment and longer and stouter aesthetasc on fourth segment, which exceeding in length the last six segments together; setal formula as follows: 1.9.4.4.1.4.4.7. No seta with articulating base or breaking plane. Seta on first segment, 1 seta on second, 2 on third, 1 on fourth, 2 on sixth, and 1 on seventh segment pinnate; all other setae smooth. Length ratios of antennular segments, from proximal end and measuring medially, 1 : 0.6 : 0.5 : 0.3 : 0.3 : 0.3 : 0.3 : 0.8. First segment ornamented with transverse row of spinules; other segments without any ornamentation visible.

Antenna (Fig. 3) comprising coxa, allobasis, 1-segmented endopod, and 3-segmented exopod. Coxa very short, about twice as wide as long, unornamented. Basis and proximal endopodal segment fused forming allobasis, without original segmentation marked by any surface suture, armed with only 1 strong pinnate seta on anterior margin; ornamented with transverse row of very long spinules between exopod and anterior margin. Single free endopodal segment with 2 surface frills subdistally; lateral armature consisting of 2 spines and 1 small seta; apical armature consisting of 1 slender seta (which bipinnate at distal end), 1 short spine, 4 strong geniculate setae, longest one bearing very long spinules around geniculation and fused basally to another, smooth slender seta; ornamentation consisting of longitudinal row of very large spinules along anterior margin, diagonal row of large spinules between lateral and apical armature elements, and diagonal row of small spinules along subapical frill. First exopodal segment unornamented and about twice as long as wide, armed with 1 pinnate subapical seta on anterior distal corner; second segment minute, unarmed and unornamented (on right antenna even partly fused to first segment (Fig. 6)), about twice as wide as long; third exopodal segment conical, ornamented with transverse row of spinules at 2/3 of its length, armed with 1 bipinnate apical seta and 1 unipinnate lateral seta, which inserted at 1/3 of segment's anterior margin.

Labrum (Fig. 4) large, rigidly sclerotized, with trapeziform free part and ornamented with 1 short row of spinules near each posterior outer corner; cutting edge slightly convex, smooth.

Mandibula (Figs. 8, 9) with broad cutting edge of coxa, armed with many pointed teeth and with 1 unipinnate seta. Basis elongate, about 2.3 times as long as wide, armed with 3 slender pinnate setae along inner margin. Endopod 1-segmented, about 1.7 times as long as wide, armed with 2 lateral and 4 apical setae. Exopod also 1-segmented but much smaller than endopod, about 1.9 times as long as wide, armed with 2 lateral and 2 apical smooth setae. Both lateral setae on endopod inserted at middle, while on exopod 1 lateral seta inserted at 1/3 and other at 2/3 of segment length.

Maxillula (Fig. 12) with large praecoxa, arthrite of which highly mobile, armed apically with 4 smooth strong spines, laterally with 2 smooth slender anterior surface setae, dorsally with 2 short pinnate setae; ornamented dorsally with 2 long spinules. Coxa small, armed with single smooth strong seta on inner margin, not reaching midlength of basis. Basis slightly longer than arthrite of praecoxa, furnished with 3 setae apically (on inner margin) and with 2 setae laterally; ornamented with longitudinal row of small spinules. Endopod 1-segmented, small, about twice as long as wide, armed with 1 lateral and 3 apical setae, median longest. Exopod also 1-segmented, about 0.7 times as long as endopod and 1.7 times as long as wide; armed with 2 plumose apical setae, outer seta being about 1.7 times as long as inner one.

Maxilla (Fig. 13) composed of syncoxa, basis, and very small 2-segmented endopod. Syncoxa ovoid, with 3 endites; proximal and middle endite each armed with 2 short subequal setae, distal endite armed with 3 subequal setae. Basis drawn out into strong claw, armed with 1 strong and 2 slender setae at base. Each endopodal segment armed with 2 slender setae. Ornamentation on maxilla consists of few small spinules on outer margin of syncoxa.

Maxilliped (Fig. 14) prehensile, 4-segmented, composed of coxa, basis, and 2-segmented endopod. Coxa reduced, unornamented. Basis ornamented with arched row of large spinules and armed with 2 pinnate setae at distal inner corner. First endopodal segment about 2.5 times as long as wide, ornamented with 2 longitudinal rows of spinules and armed with 1 lateral smooth and 1 subapical unipinnate seta. Second endopodal segment small, armed with 1 claw-like apical spine and 2 slender and much shorter subapical setae and ornamented with single subapical spinule.

All swimming legs with 3-segmented exopods and endopods (Figs. 16, 17, 18, 19). Swimming legs armature formula as follows (legend: inner/outer spine or seta; inner/terminal/outer):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	0/1	0/2/2	1/0	1/0	1/1/1
Second leg	0/1	1/1	0/2/3	1/0	1/0	1/2/1
Third leg	0/1	1/1	1/2/3	1/0	1/0	2/2/1
Fourth leg	0/1	1/1	2/2/3	1/0	1/0	1/2/1

Intercoxal sclerites of all swimming legs with concave distal margins; sclerite of first leg small and smooth (Fig. 16); sclerite of second leg armed with 2 arched rows of large spinules at distal part (Fig. 17); sclerite of third leg smooth but with pointed outer distal corners (Fig. 18); and sclerite of fourth leg smooth and with rounded outer distal corners (Fig. 19). Praecoxae of all legs with transverse row of spinules, except fourth leg smooth. Coxae ornamented with at least 2 rows of large spinules, unarmed. Basis of first swimming leg armed with 1 strong spine on inner distal corner (reaching 2/3 of first endopodal segment) and 1 moderate spine on outer margin; ornamented with 1 crescentic row of large spinules at base of inner spine, 1 similar row of spinules on distal margin, between endopod and exopod, and with short row of minute spinules on inner margin. Basis of second leg with spine on outer margin; those of third and fourth legs with strong seta. Inner distal corners of basis of second, third and fourth legs each produced distally as sharp, spiniform process; that of second leg being longest. Endopods of first, second, and third legs slightly longer than exopods, endopod of fourth leg considerably shorter than exopod. First endopodal segment of first swimming leg reaching middle of second exopodal segment (Fig. 16), about 2.4 times as long as wide. Second endopodal segments of second, third, and fourth legs each with sharply produced outer distal corner. All exopods and endopods ornamented with spinules on outer margins, and exopods also ornamented with hairs on inner margins. All armature elements very strong, except inner subapical seta on third endopodal segment of first leg.

Fifth leg (Fig. 15) biramous. Baseoendopod with outer basal seta smooth, arising from relatively short setophore. Endopodal lobe subtrapeziform, extending to 2/3 of exopod length, ornamented with few spinules on inner margin and armed with 5 armature elements; 2 inner elements very stout, spiniform, unipinnate and longer than baseoendopod; 3 outer elements also very strong, but bipinnate and shorter than baseoendopod; length ratios of 5 endopodal setae (from inner side) approximately 1 : 1.1 : 0.7 : 0.8 : 0.5. Exopod subquadrangular, about 1.6 times as long as maximum width, unornamented, and armed with 5 armature elements; 2 inner setae subequal, very strong, spiniform and bipinnate; middle seta slender, smooth and longest one; 2 outer setae subequal, very short, curved and unipinnate; length ratio of 5 exopodal setae (from inner side) 1 : 1.3 : 1.7 : 0.4 : 0.4.

Sixth legs (Fig. 7) fused, indistinct, very small cuticular plates, covering single large gonopore, armed with 2 setae each; inner seta 1.8 times as long as outer one, slender and smooth and reaching posterior end of seminal receptacles; outer seta stouter than inner one and plumose.

Male (allotype). Body length, excluding caudal setae, 0.327 mm. Habitus, ornamentation of prosomal somites, rostrum, dorsal ornamentation of urosomal somites, pseudoperculum (Fig. 20), color and nauplius eye similar to female. Genital somite about 2.6 times as wide as long. Single large, completely formed and longitudinally placed spermatophore (Fig. 22) visible inside first 2 urosomal somites. All abdominal somites ventrally with posterior rows of spinules; these rows interrupted only on preanal somite, and first 3 somites with additional pair of sensilla in each row (Fig. 21).

Caudal rami (Fig. 21) much shorter and less ornamented than in female, but with similar ventral acuminate lappets and armature. Inner apical seta smooth and slightly shorter than lateral one; ventral seta inserted at 3/4 of ramus length; middle apical seta about twice as long as outer apical one, and both setae with breaking planes.

Antennula (Fig. 23) 9-segmented (although distal part of third segment distinct lobe bearing 1 apical seta) not strongly geniculate, with geniculation visible between sixth and seventh segments, somewhat longer than in female. Aesthetascs present on fourth and ninth segments; first aesthetasc much longer and stouter. Setal formula as follows: 1.11.8.6.2.3.0.4.4. Seta on first segment and 1 seta on third segment pinnate; all other setae smooth. Only 1 seta on ninth segment articulating on basal part and no setae with breaking planes; 2 setae on sixth segment transformed into spiniform armature elements. Seventh segment with characteristic cuticular structure on grasping margin.

Antenna, labrum, mandibula, maxillula, maxilla, maxilliped, endopod, and exopod of first swimming leg, exopod of second swimming leg (Fig. 24), and fourth swimming leg similar to female.

First swimming leg (Fig. 28) with modified basis, inner margin of which rigidly sclerotized and produced distally into blunt spiniform process, at base of inner spine. Inner spine on basis somewhat smaller than in female, without spinules at its base, about 2.4 times as long as spiniform process.

Second swimming leg (Fig. 26) with transformed endopodal second and third segments. Second segment with part of inner margin protruding into smooth rounded lobe; inner seta shorter than in female. Third segment completely modified; only inner seta normally formed, stout, bipinnate, and very long. Ancestral inner apical seta smooth and very slender, shorter than inner seta. Ancestral outer apical seta transformed into strong smooth serpentine element; its distal end swollen and with 2 characteristic tips (1 apically and 1 on outer margin). Ancestral outer spine completely fused to somite, transformed into very strong and smooth thorn, which somewhat shorter than ancestral outer apical element and as long as ancestral inner apical seta; with small smooth protrusion at inner basal margin. As a result of these transformations, third segment appearing cleft medially. Exopod (Fig. 24) similar to female.

Third swimming leg (Fig. 25) with sexually dimorphic pore on third exopodal segment, at level of second outer spine, but without hyaline tubular extension.

Fifth legs (Fig. 27) with basally fused baseoendopods and without ornamentation. Endopodal lobe small, trapeziform, extending to midlength of exopod, armed with 2 very strong apical spines; inner spine about 1.1 times as long as outer one. Exopod about as long as its maximum width, pentagonal; armed with 5 elements, as in female; length ratios of these elements (from inner side) 1 : 1.5 : 1.8 : 0.3 : 0.4.

Sixth leg (Fig. 29) distinct, broad and short, cuticular plate, without ornamentation and armed with 3 elements: smooth innermost spine, slender middle seta (this seta slightly shorter than spine and also smooth) and minute outermost seta (about twice as short as spine).

Variability.—Exopod of antenna may have all three segments distinct (Fig. 3), or last two segments can be partly fused (Fig. 6). Unfortunately, only one male and one female were collected and studied.

Etymology.—The species name is taken from the name of the Republic of India, where the material was collected, i.e., as an adjective agreeing in gender with the masculine generic name.

Discussion

Compared with many other harpacticoid taxa, the subdivisions of Diosaccidae Sars, 1906, are more or less clear, despite the fact that this large family has been treated independently by Nicholls (1941) and Lang (1948). Lang was apparently unaware of Nicholls' paper when he wrote his monograph. Although Lang's system is far superior, and consequently has been adopted by all modern taxonomists, Nicholls introduced new generic names that cannot be neglected for priority reasons. Lang's second overview of this family (Lang, 1965) certainly greatly contributed to the clarity of the generic diagnoses, but some genera have not been properly assigned until recently (see Huys, 1990). Lang's (1948) view of the phylogeny of Diosaccidae has not been challenged so far, although it was supplemented by Wells *et al.* (1982) for the *Amphiascus*-related genera. Our new species clearly belongs to that evolutionary line and, in fact, in Lang's (1965) key it would outkey as *Paramphiascella* Lang, 1948, just like the genera *Paramphiascoides* Wells, 1967, and *Miscegenus* Wells, Hicks, and Coull, 1982 (see Wells, 1967; Wells *et al.*, 1982). These three genera, together with *Amphiascoides* Nicholls, 1941 [syn. *Amphiascella* Lang, 1944], are very close to the Indian freshwater representative insomuch that they share the same female swimming legs armature formula, as well as the fifth leg armature formula in both sexes. Unfortunately, the Indian species cannot be assigned to any of these four genera (or any other genus of Diosaccidae) without significantly extending their diagnoses. As that would cause systematic confusion in many other genera, we prefer to erect a new genus to accommodate it.

The genus *Amphiascoides* contains today 20 valid species, fewer than when it was originally established by Nicholls (1941). The reason for that is its junior synonym, the genus *Amphiascella*, described by Lang (1944), which diagnostic concept was much narrower and has been accepted consequently. That is why all generic comparisons should refer to Lang's (1948, 1965) perception of this group of Diosaccidae species, of course, with Nicholls' (1941) name having priority. Although a relatively close relationship between *Amphiascoides* and *Neomiscegenus*, n. gen., is evident, the former differs from the latter by some very important morphological features: the first endopodal segment of first leg is always longer than the entire exopod; the caudal rami are wider than long, and the proximal lateral seta is not moved completely ventrally; the third exopodal segment of the antenna bears more than one apical seta; the exopod of the mandibula is 3-segmented; the basis of the maxilliped is armed with 3 setae; the female antennula is much longer (at least twice, but usually more than three times, as long as the rostrum); the epicopulatory bulb on the female genital somite is present; and the endopod of the second leg in the male is much more simplified.

With 21 species currently recognized, the genus *Paramphiascella* appears to be as large as *Amphiascoides*, but the former probably contains several additional unrecognized synonyms. Regarding this genus, Lang (1965: 321) stated: "the differences between many of the species are so small that I cannot give a key to them." Whatever is the exact number of species in *Paramphiascella*, they form quite a compact entity and can be distinguished from *Neomiscegenus* by the following six characteristics: the first endopodal segment of the first leg is always longer than at least the first two exopodal segments combined; the third exopodal segment of the antenna bears more than one apical seta; the exopod of the mandibula is 2-segmented; the female antennula is much longer, when compared with the cephalothorax or rostrum, and slender; the epicopulatory bulb on the female genital double-somite is present; and the endopod of the second leg in the male ends like slender pincers, without any trace of the third segment itself. Obviously, *Paramphiascella* is much closer to *Amphiascoides* than to *Neomiscegenus*, and the only strong generic character that separates them is the appearance of the sexually dimorphic endopod of the second leg in the male (Lang 1965: 320). However, this seems to be enough, and we completely agree with Mu and Gee (2000: 129) that: "The secondary sexually dimorphic characters may assume greater significance in future revisions of the genera of Diosaccidae . . ." It should be mentioned here that some of the characters that we are using to distinguish *Neomiscegenus* from *Paramphiascella* (as well as from *Amphiascoides*) are not known in all species of the latter genus, because of the incomplete descriptions of many species, but unfortunately, that is the present situation in the majority of copepod genera. It is interesting to mention that one of the *Paramphiascella* species, *P. aquaedulcis* Dussart, 1984, was described from a similar habitat as *Neomiscegenus indicus*, n. sp., after the seasonal flooding of Rio Portuguesa in Venezuela (Dussart, 1984). Probably this evolutionary line of Diosaccidae genera is more successful in colonizing the freshwater subterranean habitats than we presently know, and further investigations of this habitat in former parts of Gondwana may reveal many new members.

The genus *Paramphiascoides* is so far monospecific. It was described from the littoral of Inhaca Island, Mozambique, by Wells (1967). Its sexually dimorphic endopod of the second leg in the male ends in slender pincers, just as in the genus *Paramphiascella*, but it has quite a different appearance. None of the two branches of this peculiar organ is movable, and also the inner setae are not so closely set as in *Paramphiascella*. The first swimming leg of the genus *Paramphiascoides* is very similar to that of *Neomiscegenus*, and the female antennulae are also very short. However, *Paramphiascoides* can be easily distinguished from the new taxon by the following characters: the distalmost exopodal segment of the antenna bears more than one apical seta; the exopod of the mandibula is 3-segmented; the epicopulatory bulb is present; the exopod of the maxillula bears three setae; and, most importantly, the endopod of the second leg in the male is quite different from that in *Neomiscegenus*.

As its name suggests, *Neomiscegenus* is morphologically most similar to the genus *Miscegenus*, which is also known from a single species. This species, *Miscegenus hereatunga* Wells, Hicks, and Coull, 1982, was described from several estuaries and bays from New Zealand by Wells *et al*. (1982). It shares with *Neomiscegenus indicus* a number of important characters, including the short antennulae; fusiform habitus; similar caudal rami (with the ancestral proximal lateral seta moved ventrally, and a ventral lappet between the outer and middle apical setae); the same armature formula of all the swimming legs and the fifth legs; similar maxilliped, the endopod of the second leg in the male with similar basic structure; and even extremely similar ornamentation of urosomal somites, in both female and male. Because it would be impossible to consider all these morphological similarities as convergencies, the two genera must have a close phylogenetic relationship. Nevertheless, a few very important characters preclude us from assigning the new Indian species to the genus *Miscegenus*. The most important one is certainly the absence of an epicopulatory bulb in the Indian representative (Fig. 7), because *Miscegenus* possesses a large bulb on the female genital segment, which is much more like that in the genus *Schizopera* Sars, 1905, than in *Amphiascoides*, *Paramphiascella*, or *Metamphiascopsis* Lang, 1948 (see Ohtsuka and Iwasaki, 1998). Although the function of this female sexual structure is unknown, Huys and Boxshall (1991) considered it as a "novel structure" in Harpacticoida. That all 70 species and subspecies of the genus *Schizopera* have this structure, which can even be used sometimes as one of the additional characters in distinguishing closely related species (Karanovic, 2004), is proven. It is hard to imagine that the epicopulatory bulb arose independently a number of times within the Diosaccidae. Because the condition in the female genital field is not one of the common stygomorphies (character states, usually reductions, caused by a subterranean aquatic life) in copepods, we consider it as a good generic character. The endopod of the second leg in the male is similar in both *Miscegenus* and *Neomiscegenus*, but it has several very important differences: the third segment with only one lateral seta in *Neomiscegenus* (*versus* two in *Miscegenus*); the apical seta on it shorter than lateral (longer in *Miscegenus*); and the ancestral outer apical seta transformed into a serpentine element with two characteristic tips in *Neomiscegenus* (almost straight in *Miscegenus* and without any tips). This scale of differences is not known within any of the Diosaccidae genera, so we consider it as a generic feature as well. However, tips on the second leg endopod of *Neomiscegenus* are not an autapomorphy, but rather a plesiomorphy, because they can be found in the genera *Amphiascus* Sars, 1905 (see Wells, 1968: 406; Bodin, 1977: 317) and *Typhlamphiascus* Lang, 1948 (see Por, 1963; 206). Both of these genera, as well as all the other genera of Diosaccidae, are more distant from *Neomiscegenus* than are the four genera discussed above. *Miscegenus* can be additionally distinguished from the new genus by the following features: the distalmost exopodal segment of the antenna has more than one apical seta; the exopod of the mandibula is 2-segmented; the first endopodal segment of the first leg is longer than the first two exopodal segments; and all seta on the fifth leg are much shorter in both sexes. However, the last two characters are more on the specific than on the generic level.

Although almost all autapomorphies of the new genus (the distalmost exopodal segment of the antenna with only one seta; the exopod of the mandibula 1-segmented; and the epicopulatory bulb lacking) are obviously reductions from the ancestral stage, which are never fully reliable characters for erecting new genera, we believe that at least the absence of the copulatory bulb cannot be explained as a stygomorphy. That, together with the caudal rami shape (which is a synapomorphy with the genus *Miscegenus*) and the appearance of the second leg endopod in male (probably a plesiomorphy), is sufficient justification for establishing the new genus. Gee and Fleeger (1990: 296) suggested "that sexual dimorphism of P3 exopod 3 may be characteristic of the *Robertgurneya-Amphiascus-Paramphiascella* evolutionary line," and indeed the male of *N. indicus* possesses a sexually dimorphic cuticular pore on the third exopodal segment of the third leg (Fig. 25), although without the usual tubular extension. Many new microcharacters should be investigated and considered while trying to present a possible phylogeny of the Diosaccidae. We also think that the modifications of Lang's (1948) phylogenetic tree made by Wells *et al.* (1982) are not acceptable, because they are focused on one character only and, as a result, the genus *Miscegenus* is misplaced. We think that the genera *Amphiascoides*, *Paramphiascella*, *Paramphiascoides*, *Miscegenus*, and *Neomiscegenus* have the same common ancestor. Within this line, during their evolutionary history, the genera *Miscegenus* and *Neomiscegenus* have separated relatively early from the other branch, which evolved later into the genera *Amphiascoides*, *Paramphiascella*, and *Paramphiascoides*.

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