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Biogeography and phylogeny of *Dermoergasilus* Ho & Do, 1982 (Copepoda: Ergasilidae), with descriptions of three new species

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Abstract

Three new species of *Dermoergasilus* are described from six species of grey mullet hosts. *Dermoergasilus longiabdominalis* n. sp. was found on *Valamugil engeli* (Bleeker) from the Philippines and Madagascar and on *V. cunnesius* (Valenciennes) from the Philippines and Mangalore, India. *D. semiamplectens* n. sp. occurred on *Sicamugil hamiltoni* (Day) from the Sittang River, Burma, on *Liza subviridis* (Valenciennes) and *L. parsia* (Hamilton Buchanan) from Calcutta, India, and on *V. cunnesius* (Valenciennes) from China. *D. curtus* n. sp. parasitised *Rhinomugil squamipinnis* (Swainson) from Alahabad, India. A key to the ten currently accepted species of *Dermoergasilus* is given. The biogeographical distribution of *Dermoergasilus* species is analysed and levels of host-specificity are surveyed within the genus. The phylogenetic relationships between the species of *Dermoergasilus* are also analysed.

Introduction

The genus *Dermoergasilus* was proposed by Ho & Do in 1982 to accommodate *Ergasilus amplectens* Dogiel & Akhmerov, 1952 (reported from *Mugil cephalus* L. from Russia and Japan), *Dermoergasilus coleus* (Cressey, 1970) (on needlefishes from the Philippines, Borneo and India) and *D. semicoleus* (Cressey, 1970) (on needlefishes from Australia). Subsequently, Byrnes (1986) described a new species, *D. acanthopagri*, from three species of bream from Australia and a fifth species, *D. mugilis*, was added by Oldewage & van As (1988) from *Mugil cephalus* in South Africa. Kabata (1992) described a species of *Ergasilus* Nordmann, *E. intermedius*, from several hosts belonging to the families Clupeidae, Plotosidae and Perichthyidae. He named this species to reflect its intermediate nature between the genera *Ergasilus* and *Dermoergasilus*. This species was later transferred to *Dermoergasilus* by El-Rashidy & Boxshall (1999). Ho et al. (1992) reported *D. amplectens* on *Valamugil seheli* and on five other hosts belonging to the families Cichlidae, Gerreidae, Hemiramphidae, Megalopidae and Chanidae from India, in addition to describing a new species, *D. varicoleus* Ho, Jayarajan & Radhakrishnan, 1992, found on *Liza tade* (Forsskål). This new species was subsequently reported on a second mugilid host, *Liza abu* (Heckel), from Iraq (Ho et al., 1996).

The present paper describes three new *Dermoergasilus* species, all of which occur on grey mullet (Mugilidae). Additional new localities and new host records are presented for *D. amplectens* and *D. varicoleus*, together with a key to the ten currently accepted *Dermoergasilus* species. This genus is confined to the Indian and Indo-West Pacific regions. The phylogenetic relationships of species within the genus *Dermoergasilus* were analysed using PAUP. We consider that the status of the genus *Dermoergasilus* is still uncertain. However, validation of the genus can only be achieved in the context of a full generic level revision of the entire family Ergasilidae, given that the most speciose genus, *Ergasilus*, is certainly paraphyletic (El-Rashidy, 1999). No changes will be proposed here.

Materials and methods

Material was collected from the gills of grey mullet deposited in the fish collection of The Natural His-

tory Museum, London (BMNH). The copepods were removed from the gill filaments, dissected, mounted in lactophenol as temporary slide preparations. Measurements were made using an ocular micrometer and drawings were made with the aid of camera lucida on an Olympus BH2 microscope equipped with differential interference contrast.

***Dermoergasilus longiabdominalis* n. sp.**
(Figures 1–4)

Type-material: Female holotype (BMNH Reg. No. 1999.1318), 11 female paratypes (BMNH Reg. Nos 1999. 1319-1329).
Type-locality: Calabato, Mindanao, Philippines.
Type-host: *Valamugil engeli* (Bleeker).
Records of infected hosts: *V. engeli* (Mindanao, Philippines; Tamatave, Madagascar), *V. cunnesius* (Valenciennes) (Mindanao, Philippines; Mangalore, India).
Etymology: The specific name refers to the elongate urosome.

Description of female

Mean body length 0.89 ± 0.08 mm, mean body width 0.24 ± 0.01 mm ($n = 3$). Cephalothorax constituting about half body length (excluding caudal setae); anterior part narrow, delimited by posterior margin of dorsal cephalic shield, ornamented with inverted T-shaped marking (Figure 1A). First pedigerous somite partly delimited by dorsal constriction visible in lateral view (Figure 1B) and with median longitudinal fold dorsally. Free second to fourth pedigerous somites narrowing posteriorly. Rostrum small, rectangular. Thick block of muscles extending from dorsal origin on mid-line to base of antennae (Figure 1C).

Genital double-somite elongate, 1.2-1.5 times longer than first abdominal somite; anterior part wider than posterior; rows of spinules present ventrally in anterior part (Figure 1D). First free abdominal somite 1.5-1.7 times longer than wide, and nearly 1.5 times longer than second and third abdominal somites and caudal rami combined, ornamented with row of spinules ventrally in anterior part. Second free abdominal somite nearly as long as anal somite and caudal rami combined, with row of spinules ventrally along posterior margin. Anal somite deeply incised medially; ornamented with posterior spinule row. Caudal rami nearly 2/3 length of anal somite, produced disto-ventrally into narrow digitiform process bearing minute terminal seta; process 2.4-2.8 times longer than ramus; longest caudal seta armed with rows of spinules; 2 lateral setae longer than digitiform process; longer lateral seta sparsely plumose.

Antennule small, 6-segmented (Figure 2A), tapering distally; setal formula: 3: 10: 5: 4+ae: 2+ae: 7+ae.

Antenna 4-segmented (Figure 2B), comprising short coxobasis and 3-segmented endopod bearing curved claw. Base of antenna elevated, carried on strongly developed pedestal (arrowed in Figure 2B) nearly half as long as coxobasis. Second segment (first endopodal segment) nearly twice as long as coxobasis. Second endopodal segment long, armed with small spine nearly at mid-length of concave margin. Third endopodal segment very small, represented by incomplete sclerite. Second plus third endopodal segments together comprising nearly 85% length of first endopodal segment. Curved claw nearly 2/3 length of second endopodal segment, fitting into distal socket, located in inflated cuticular membrane surrounding first endopodal segment of opposing antenna.

Mandible unsegmented, bearing anterior, distal and posterior blades; small anterior blade with teeth on anterior margin; distal blade with teeth along both margins; posterior one with teeth on posterior margin. Maxillule lobate with medial process plus 2 distal setae and minute inner seta. Maxilla consisting of large syncoxa tapering distally and small spatula-shaped basis, armed anteriorly with rows of sharp teeth (Figure 3A).

Legs 1-4 (Figures 3B; 4A-B) with all rami 3-segmented except 2-segmented fourth exopod. Basis with row of spinules along posterior margin in legs 2-4. Lateral margins of both rami spinulate in all legs. Setules present on unarmed inner margin of first exopodal segment of all legs. Interpodal sternites not ornamented (Figure 4C). Armature of legs as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	I-0; 0-1; II,5	0-1; 0-1; II,4
Leg 2	0-0	1-0	I-0; 0-1; 6	0-1; 0-1; I,4
Leg 3	0-0	1-0	I-0; 0-1; 6	0-1; 0-1; I,4
Leg 4	0-0	1-0	I-0; 5	0-1; 0-2; I,3

Fifth leg 2-segmented; short protopodal segment bearing outer seta; free exopodal segment with short lateral seta plus 2 terminal setae (Figure 3C).

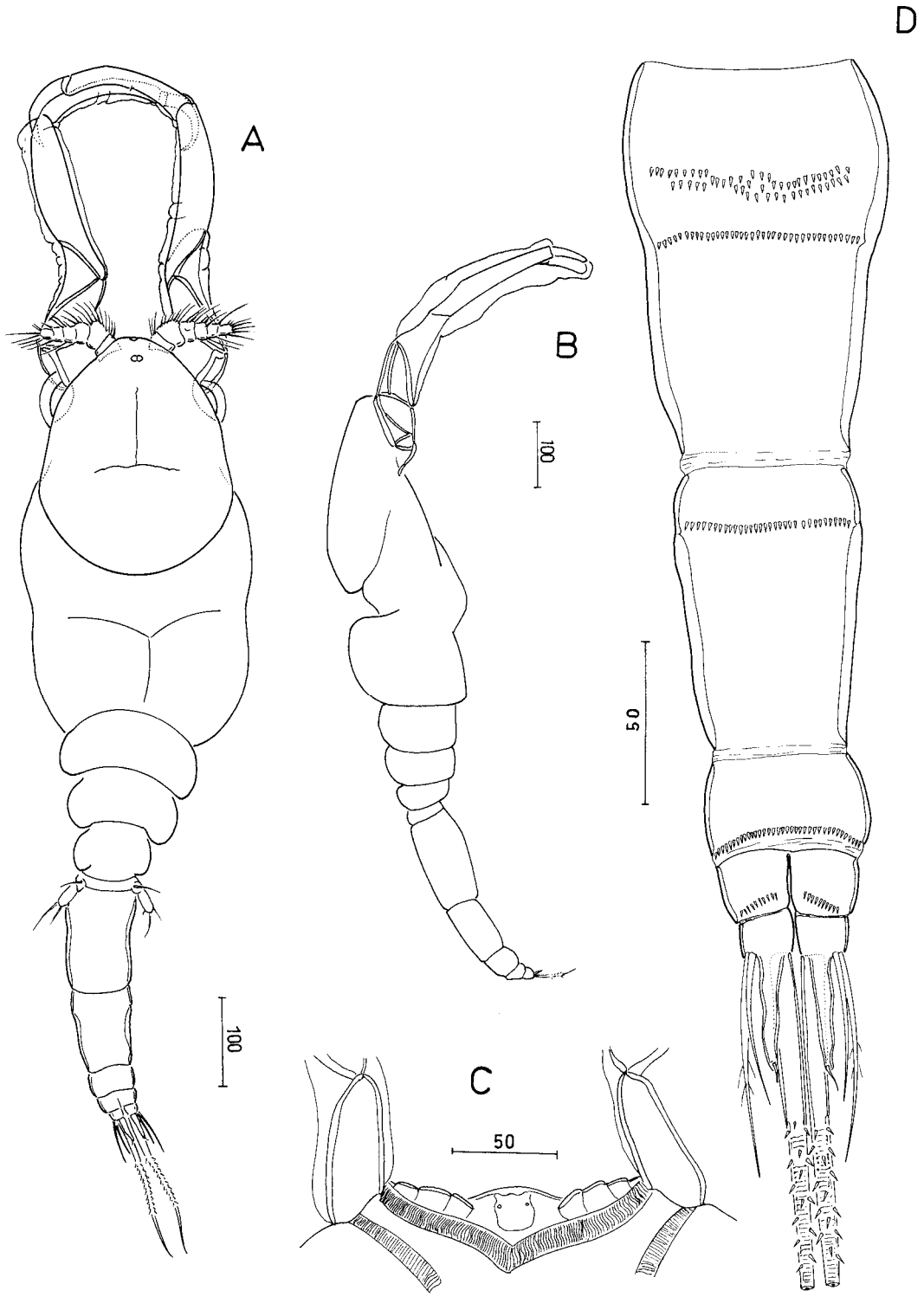

Figure 1. Dermoergasilus longiabdominalis n. sp. Adult female. A, dorsal view; B, lateral view; C, rostrum, ventral; D, urosome, ventral. Scale-bars in μm.

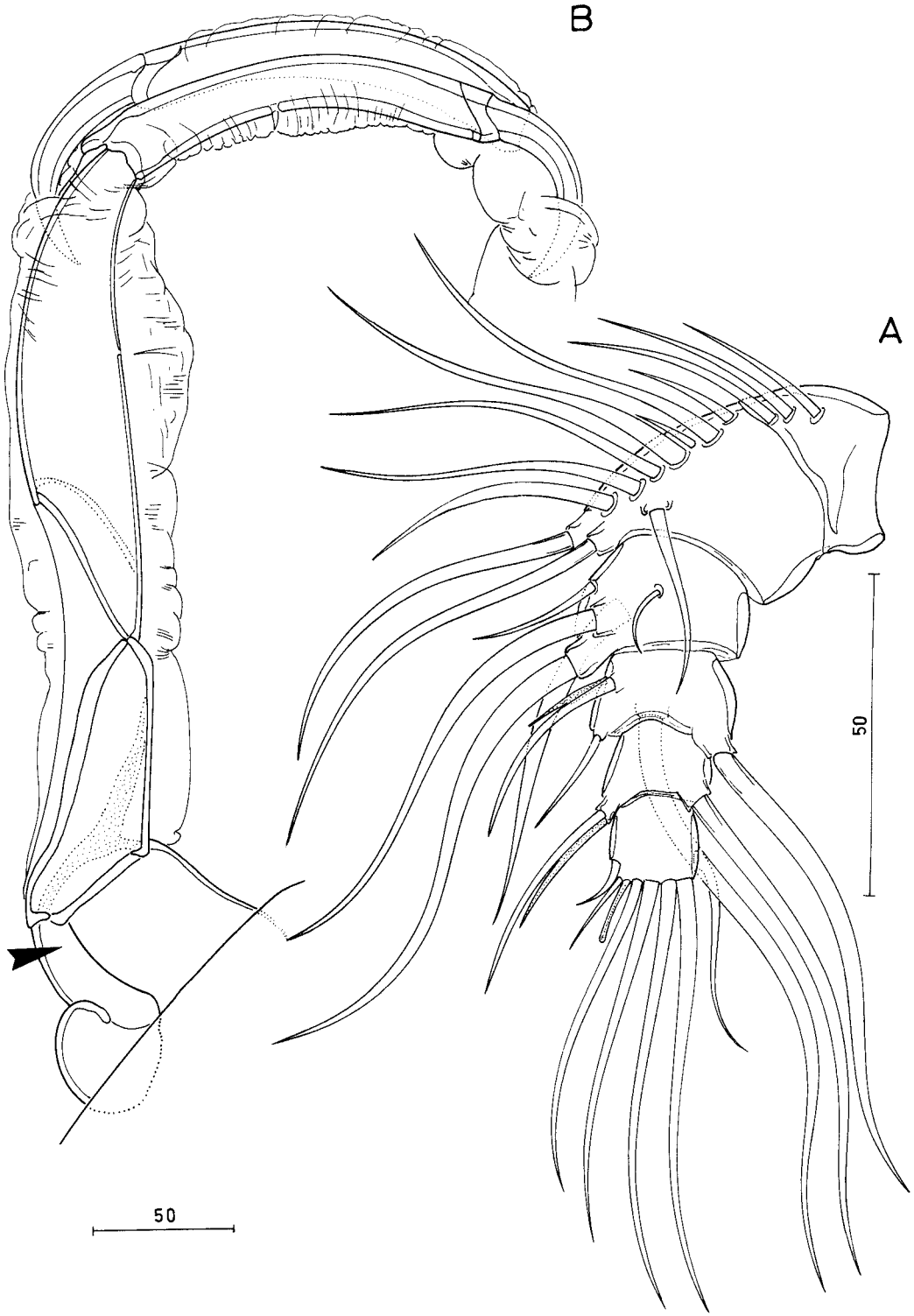

Figure 2. Dermoergasilus longiabdominalis n. sp. Adult female. A, antennule; B, antenna, with pedestal arrowed. Scale-bars in μm.

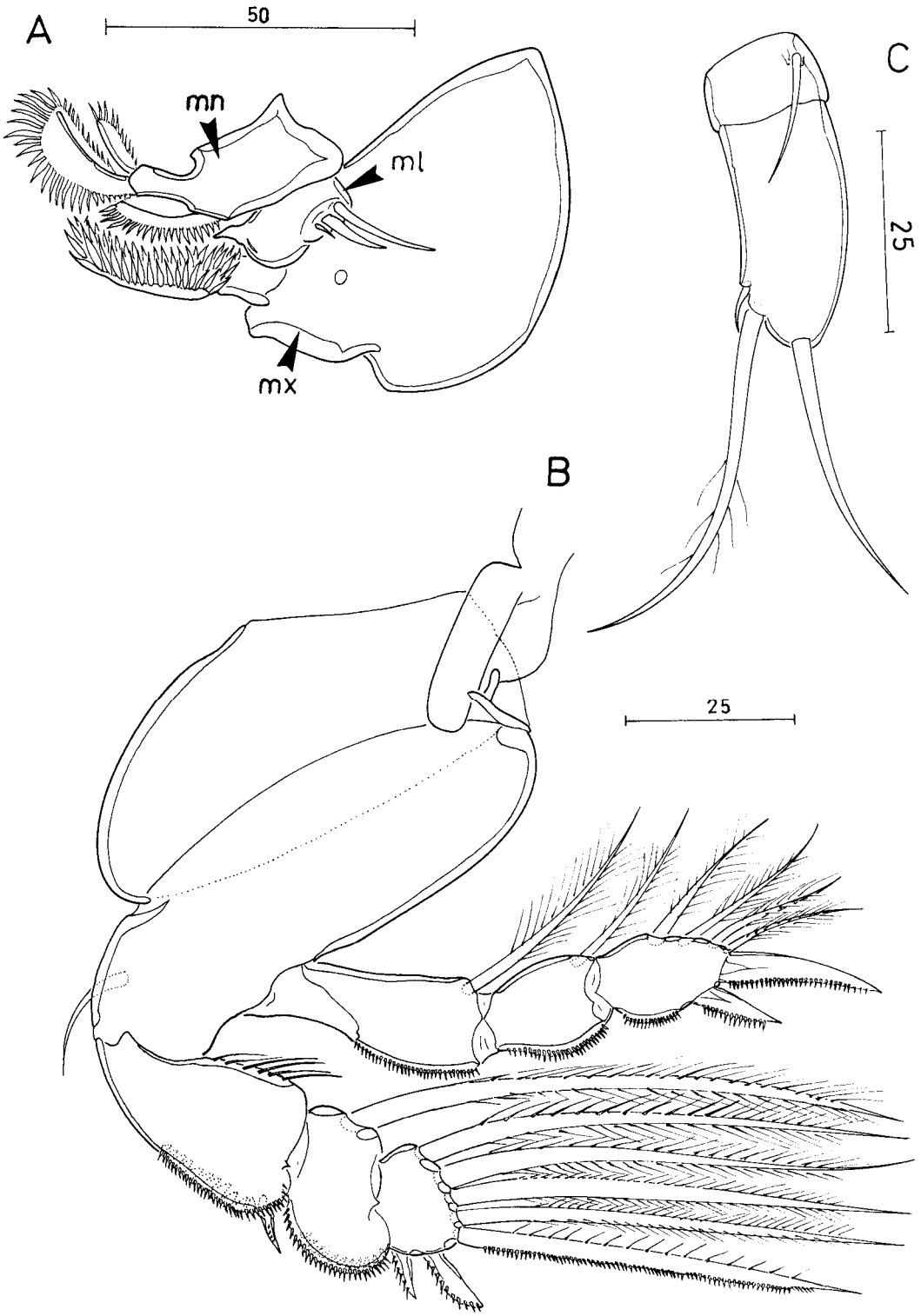

Figure 3. Dermoergasilus longiabdominalis n. sp. Adult female. A, mouthparts; B, first swimming leg, anterior; C, fifth swimming leg. Scale-bars in μm. (mn = mandible, ml = maxillule, mx = maxilla).

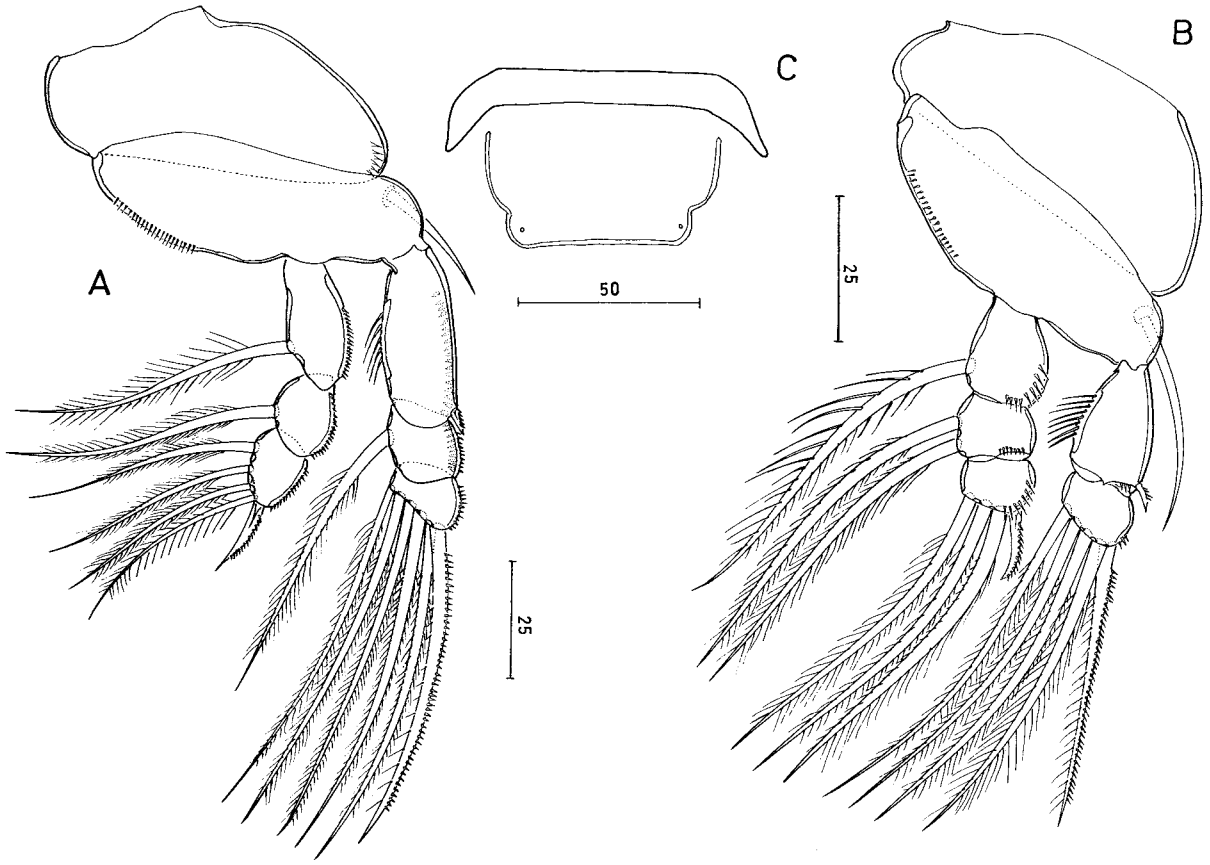

Figure 4. Dermoergasilus longiabdominalis n. sp. Adult female. A, second swimming leg; anterior; B, fourth swimming leg, anterior; C, interpodal sternite of second swimming leg. Scale-bars in μm.

Remarks

The new species shares an elongate urosome with *D. mugilis*, *D. acanthopagri*, *D. amplectens* and *D. varicoleus*. The South African species, *D. mugilis*, differs from the new species in the setation of the antennule (but this needs verification) as well as in the setal formula of the swimming legs. The new species differs from *D. acanthopagri* in the antennulary setation and in the presence of five setae on the terminal exopodal segment of leg 4, compared with six in *D. acanthopagri*.

The new species resembles *D. amplectens* in the setal formula of the swimming legs and in the ornamentation of the first exopodal segment of legs 1-4. It differs from *D. amplectens* in the antennulary setation and in having a first free abdominal somite that is longer than wide (that of *D. amplectens* is only nearly as long as wide). The coxobasis of the antenna is carried on an elevated anterolateral pedestal in both species, but it is smaller in the new species than in *D. amplectens*. The caudal digitiform process of the new species is long and narrow, whereas that of *D. amplectens* is relatively short and wide. A small terminal seta is present on the digitiform process in both species but has not previously been reported in *D. amplectens* (it was overlooked in the original description, see below).

The new species is closely related to *D. varicoleus* with which it shares the leg setation formula and elongate urosome, but it differs particularly in the proportional lengths of the antennal segments. The tip of the digitiform process on the caudal ramus is rounded and bears a small seta. It is similar to that of *D. varicoleus* (which is present although not mentioned in the original description). The lateral caudal setae in the new species are longer than the digitiform process, but are shorter than it in *D. varicoleus*.

***Dermoergasilus semiamplectens* n. sp.** (Figures 5-8)

Type-material: Female holotype (BMNH Reg. No. 1999.1340), 38 female paratypes (BMNH Reg. Nos. 1999.1341-1378).
Type-locality: Sittang River, Burma.
Type-host: *Sicamugil hamiltoni* (Day).
Records of infected hosts: *S. hamiltoni* (Sittang River, Burma), *Valamugil cunnesius* (China), *Liza subviridis* (Calcutta, India) and *Liza parsia* (Hamilton Buchanan) (Calcutta).
Etymology: The specific name refers to the close resemblance between the new species and *D. amplectens*.

Description of female

Mean body length 0.70 ± 0.04 mm; range 0.65–0.77 mm. Mean body width 0.23 ± 0.01 mm; range 0.21–0.26 mm (n = 10). Cephalothorax oblong, slightly constricted in posterior third; dorsal surface ornamented anteriorly with inverted T-shaped marking (Figures 5A, B). Boundary between cephalosome and first pedigerous somite indistinct. Free second to fourth pedigerous somites narrowing posteriorly. Rostrum with 6 sensilla and 3 integumental pores (Figure 5C).

Genital double-somite slightly longer than 3 free abdominal somites combined; anterior part wider than posterior; ventral spinule row present at level of genital openings (Figure 5D). First free abdominal somite constituting about 55–66% length of genital double-somite, just wider than long, and slightly longer than second and third free abdominal somites plus caudal rami combined; transverse row of spinules present ventrally in anterior third of somite. Second free abdominal somite slightly longer than anal somite, ornamented with transverse row of spinules ventrally. Anal somite deeply incised medially and ornamented ventrally with incomplete row of spinules along posterior margin. Caudal rami (Figure 5D) about equal in length to anal somite; each produced distoventrally into stout digitiform process, about 1.8 times longer than ramus, bearing short seta; longest seta ornamented with spinule rows; 2 lateral setae longer than digitiform process.

Antennule small, 6-segmented (Figure 6A), tapering distally; setal formula: 3: 10: 5: 4+ae: 2+ae: 7+ae.

Antenna 4-segmented (Figure 6B), comprising coxobasis, 3 endopodal segments and curved claw. Base of antenna elevated on weak pedestal. Second segment (first endopodal segment) nearly 2.2 times longer than coxobasis (excluding pedestal elevating coxobasis); second and third endopodal segments together equal to 60% length of first endopodal segment. Curved claw about 2/3 length of second plus third endopodal segments combined; tip fitting into distal part of first endopodal segment of opposing antenna. Antennal segments enclosed by loose, hyaline, cuticular membrane.

Mandible unsegmented, bearing 3 blades; anterior blade with teeth on anterior margin; large distal blade carrying teeth on both margins; posterior blade with teeth only on posterior margin. Maxillule lobate, ornamented with spinules, bearing 2 long distal setae, minute inner seta and tapering medial process. Maxilla consisting of large tapering syncoxa and small spatula-shaped basis, armed anteriorly with irregular rows of sharp teeth (Figure 7A).

Legs 1-4 (Figures 7B, 8A-B) with all rami 3-segmented except 2-segmented fourth exopod. Basis with row of spinules along inner margin in legs 2-4. Lateral margins of both rami spinulate in all legs. Setules present on inner margin of first exopodal segment of all legs. Interpodal sternites spinulate (Figure 7B). Spine and setal formula of legs 1-4 as in *D. longiabdominalis* n. sp.

Fifth leg 2-segmented; protopodal segment short with outer seta; free exopod with short lateral seta plus 2 setae of unequal length at apex (Figure 7C).

Remarks

The new species is closely related to *D. amplectens*. It possesses the same swimming leg setation, the first abdominal somite is about as long as wide, the base of the digitiform process on caudal ramus is broad, and the process itself is short. It differs from *D. amplectens* in its antennulary setation and in the reduction of the anterolateral cephalic pedestal bearing the antenna which causes the antenna to appear to be 5-segmented in *D. amplectens*.

The new species differs from *D. varicoleus* in the proportional lengths of the first free abdominal somite and genital double-somite: it represents up to two-thirds of the genital double-somite length in the new species but about three-quarters in *D. varicoleus*. The first abdominal somite is nearly as long as wide in the new species, whereas it is 1.7 times longer than wide in *D. varicoleus*. Finally, the digitiform process on the caudal ramus is relatively longer in *D. varicoleus*.

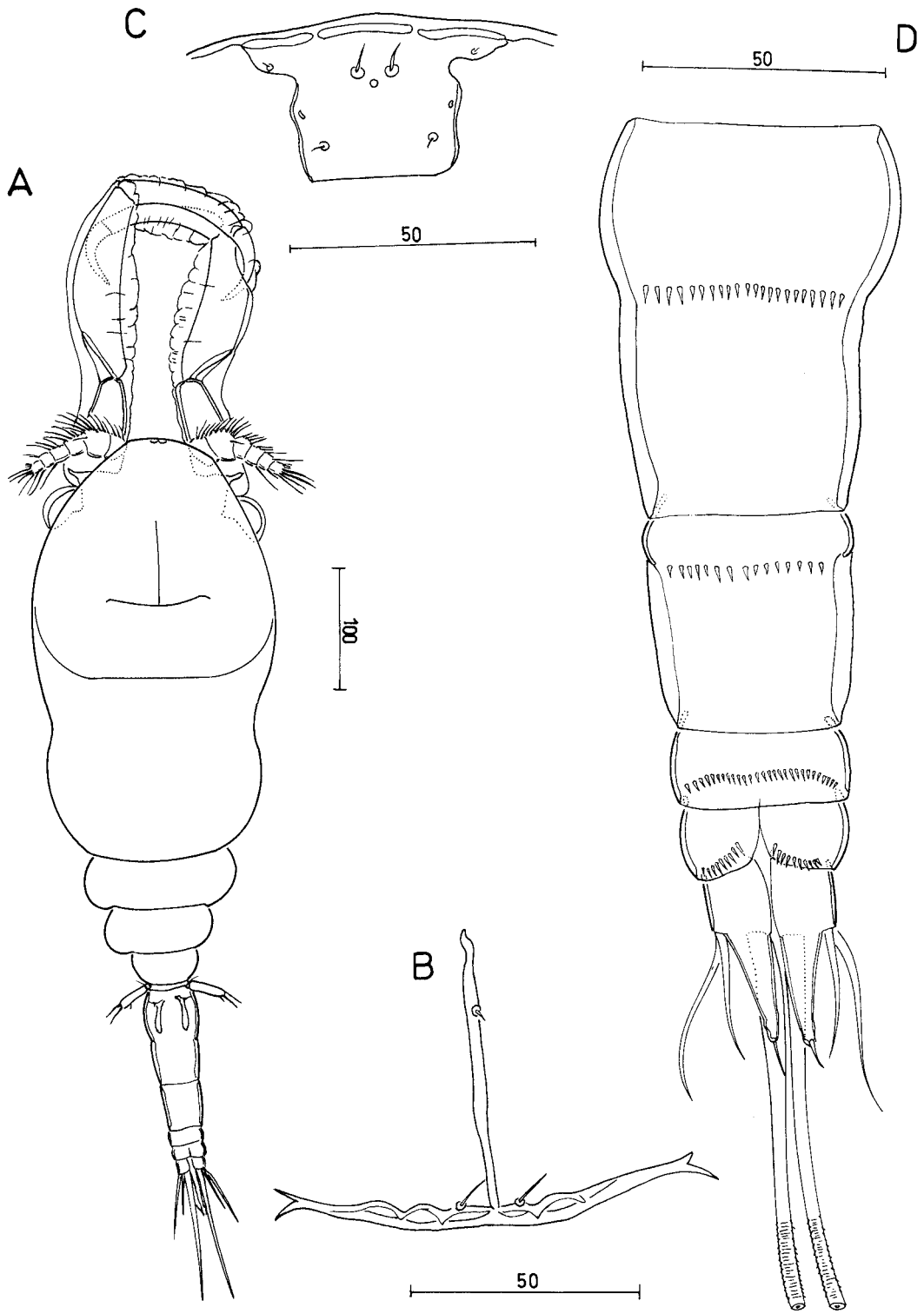

Figure 5. Dermoergasilus semiamplectens n. sp. Adult female. A, dorsal view; B, inverted T-shaped marking; C, rostrum, ventral; D, urosome, ventral. Scale-bars in μm.

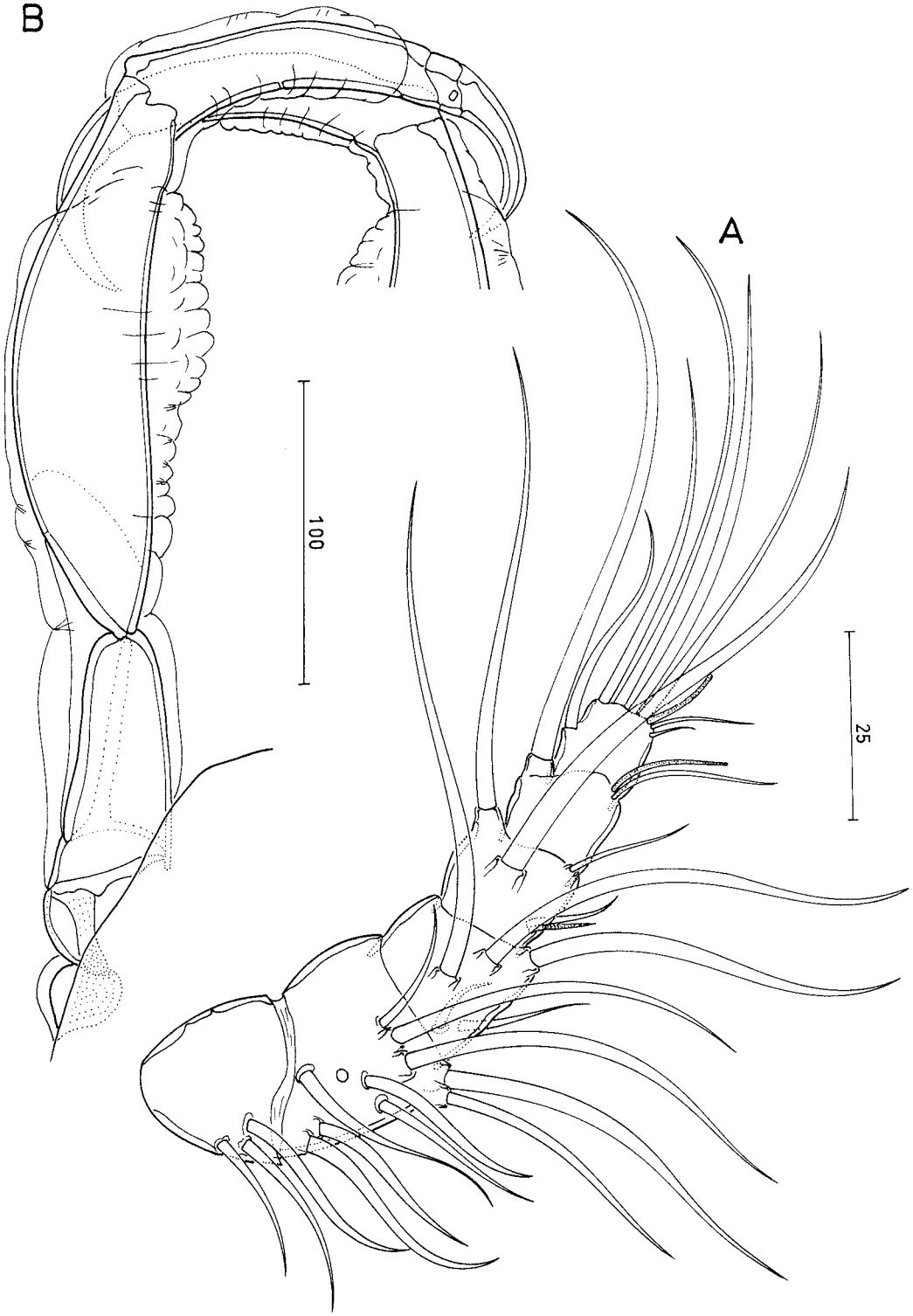

Figure 6. Dermoergasilus semiamplectens n. sp. Adult female. A, antennule; B, antenna. Scale-bars in μm.

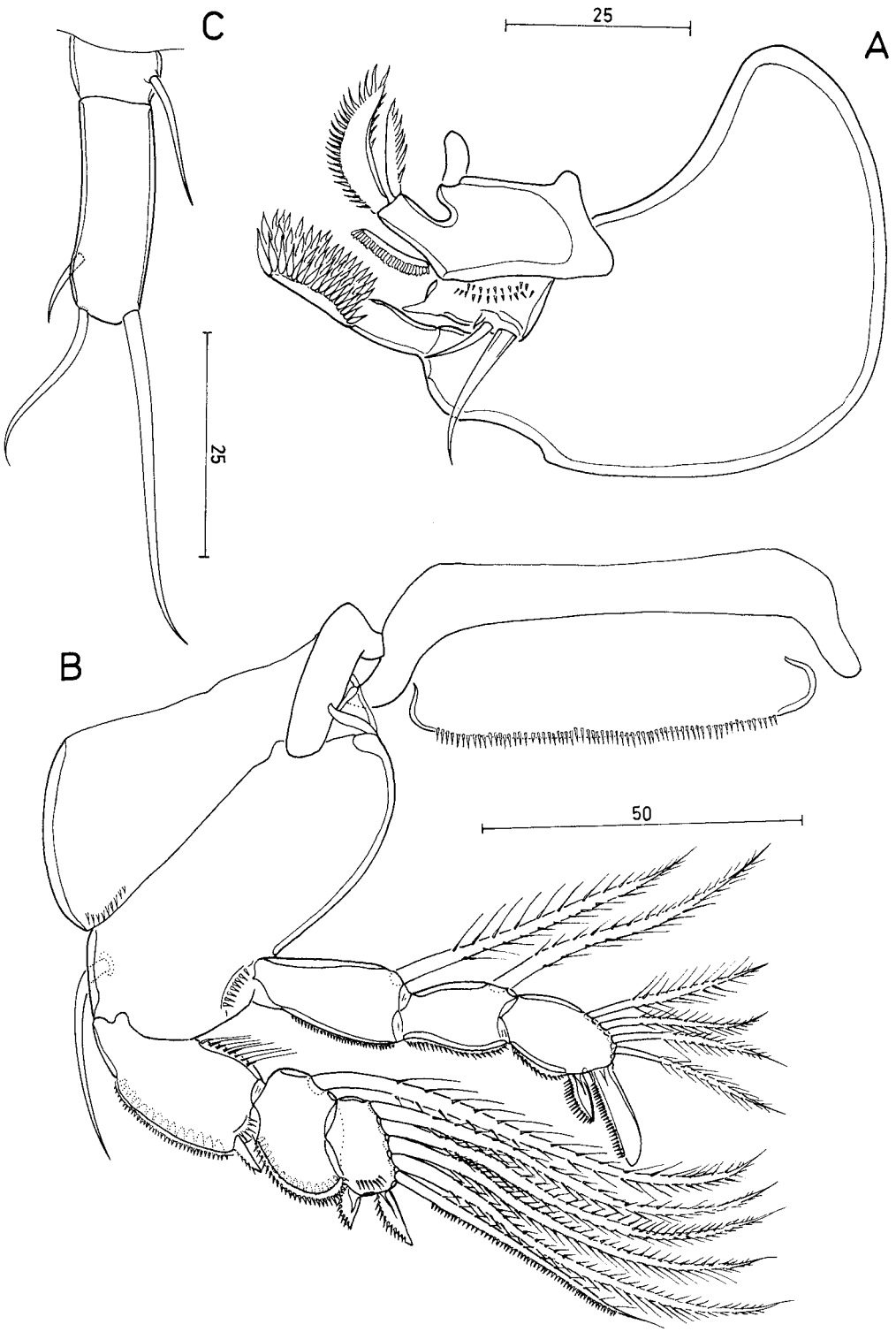

Figure 7. Dermoergasilus semiamplectens n. sp. Adult female. A, mouthparts; B, first swimming leg and interpodal sternite, anterior; C, fifth swimming leg. Scale-bars in μm.

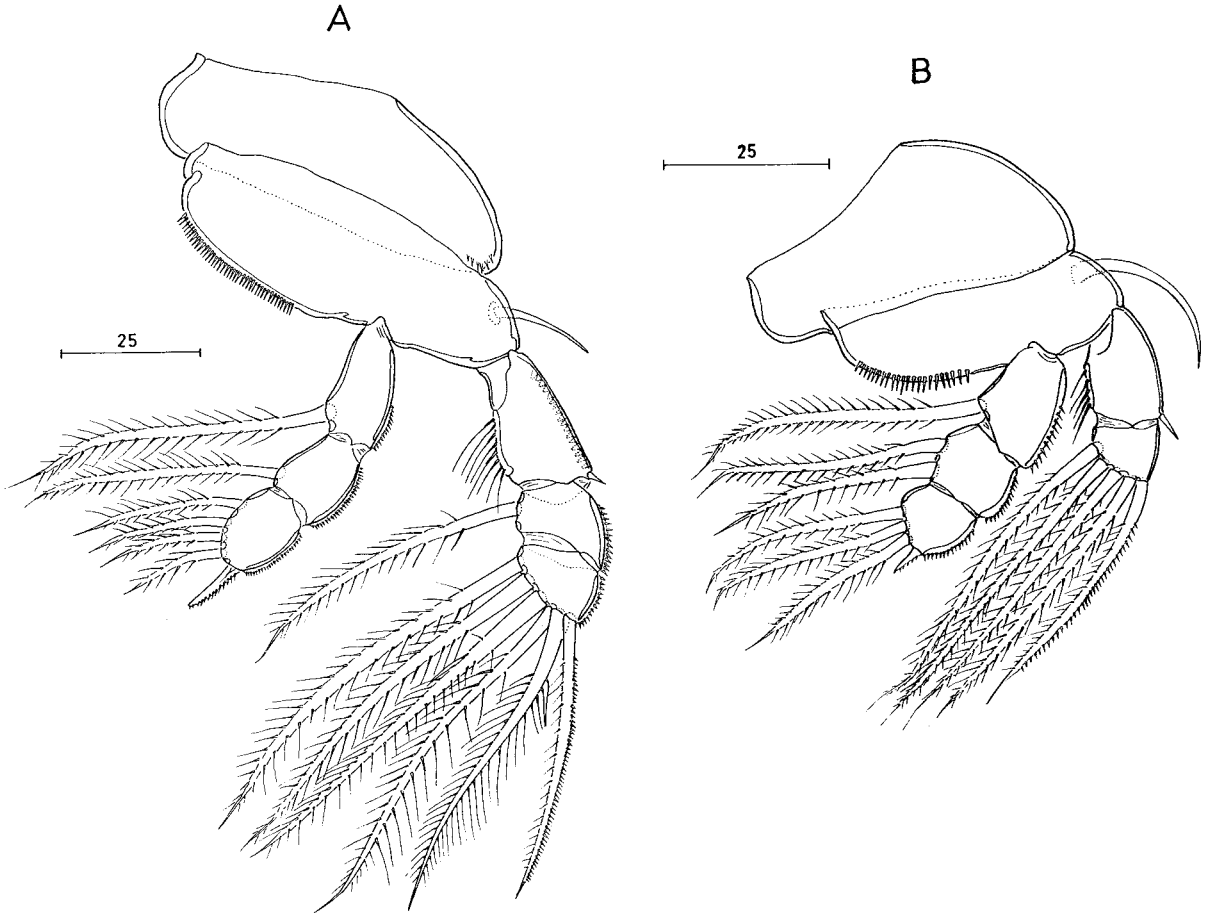

Figure 8. Dermoergasilus semiamplectens n. sp. Adult female. A, second swimming leg; anterior; B, fourth swimming leg, anterior. Scale-bars in μm.

***Dermoergasilus curtus* n. sp.** (Figures 9-12)

Type-material: Female holotype (BMNH Reg. No. 1999.1628).
Type-locality: Alahabad, India.
Type-host: *Rhinomugil squamipinnis* (Swainson).
Etymology: The specific name refers to the short urosome of the female.

Description of holotype female

Body length 0.76 mm, body width 0.24 mm. Cephalothorax oblong, ornamented with inverted T-shaped marking anteriorly (Figure 9A). Free second to fourth pedigerous somites narrowing posteriorly.

Genital double-somite globular, wider than long, nearly 2.2 times longer than first free abdominal somite, and nearly as long as second and anal somites combined; ornamented with 3 transverse rows of spinules ventrally (Figure 10A). Folded membrane present between genital double-somite and following somite. First free abdominal somite nearly twice as wide as long; ventral spinule row present along posterior margin; folded membrane present between first and second free abdominal somites. Second somite nearly twice as wide as long, with ventral row of spinules along posterior margin. Anal somite 1.5 times wider than long, incised medially; ventral row of spinules present along posterior margin. Caudal rami produced distally into digitiform process bearing minute terminal seta; process nearly twice as long as ramus; long medial seta on posterior margin armed with spinule rows; 2 lateral setae shorter than digitiform process.

Antennule small, 6-segmented (Figure 10B), tapering distally; setal formula: 3: 10: 5: 4+ae : 2+ae: 7+ae.

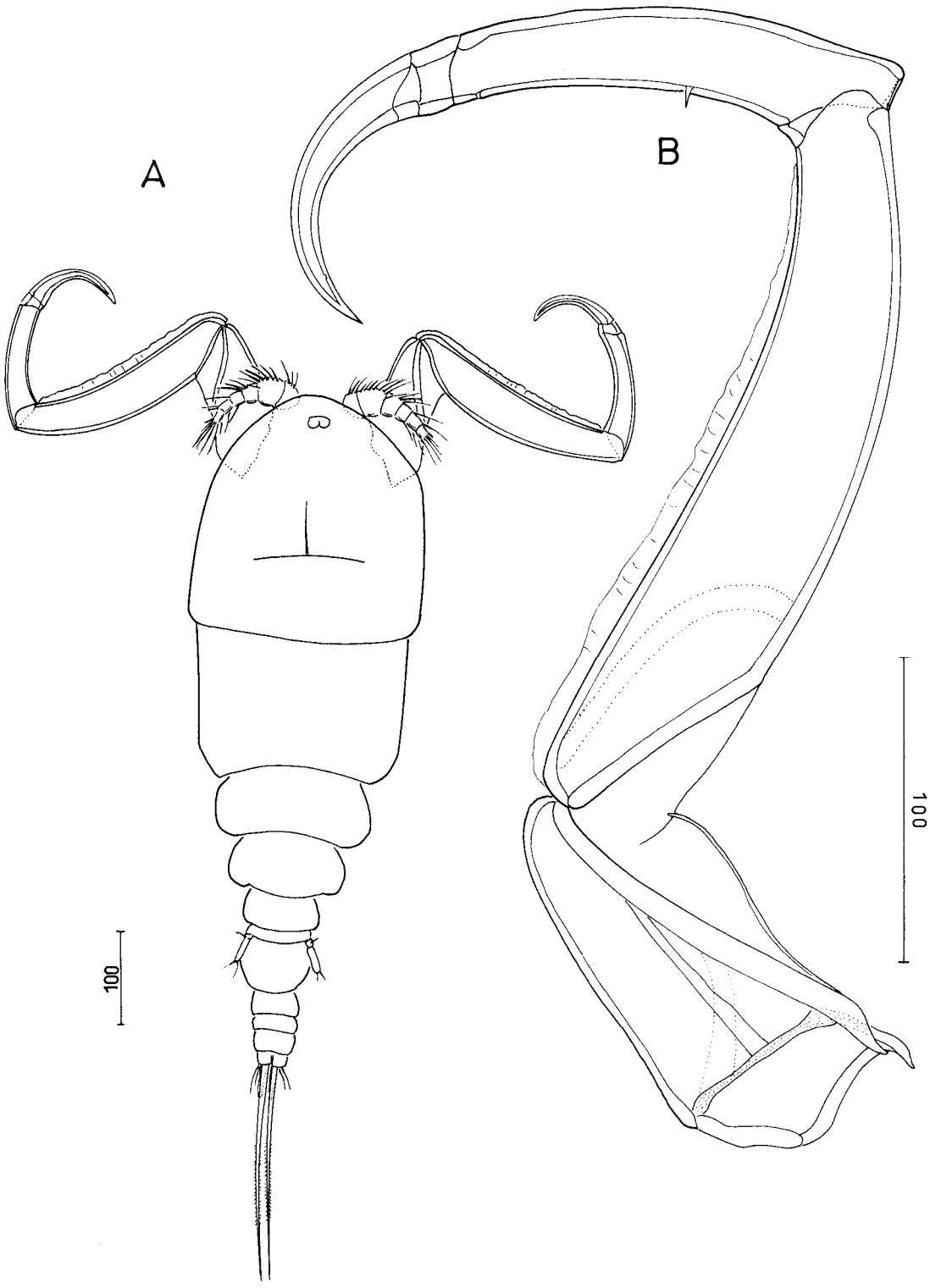

Figure 9. Dermoergasilus curtus n. sp. Adult female. A, dorsal view; B, antenna. Scale-bars in μm.

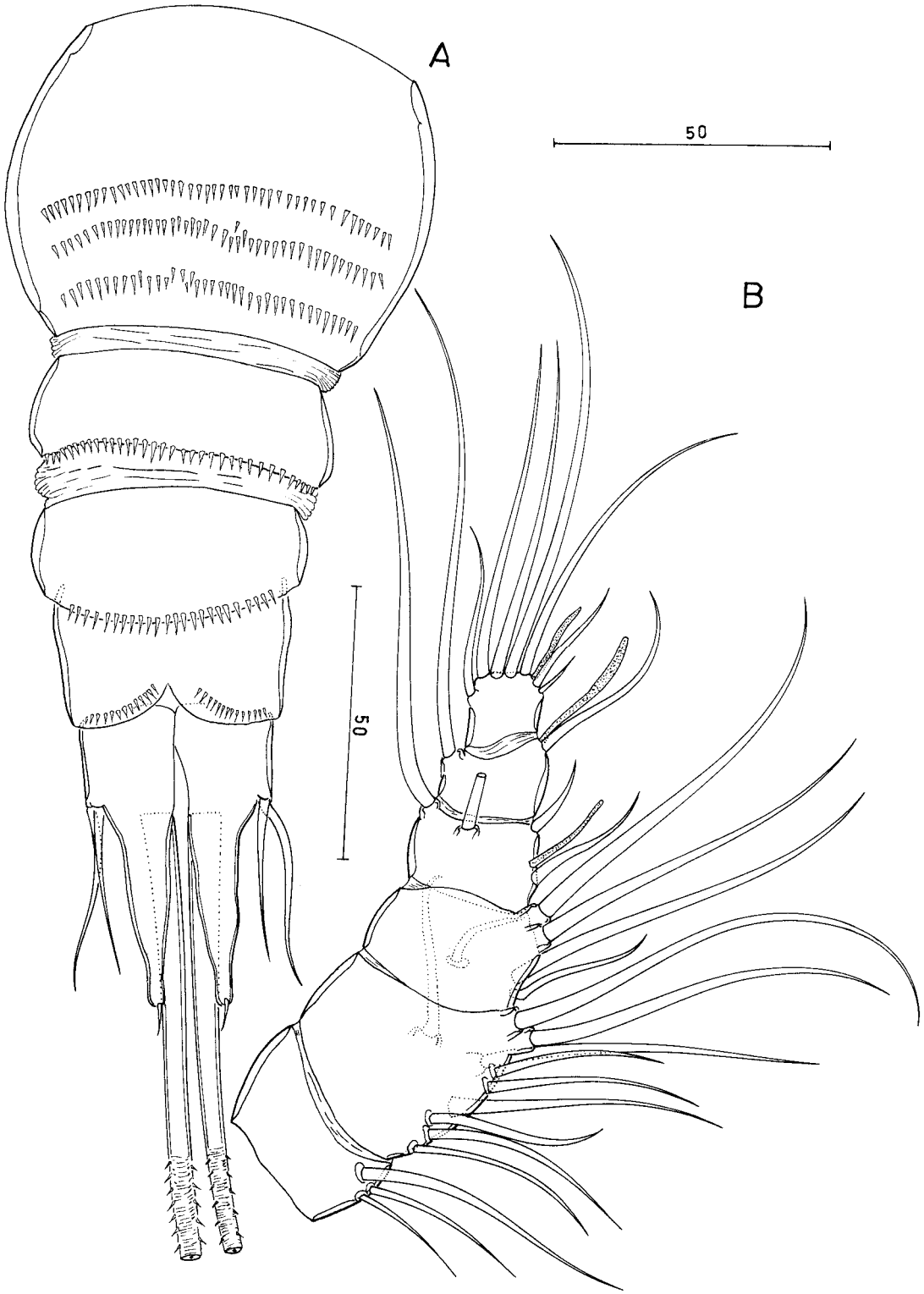

Figure 10. Dermoergasilus curtus n. sp. Adult female. A, urosome; B, antennule. Scale-bars in μm.

Antenna 4-segmented (Figure 9B), comprising coxobasis, 3-segmented endopod and curved claw. Coxobasis on slightly elevated pedestal. Second segment (first endopodal segment) nearly 1.8 times longer than coxobasis; long second plus third endopodal segments together comprising about 70% of length of first endopodal segment; curved claw about 3/4 length of second plus third endopodal segments combined; antenna with slightly inflated cuticle around first endopodal segment only; second endopodal segment with minute seta proximally on inner margin.

Mandible unsegmented, bearing anterior, distal and posterior blades; teeth present on anterior margin of anterior blade, both margins of distal blade and on posterior margin of posterior blade. Maxillule lobate, ornamented with spinules, bearing 2 long distal setae, minute inner seta and small medial process. Maxilla consisting of large syncoxa tapering distally and small, spatula-shaped basis armed anteriorly with rows of sharp teeth (Figure 11A).

Legs 1-4 (Figures 11B-C, 12A-B) with all rami 3-segmented except 2-segmented fourth exopod. Basis with row of spinules along posterior margin in legs 2-4. Lateral margins of both rami spinulate in all legs. Setules present on inner margin of first exopodal segment of all legs. Interpodal sternites spinulate (Figure 12C). Setal formula of legs as in *D. longiabdominalis* n. sp.

Fifth leg 2-segmented; short protopodal segment bearing outer seta; free exopodal segment with one short lateral seta plus 2 terminal setae (Figure 12D).

Remarks

This species differs from all other *Dermoergasilus* species, except for *D. intermedius* and *D. semicoleus*, in the presence of the hyaline inflated cuticle only around the first endopodal segment of the antenna, and by the small urosome with its short barrel-shaped genital double-somite and first free abdominal somite. The presence of zones of folded membrane between the genital double-somite and first free abdominal somite, and the first and second free abdominal somites, might be interpreted as evidence that the urosomal configuration of this species is somewhat intermediate between *Ergasilus* and typical *Dermoergasilus*.

The new species differs from *D. semicoleus* in the armature of the terminal endopodal segment of leg 1, in carrying two outer spines and four inner setae instead of two spines and five setae, respectively. The terminal exopodal segment of leg 2 is armed with six setae in *D. curtus* n. sp. compared to five in *D. semicoleus*, and the terminal endopodal segment of leg 2 carries a spine and four inner setae rather than a spine and three inner setae as in *D. semicoleus*.

The new species shares with *D. intermedius* the setation of the swimming legs; but it is relatively smaller (*D. intermedius* is 0.9-1.04 mm) and the anterior margin of the cephalothorax is different (in *D. intermedius* it is flat and the antennules are widely separated). Additional differences include the shape of the first endopodal segment of the antenna (which is more curved than that of *D. intermedius*), and the lateral seta on leg 5 is relatively longer than the knob-like lateral seta of *D. intermedius*; furthermore, the folded membranes between the genital double-somite and the first free abdominal somite, and between first and second free abdominal somites, are absent in *D. intermedius*. The lateral caudal setae are also both shorter than the digitiform process in *D. curtus*, whereas they are of unequal lengths, with the outer being longer than the digitiform process, in *D. intermedius*.

***Dermoergasilus amplectens* (Dogiel & Akhmerov, 1952)** (Figures 13-14)

Previous records: This species was originally recorded from the mouth of River Tumen-Ula in Russia, on *Mugil cephalus* L. (see Dogiel & Akhmerov, 1952). It has subsequently been recorded on the same host from Kojima Bay, Okayama, Japan, by Ho & Do (1982). It has also been reported from many localities around Australia (Kabata, 1992) and India (Ho et al., 1992).
Present records: Wakanoura and Tsu Shima, Japan; Kowie River, South Africa; all on *Mugil cephalus*.

Remarks

The specimens from Wakanoura are relatively smaller (0.91 ± 0.04 mm long, 0.30 ± 0.02 mm wide) than those from Tsu Shima (1.2 ± 0.2 mm long, 0.31 ± 0.01 mm wide). The markings on the cephalothorax are the same as in other *Dermoergasilus* species (Figure 13A). The genital double-somite and the first abdominal somite have a sclerotised cuticle and the two posterior abdominal somites are always reflexed anteriorly in fixed specimens (Figure 13B). The caudal rami are wide and the digitiform process is nearly twice as long as the ramus (Figure 13C). The material differs from previous descriptions in the presence of a minute terminal seta on the digitiform process, but this seta was probably overlooked by previous authors.

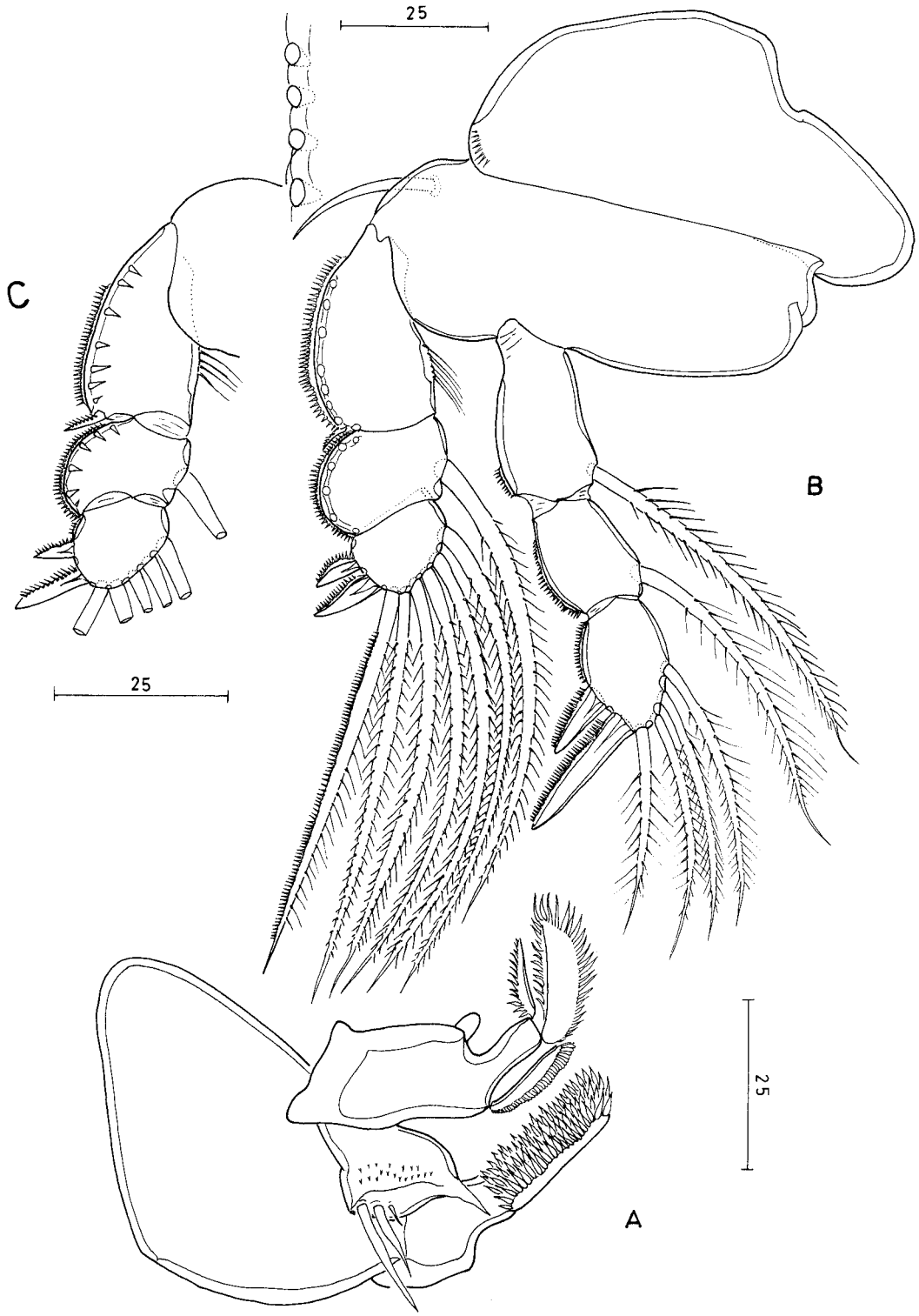

Figure 11. Dermoergasilus curtus n. sp. Adult female. A, mouthparts; B, first swimming leg, anterior; C, exopod of first swimming leg, posterior. Scale-bars in μm.

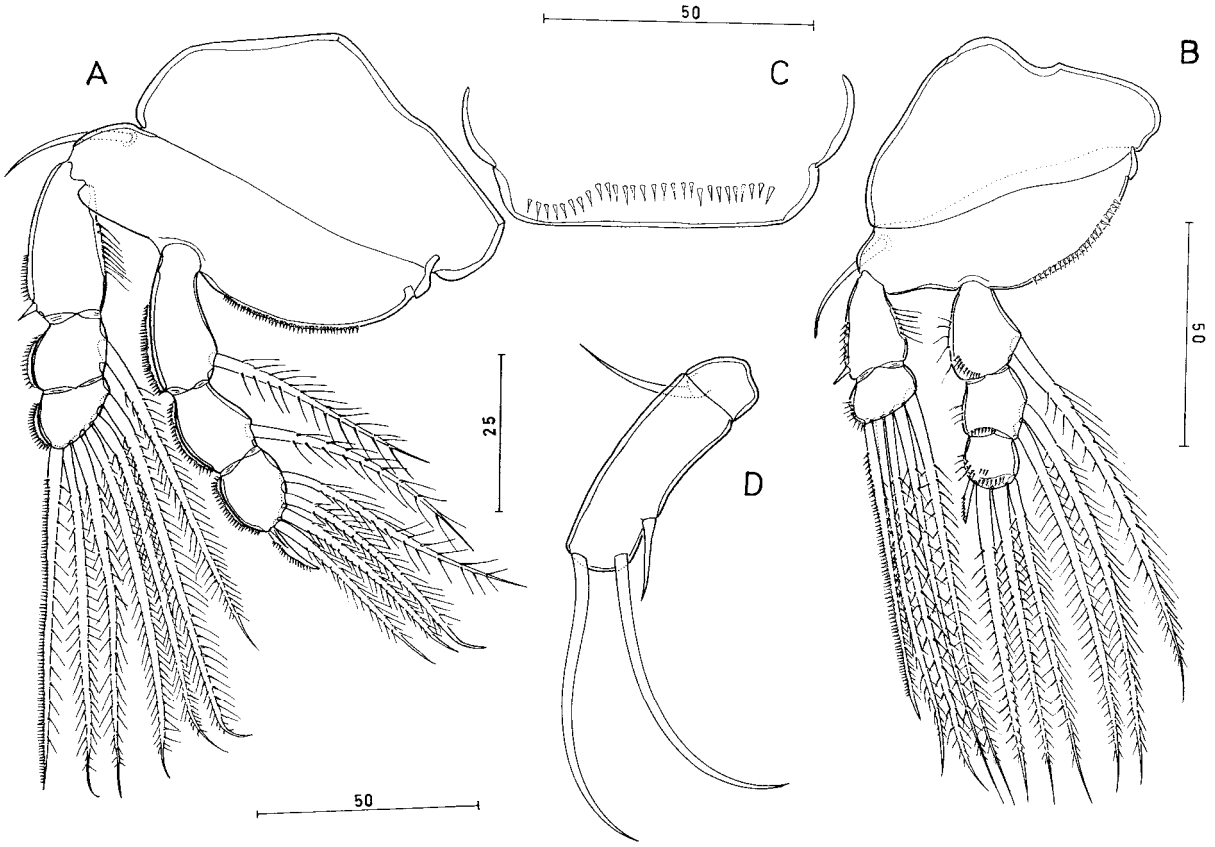

Figure 12. Dermoergasilus curtus n. sp. Adult female. A, second swimming leg, anterior; B, fourth swimming leg, anterior; C, interpodal sternite of the second swimming leg; D, fifth swimming leg. Scale-bars in μm.

The swimming leg setation is the same as in *D. longiabdominalis* n. sp. and leg 1 is characterised (Figure 13D) by the relative lengths of the outer margin spines in the exopod and the distal spines on the endopod.

The present specimens have a 6-segmented antennule, with setation as described by previous authors, and the antenna is completely ensheathed with inflated cuticle except for the claw. The coxobasis is elevated on a long anterolateral pedestal, and both anterior and lateral blocks of muscle are visible (Figure 14A, B).

The material from Kowie River, South Africa, has a mean length of 0.94 $\pm$ 0.04 mm and mean width of 0.36 $\pm$ 0.01 mm. This material closely resembles the Japanese material, but the anterolateral pedestal bearing the antenna is less well developed (Figure 14C).

***Dermoergasilus varicoleus* Ho, Jayarajan & Radhakrishnan, 1992** (Figure 15)

Previous records: This species was originally recorded on *Liza tade* (Forsskål) from Veli Lake, Trivandrum, India (Ho et al., 1992) and subsequently from *Liza abu* (Heckel) in Iraq (Ho et al., 1996).

Present records: *Liza subviridis* (Val.) (Calcutta, Orissa, Madras and Bombay).

Material

The paratype material (USNM Reg. No. 254502) was re-examined. It was confirmed that the second endopodal segment of the antenna comprises about 60% of the length of the first endopodal segment (Figure 15A) and that the first free abdominal somite constitutes nearly three-quarters the length of the genital double-somite. The digitiform process on the caudal ramus bears a minute terminal seta (Figure 15B).

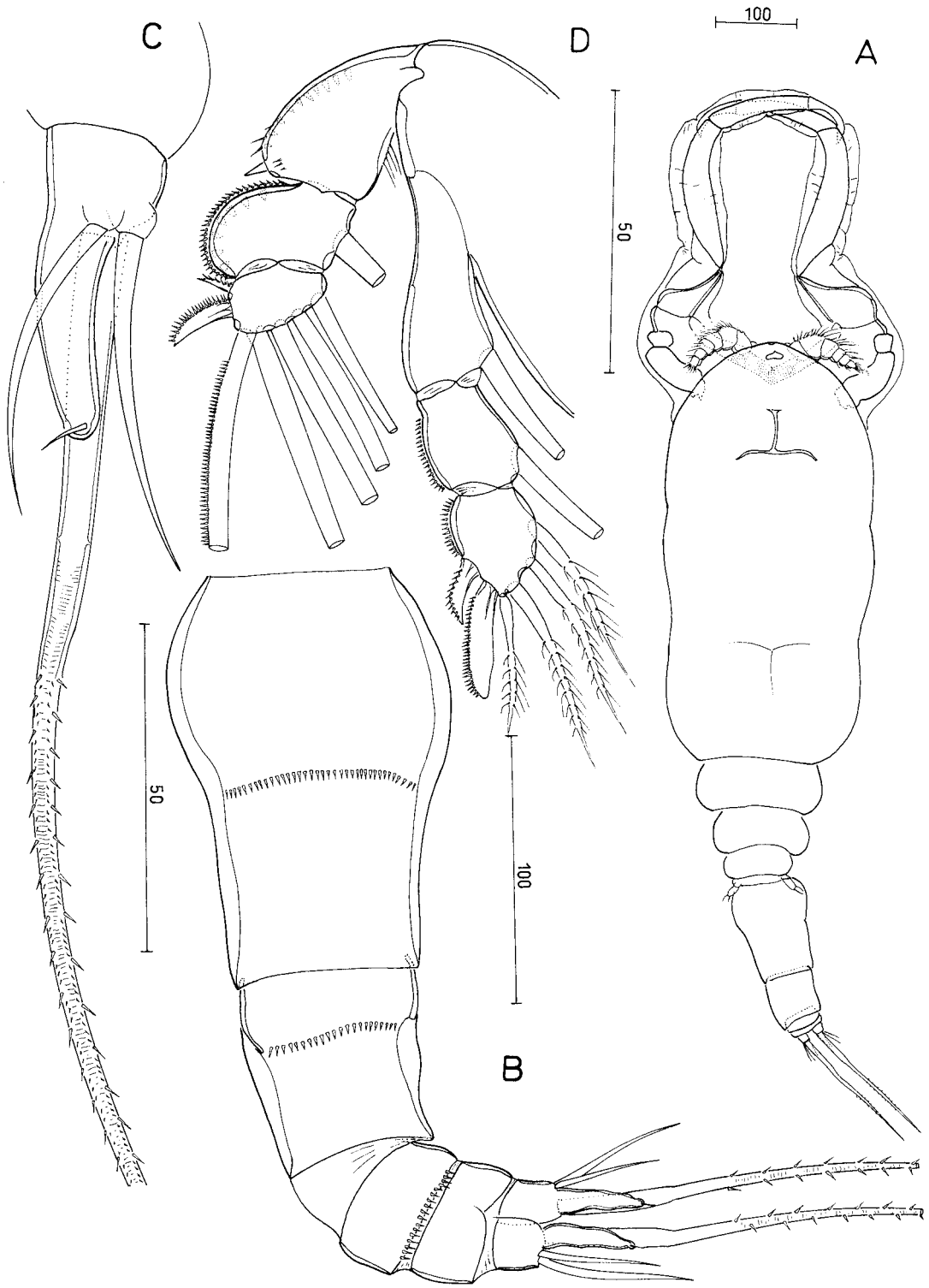

Figure 13. Dermoergasilus amplectens. Adult female. A, dorsal view; B, urosome; C, caudal ramus and digitiform process, lateral; D, first swimming leg, anterior. Scale-bars in μm.

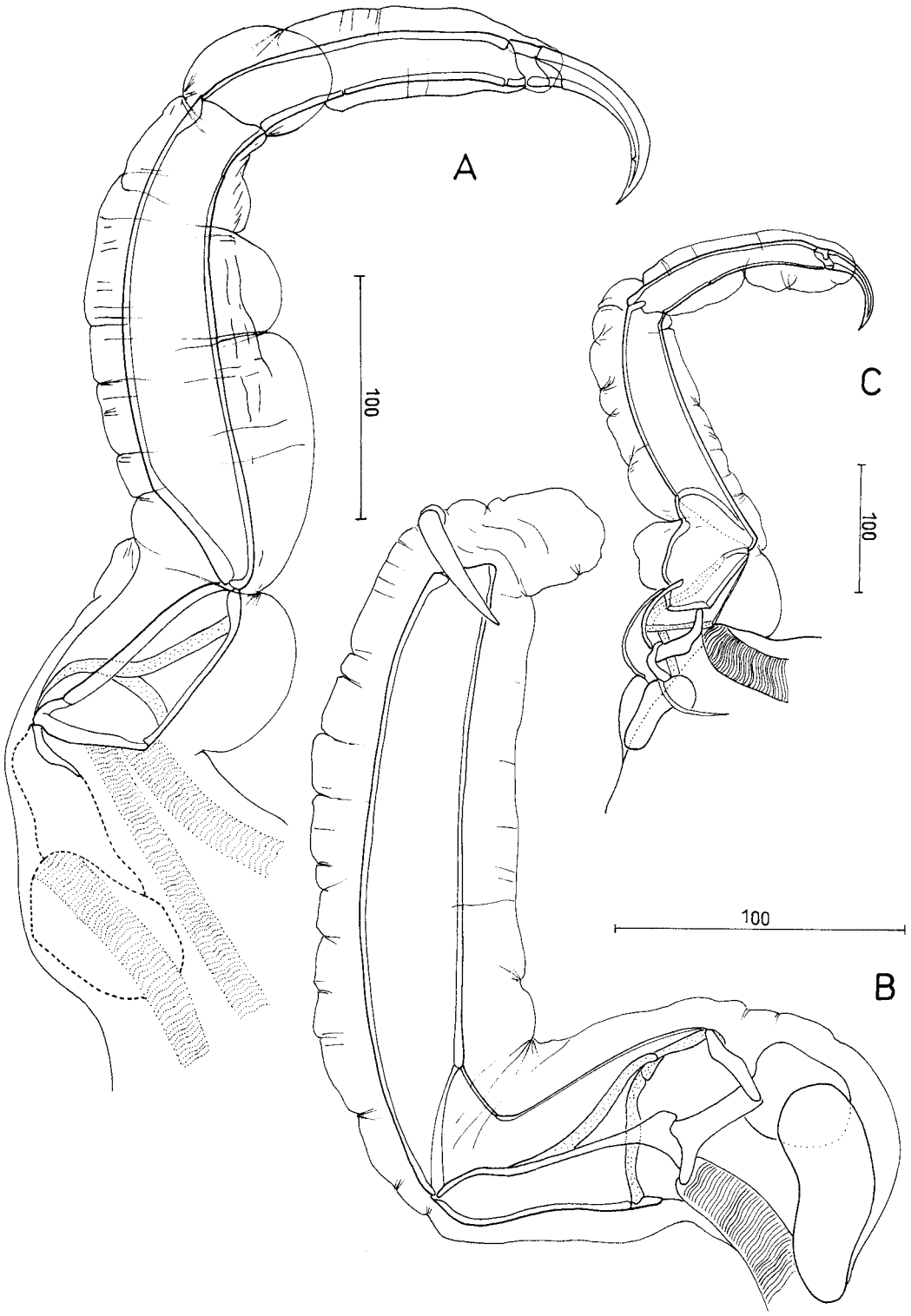

Figure 14. Dermoergasilus amplectens. Adult female. A, antenna, dorsal; B, antenna, lateral; C, antenna, ventral. Scale-bars in μm.

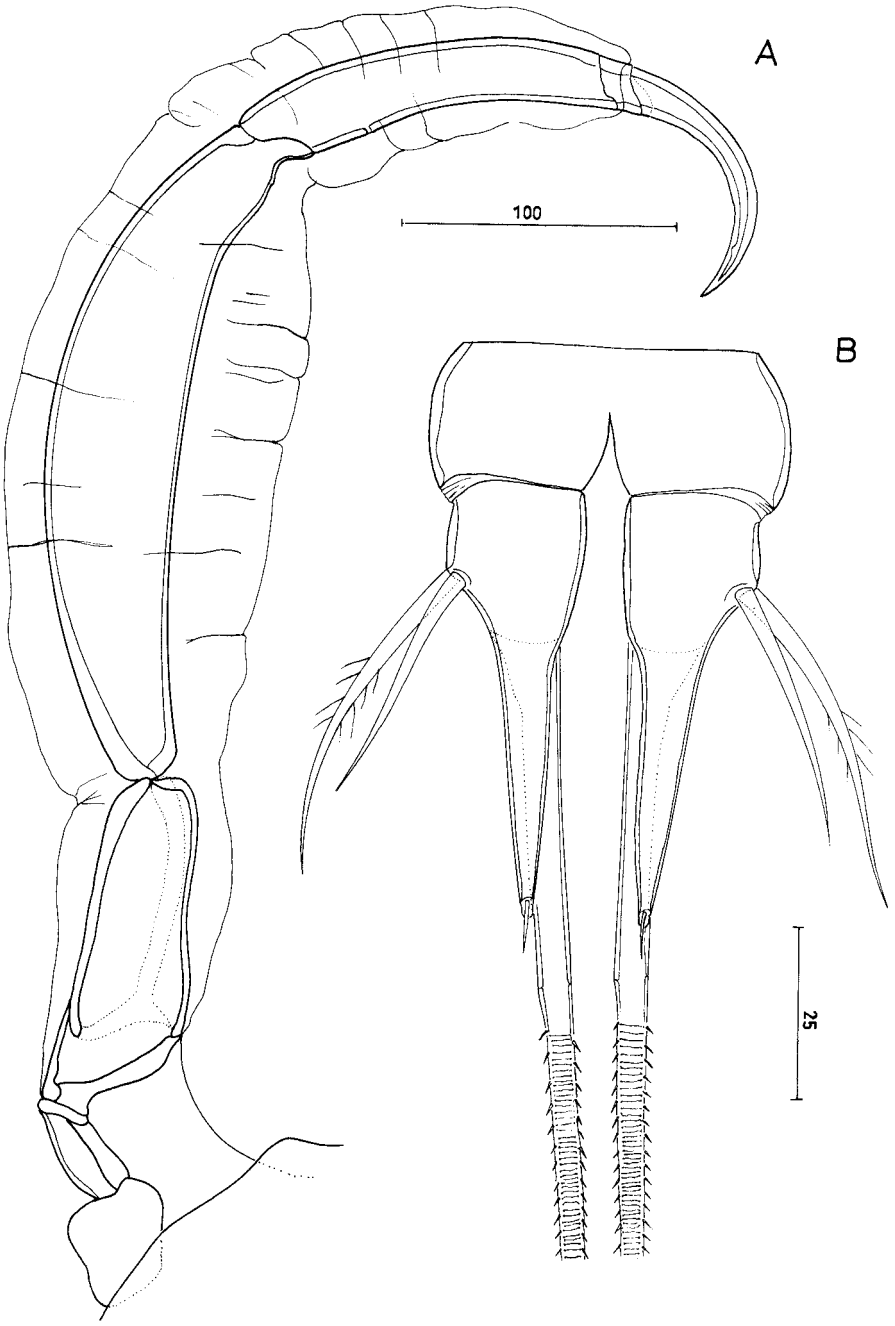

Figure 15. Dermoergasilus varicoleus. Adult female. A, antenna; B, anal somite and caudal rami. Scale bars in μm.

Key to the species of *Dermoergasilus*

1 Genital double-somite elongate (more than 1.3 times longer than wide) 2
– Genital-double somite short or ensheathed with membrane 7

2 Long anterolateral pedestal elevating base of antenna (Figure 14A-B); loose, cuticular membrane completely ensheathing antennal segments ..... *amplectens*

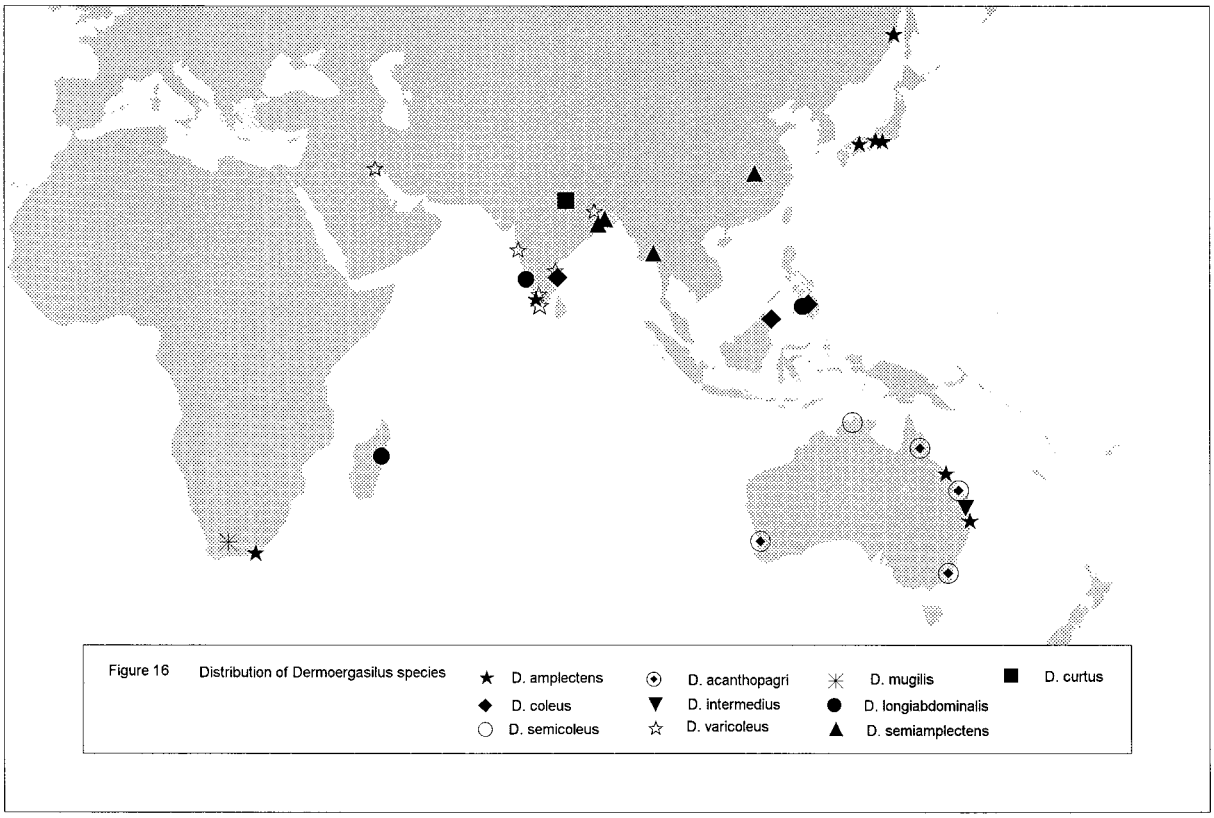

Figure 16. The reported geographical distributions of *Dermoergasilus* species.

– Short pedestal elevating base of antenna; cuticular membrane not completely ensheathing antennal segments 3
3 Second exopodal segment of leg 4 with 6 setae ..... *acanthopagri*
– Second exopodal segment of leg 4 with 5 setae 4
4 First endopodal segment of legs 1-4 without inner seta ..... *mugilis*
– First endopodal segment of legs 1-4 with inner seta 5
5 First abdominal somite about as long as wide; digitiform process on caudal ramus short (Figure 5D) ..... *semiamplectens*
– First abdominal somite longer than wide; digitiform process on caudal ramus long (Figure 1D) 6
6 Second plus small third endopodal segments of antenna long, curved, about 75% of first endopodal segment ..... *longiabdominalis*
– Second plus small third endopodal segments of antenna short, about 60% of first endopodal segment ..... *varicoleus*
7 Genital double-somite ensheathed by cuticular membrane ..... *coleus*
– Genital double-somite not ensheathed by cuticular membrane 8
8 Terminal endopodal segment of leg 1 with 5 setae; leg 2 with 5 setae on terminal exopodal segment and 3 on terminal endopodal segment. *semicoleus*
– Terminal endopodal segment of leg 1 with 4 setae; leg 2 with 6 setae on terminal exopodal segment and 4 on terminal endopodal segment 9
9 Antennules widely separated; first endopodal segment of antenna fairly straight; cuticular membrane not inflated, but loosely ensheathing all antennal segments; lateral seta on leg 5 knob-like; folded membrane not present between urosomites ..... *intermedius*
– Antennules not widely separated; first endopodal segment of antenna slightly curved; cuticular

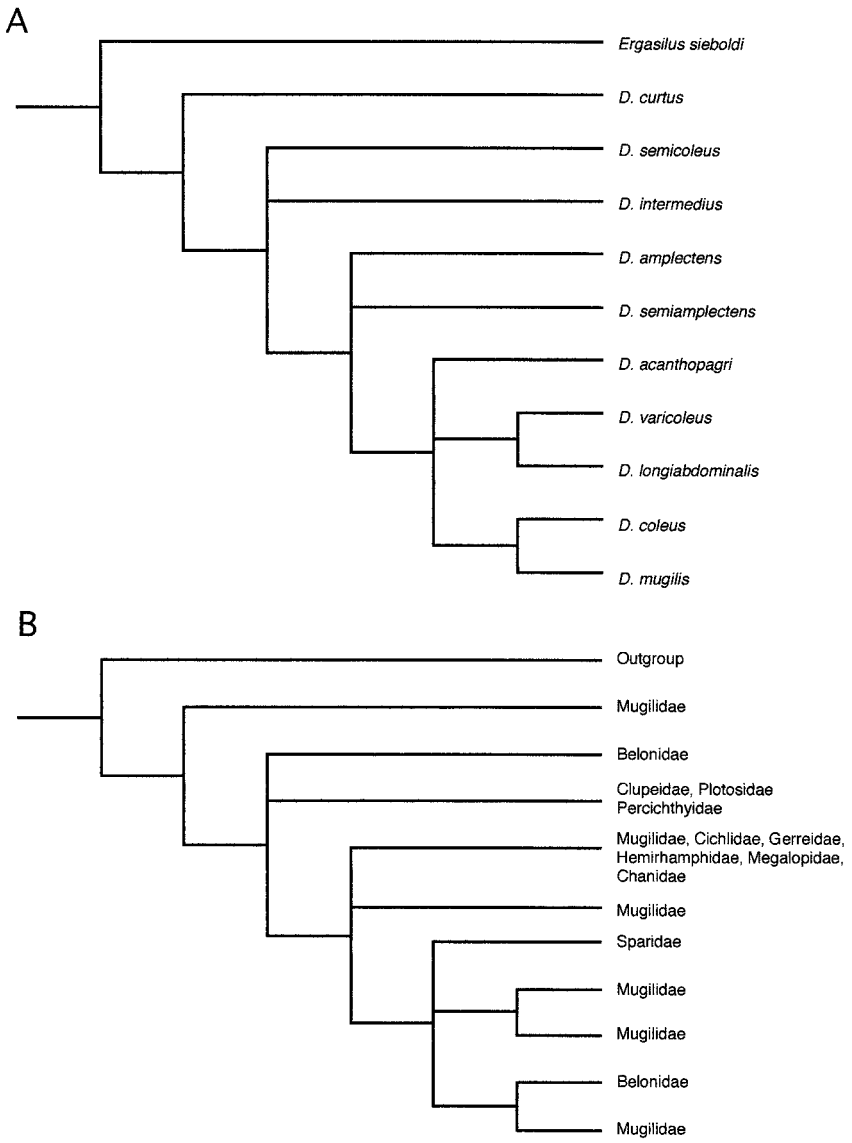

Figure 17. A. Single cladogram of *Dermoergasilus* species obtained from phylogenetic analysis using PAUP 3.1.1, Branch and Bound search. B. Host family utilisation of *Dermoergasilus* species.

membrane limited, developed only on inner surface of first endopodal segment of antenna; lateral seta on leg 5 not knob-like; folded membrane present between urosomites ..... *curtus*

Distribution of *Dermoergasilus* species and host utilisation

Five species of *Dermoergasilus* were recorded on hosts from the Indo-West Pacific region (Figure 16), three which are new. *D. longiabdominalis* n. sp. was found on three species of *Valamugil: V. engeli* from the Philippines and Madagascar; *V. cunnesius* from the Philippines and India (Figure 16); and *V. seheli* from Sri Lanka. *D. semiamplectens* n. sp. was recorded on four host species belonging to three genera of grey mullet: *Sicamugil hamiltoni* from Burma; *V. cunnesius* from China; and *Liza subviridis* and *Liza parsia* from India. *D. curtus* n. sp. was found on *Rhinomugil squamipinnis* from India.

D. amplectens was found on *Mugil cephalus* from Japan and S. Africa, and *D. varicoleus* recorded on *L.*

Table 1. Character matrix for phylogenetic analysis of *Dermoergasilus* species.

Character number *Taxon name*	1	2	3	4	5	6	7	8	9	10	11	12
D. amplectans	1	0	0	0	0	0	0	0	0	2	1	0
D. varicoleus	1	0	0	0	0	0	0	0	1	2	1	1
D. acanthopagri	1	0	0	0	0	0	0	0	1	2	1	0
D. coleus	?	0	1	0	1	1	0	1	?	2	1	1
D. semicoleus	0	1	0	1	0	0	1	0	0	1	1	1
D. mugilis	1	1	1	1	1	1	1	1	1	2	1	0
D. intermedius	0	0	0	0	0	0	0	0	0	1	1	0
D. longiabdominalis	1	0	0	0	0	0	0	0	1	2	1	1
D. semiamplectans	1	0	0	0	0	0	0	0	0	2	1	0
D. curtus	0	0	0	0	0	0	0	0	0	0	1	0
Ergasilus sieboldi	0	0	0	0	0	0	0	0	0	0	0	?

Table 2. Characters and character states of *Dermoergasilus* species used in phylogenetic analysis (using PAUP 3.1.1).

No	Character	States
1	Genital double-somite shape	0 = not elongate, 1 = elongate
2	Inner seta on endopod segment 1, leg 1	0 = present, 1 = absent
3	Outer spine on exopod segment 1, leg 2	0 = present, 1 = absent
4	Inner seta on endopod segment 1, leg 2	0 = present, 1 = absent
5	Outer spine on exopod segment 1, leg 3	0 = present, 1 = absent
6	Inner proximal seta on exopod segment 3 of leg 3	0 = present (5 setae), 1 = absent (4 setae)
7	Inner seta on endopod segment 1, leg 3	0 = present, 1 = absent
8	Outer spine on exopod segment 1, leg 4	0 = present, 1 = absent
9	First abdominal somite	0 = shorter than wide, 1 = longer than wide
10	Cuticular membrane around antenna	0 = absent or restricted to inner surface of first endopodal segment, 1 = ensheathing at least first endopodal segment but not inflated, 2 = extensive inflated membrane ensheathing most of limb
11	Digitiform process on caudal ramus	0 = absent, 1 = present
12	Digitiform process on caudal ramus	0 = less than twice as long as ramus, 1 = more than twice as long as ramus

subviridis from various localities around India (Figure 16). *D. amplectens* had previously been found on other grey mullet, including *Liza argentea*, *Valamugil seheli* and *M. cephalus* from Australia (Kabata, 1992). In India it occurs on the grey mullet, *V. seheli* and as well as on hosts of other families, including the Cichlidae (*Etroplus maculatus* (Bloch)), Gerreidae (*Gerres steifer* (Hamilton)), Hemiramphidae (*Hyporamphus xanthopterus* (Cuvier & Valenciennes)), Chanidae (*Chanos chanos* (Forsskål)) and Megalopidae (*Megalos cyprinoides* (Broussonet)) (Ho et al., 1992).

D. varicoleus was recorded on *Liza subviridis* in the present work, but it has been previously recorded on two other grey mullet, *L. tade* and *L. abu*, from India and Iraq, respectively (Ho et al., 1992; Ho et al., 1996). *D. mugilis* was originally recorded from *M. cephalus* in S. Africa (Oldewage & van As, 1988).

The remaining *Dermoergasilus* species are reported only from other host families. Three species from Australia have been reported on different fam-

ilies of coastal fishes: *D. intermedius* on members of the Plotosidae, Clupeidae and Percichthyidae (Kabata, 1992); *D. acanthopagri* on Sparidae (Byrnes, 1986); and *D. semicoleus* on one species of the family Belonidae (Cressey & Collette, 1970). *D. coleus* was known from three species of belonids from the Philippines (Cressey & Collette, 1970).

Dermoergasilus species are currently known to utilise 27 species of fishes representing 11 different host families (Figure 17B). Such a wide range of hosts reflects a low degree of host-specificity both at the family and at the species level. Its distribution is confined to the Old World, extending through the Palaearctic, Oriental, Australasian and Ethiopian regions.

Phylogenetic relationships of *Dermoergasilus* species

The phylogenetic analysis was based on a data-matrix (Table 1) of 12 morphological characters (Table 2) and 11 species (including the outgroup). The type-species of *Ergasilus, E. sieboldi* Nordmann, was chosen as the outgroup. The analysis was performed using PAUP 3.1.1. and the options employed were BRANCH AND BOUND search, with characters set as IRREVERSIBLE-UP. The analysis generated a single tree with branch length = 18, CI = 0.722 and f value = 16.

The single tree (Figure 17A) shows three unresolved trichotomies, but the ingroup, *Dermoergasilus*, is defined as monophyletic by the presence of the digitiform process on the caudal ramus. The first offshoot from the main lineage is *D. curtus*, which lacks the loose cuticular membrane ensheathing at least the first endopodal segment of the antenna in all other species. In *D. curtus* the loose cuticle is restricted to a small region on the inner surface of that segment. Next to diverge from the main clade, at an unresolved trichotomy, are *D. semicoleus* and *D. intermedius*. Both these species have loose membrane ensheathing the first endopodal segment of the antenna, but it is not as extensive or inflated as in all remaining species. These two species also retain a barrel-shaped genital double-somite in the female and lack the elongate genital double-somite that characterises the more derived species, from *D. amplectens* to *D. mugilis*. The species of this main clade share the following two apomorphies, an elongate genital double-somite and the presence of a well-developed membrane ensheathing the antenna. Within this derived clade the *D. acanthopagri* to *D. mugilis* group is defined by the elongate first free abdominal somite. *D. amplectens* and *D. semiamplectens* both retain the short first free abdominal somite. The *D. coleus-D. mugilis* group is defined by the loss of the outer spine on the first exopodal segment of legs 2 to 4. The *D. varicoleus-D. longiabdominalis* group is defined by the digitiform process on the ramus being more than twice as long as the caudal ramus. According to the tree topology, this apomorphy also arose independently in *D. coleus* and in *D. semicoleus*.

A simple host summary cladogram for *Dermoergasilus* (Figure 17B) is produced by replacing each species name with the host families utilised. Five of the species of *Dermoergasilus* included in the main clade occurred on members of the Mugilidae (*D. amplectens*, *D. semiamplectens*, *D. varicoleus*, *D. longiabdominalis* and *D. mugilis*). The clustering in a single clade suggests that their common ancestor may have already colonised mugilids as hosts. Further, the utilisation of a mugilid as host by the most plesiomorphic *Dermoergasilus* species, *D. curtus*, may be interpreted as evidence that the ancestor of *Dermoergasilus* ocurred on a mugilid host. Indeed, El-Rashidy (1999, figure 6.27) inferred that the genus *Dermoergasilus* belonged to a much larger clade which also included an as yet undescribed new species of *Ergasilus* (referred to under manuscript name of *E. extensus* in El-Rashidy, 1999), *Nipergasilus parabora* El-Rashidy & Boxshall and *Nipergasilus bora* (Yamaguti). The members of this larger clade occurred primarily on mugilid hosts. It is inferred here that *Dermoergasilus* species, such as *D. acanthopagri* and *D. coleus*, which occur on other families of coastal fishes (e.g. Sparidae and Belonidae) have probably switched hosts secondarily from the Mugilidae.

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