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The mesoparasitic genera of the Ergasilidae (Copepoda): with descriptions of new species of *Paeonodes* Wilson and *Therodamas* Krøyer

H. El-Rashidy[1,2] & G A. Boxshall[1]
[1]*Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[2]*Queen Mary and Westfield College, Mile End Road, London E1 4NS, UK*

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Abstract

One species of each of the three mesoparasitic ergasilid genera, *Therodamas* Krøyer, *Mugilicola* Tripathi and *Paeonodes* Wilson, is described in detail. The descriptions of *P. subviridis* n. sp. and *Mugilicola bulbosus* Tripathi are based on new material collected from *Liza subviridis* (Valenciennes) from Guam and India, respectively. The description of *Therodamas frontalis* n. sp. is based on material from *Mugil cephalus* L. in Brazil and the redescription of *Therodamas serrani* Krøyer is based on examination of syntype material. The geographical distributions of all three genera are summarised. Analysis of the phylogenetic relationships between species of these three genera indicates that *Paeonodes* and *Mugilicola* form a single clade and that *Paeonodes*, as currently constituted, is paraphyletic.

Introduction

There are three mesoparasitic genera of copepods within the family Ergasilidae, *Therodamas* Krøyer, *Paeonodes* Wilson and *Mugilicola* Tripathi. *Therodamas* was established by Krøyer (1863) to accommodate a new species, *T. serrani* Krøyer, 1863. The genus was placed in the family Lernaeidae by Wilson (1917), but was later transferred by Thomsen (1949) to the family Ergasilidae, based on similarities in the legs and mouthparts. Wilson (1944) described a new ergasilid with a long neck and established *Paeonodes* to accommodate his new species, *Paeonodes exiguus*. In 1960, Tripathi proposed a new family, the Therodamasidae, to accommodate *Therodamas* and another new genus, *Mugilicola* Tripathi, but he commented that this new family is closely related to the Ergasilidae. Hewitt (1969) described a second *Paeonodes* species, *P. nemaformis*, from New Zealand, accepted Tripathi's view and transferred *Paeonodes* to the family Therodamasidae. Cressey (1972) indicated that the morphology of the appendages of *Therodamas* is typically ergasilid, and that the neck-like separation of the anterior cephalic appendages from the mouthparts of *Therodamas* is unique within the ergasilids. Cressey suggested separating this genus from other ergasilids only at the subfamily level. Boxshall (1986) described a new species of *Mugilicola* from Australia and called attention to the different origins of the necks of *Mugilicola* and *Paeonodes* from that of *Therodamas*. He stressed the affinities of these genera with ergasilids, particularly in the form of the cephalic appendages and in the absence of maxillipeds in adult females. Based on Boxshall's (1986) discussion and Motta Amado's (1992) phylogenetic analysis, Motta Amado et al. (1995) discarded the family Therodamasidae and transferred its genera, *Therodamas*, *Mugilicola* and *Paeonodes*, to the Ergasilidae. Motta Amado (1992) and Abdelhalim et al. (1993) independently recognised that *Amazonicopeus* Thatcher, 1986 was synonymous with *Therodamas*.

The present paper describes new species of *Paeonodes* and *Therodamas*, and redescribes two species, *Mugilicola bulbosus* Tripathi, 1960 and *Therodamas serrani* Krøyer, 1863. The phylogenetic relationships are also examined between these three genera and *Teredophilus* Rancurel, the four of which were identified as a monophyletic group by the analysis of Motta Amado et al. (1995).

Materials and methods

Material was collected from the gills of grey mullet deposited in the fish collection of The Natural History Museum, London (BMNH). The copepods were removed from the gill arches, dissected and mounted in lactophenol as temporary slide preparations. Measurements were made with an ocular micrometer and drawings were made with the aid of a camera lucida on an Olympus BH2 microscope using differential interference contrast.

Mugilicola Tripathi, 1960

***Mugilicola bulbosus* Tripathi, 1960** (Figures 1A-F, 2A-D)
Syn. *Paeonodes mugilis* Pillai & Jayasree, 1978

Locality: Bombay.
Host: *Liza subviridis* (Valenciennes).

Description of female

Body comprising head, neck and trunk (Figure 1A). Mean body length 3.5 mm (n = 2). Head small, ovoid with prominent swelling dorsally (Figure 1B); rostrum elevated on produced frontal region also bearing antennules and antennae. Mouthparts located ventrally in middle of head.

Neck long and slender, comprising about 2/3 of total body length (Figure 1A); usually ensheathed within loose, folded tissue layer of host origin.

Trunk (Figure 1A) pear-shaped, constituting nearly 20% of total body length, bearing 3 pairs of biramous swimming legs. Leg 1 located just anterior to mid-level of trunk; legs 2 and 3 located posteriorly. Two setae present on surface of somite posterior to leg 3 (arrowed in Figure 1C): homology of setae difficult to establish (see 'Remarks' below).

Urosome small (Figure 1D), consisting of genital complex, (apparently comprising genital plus first and second abdominal somites), 2 free abdominal somites and caudal rami. Genital complex constituting 75% of urosome length; ornamented ventrally with 3 rows of spinules. Single row of spinules present on posterior margin of free abdominal and anal somites. Anal somite deeply incised. Caudal rami armed with 4 setae, ornamented with incomplete spinule row.

Antennule 5-segmented (Figure 2C), with first segment largest; setal formula as follows: 11: 6: 4: 2+ae: 6+ae.

Antenna 4-segmented with almost straight terminal claw (Figure 2D). Coxobasis short, robust, unarmed; second segment (= first endopodal segment) about 2.5 times longer than average width; armed with sclerotised spine medially. Second endopodal segment short, constituting nearly 1/3 of length of preceding segment; third endopodal segment very reduced, represented by minute sclerite. Claw robust and nearly twice as long as second endopodal segment.

Mouthparts (Figure 1E-F): mandible small, with anterior, mid and posterior blades. Maxillule small, with 2 setae and minute medial process. Maxilla (Figure 1E) comprising large syncoxa and small spatulate basis bearing teeth anteriorly.

Swimming legs 1-3 (Figure 2A-B) biramous, with 3-segmented rami. Spine and seta formula of legs as follows:

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

Two setae present on surface of somite posterior to leg 3 (arrowed in Figure 1C) representing leg 4 or leg 5 (see below).

Remarks

Four species of *Mugilicola* have been established to date: *M. bulbosus* from India (Tripathi, 1960), *M. smithae* Jones & Hine, 1978 from South Africa (Jones & Hine, 1978) and redescribed by Kruger et al. (1998) from Natal, *M. australiensis* Boxshall, 1986 from New South Wales, Australia (Boxshall, 1986) and *M. kabatai* Piasecki, Khamees & Mhaisen, 1991, from Iraq (Piasecki et al., 1991; Ho et al., 1996). All previous descriptions of *Mugilicola* reported that no traces of any legs posterior to the third pair of swimming legs could be found. The two setae present on the body surface posterior to leg 3 have probably been overlooked before. The homology of these two setae is difficult to establish, since they could represent either leg 4, or leg 5, or both. The close proximity of the two setae, and their positioning on the same transverse plane suggests that they represent a single leg, rather than both legs. Their position immediately anterior to the genital double-somite (Figure 1D) and their close resemblance to leg 5 in *Paeonodes* is here interpreted as evidence that they represent leg 5. Leg 4 is, therefore, regarded as absent in *Mugilicola*.

The caudal rami are armed with four setae in the present material instead of three setae as reported in

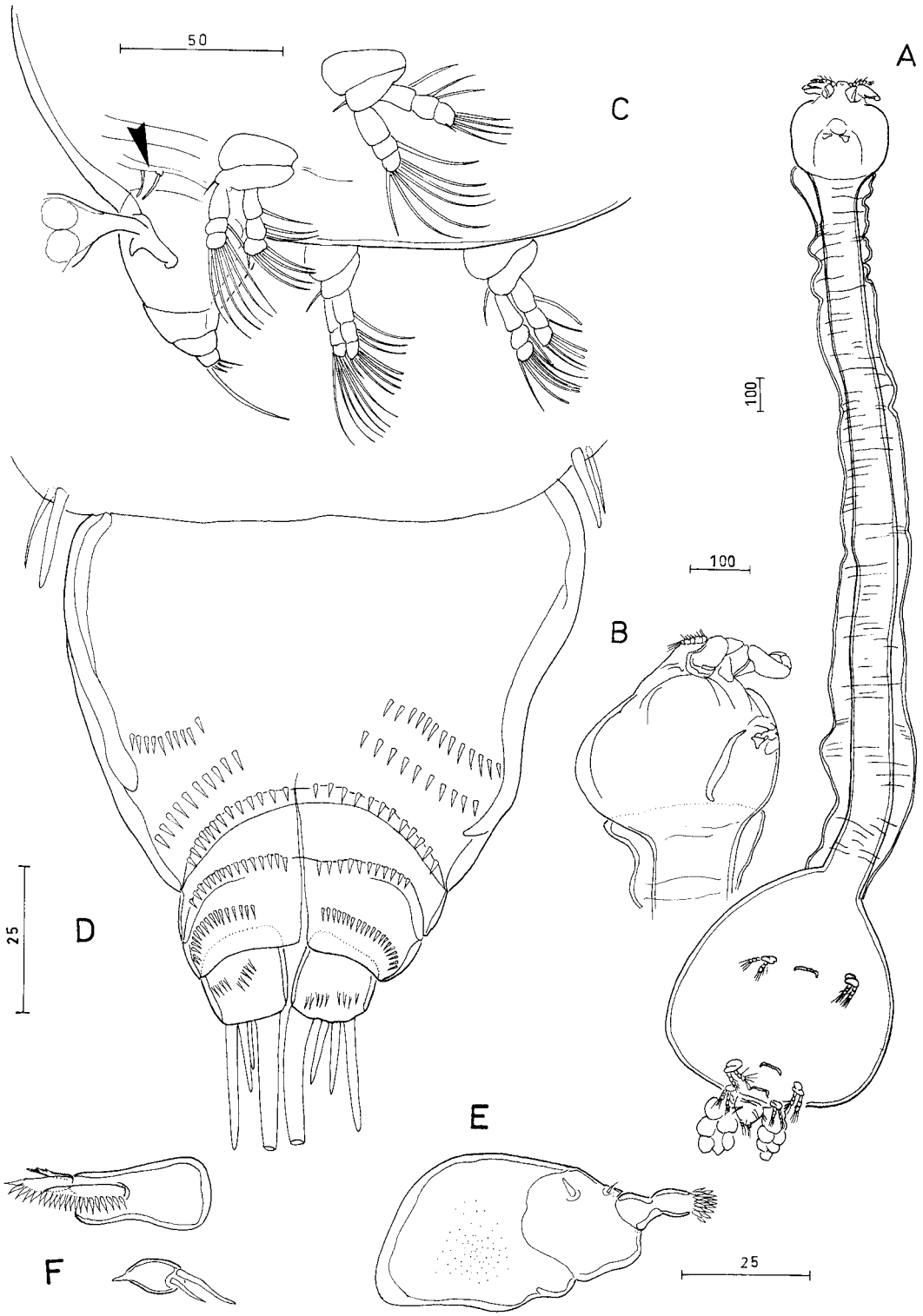

Figure 1. Mugilicola bulbosus Tripathi, 1960, adult female. A, vertral view ; B, head, lateral; C, lateral view of posterior part of trunk and urosome showing swimming legs 2 and 3, isolated setae on surface arrowed; D, urosome with leg 5,ventral; E, maxilla; F, mandible and maxillule. Scale-bars in micrometres.

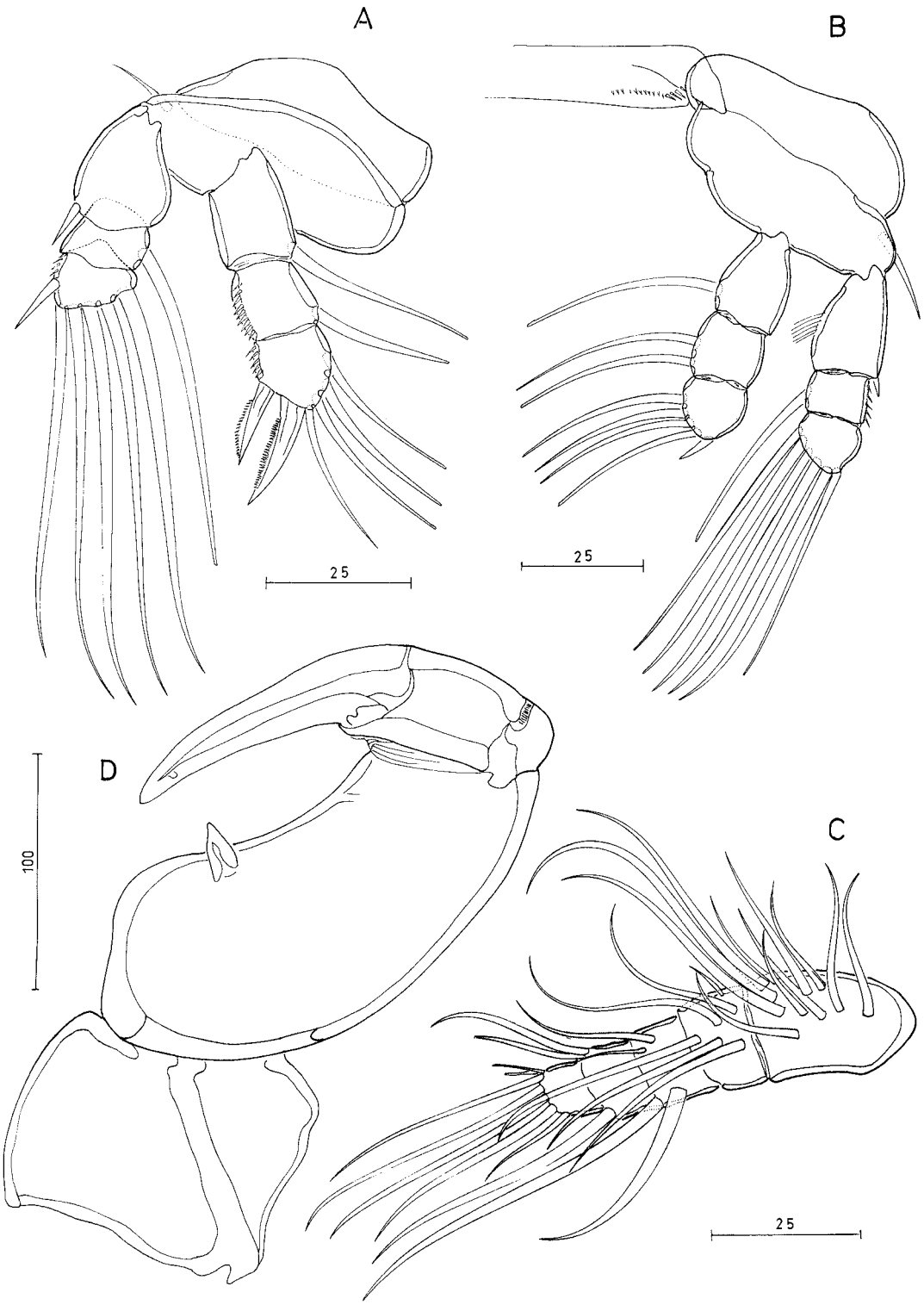

Figure 2. Mugilicola bulbosus Tripathi, 1960, adult female. A, first swimming leg, anterior; B, second swimming leg, anterior; C, antennule; D, antenna; Scale-bars in micrometres.

all previous descriptions of *Mugilicola* species, but these setae are fragile and easily broken. The present material resembles *M. kabatai* and *M. australiensis* in possessing an ovoid head and two free abdominal somites, but differs from them in the armature of the swimming legs. The armature of swimming legs of *M. smithae* is similar to that of the present material, but these two species can be readily distinguished since the posterior margin of the head of *M. smithae* is provided with trilobate processes on both sides. The present material is identified as *M. bulbosus*, since it has similar head and body morphology and occurred on the same host genus (*Liza*) in the same general locality (India). The apparent differences in the armature of the swimming legs are probably due to inaccuracies in the original description, because the legs are usually covered with mucus, and the setae are fragile and easily broken.

The species of *Paeonodes* described as new by Pillai & Jayasree (1978), *P. mugilis*, is here recognised as a synonym of *Mugilicola bulbosus*. It carries three pairs of biramous swimming legs and Pillai & Jayasree (1978) reported no trace of the fourth legs. This character indicates that its affinities lie with the species traditionally placed in *Mugilicola*, rather than with *Paeonodes*. It has similar gross morphology and very similar antennae to *M. bulbosus*, and the apparent differences in the armature of the swimming legs are probably due to inaccuracies in the original descriptions. For example, Pillai & Jayasree (1978, figure 12) show an inner seta on the first exopodal segment of leg 2, but a seta in this position is unknown throughout the entire order Poecilostomatoida (Huys & Boxshall, 1991).

Paeonodes Wilson, 1944

***Paeonodes subviridis* n. sp.** (Figures 3A-F, 4A-H)

Type-material: Female holotype (BMNH Reg. No. 1999. 1529); female paratypes (BMNH Reg. Nos. 1999. 1530-1531).
Type-locality: Guam.
Type-host: *Liza subviridis* (Valenciennes).
Etymology: The specific name refers to the type-host.

Description of female

Body comprising head, neck and trunk (Figure 3A). Mean body length 4.0 mm (n = 2). Head small (Figure 3D) with inverted T-shaped marking; rostrum elevated, antennules and antennae located frontally. Mouthparts located ventrally in middle of head.

Neck long and slender, comprising nearly 70% of total body length (Figure 3A); usually ensheathed within tube of folded tissue of host origin.

Trunk pear-shaped, constituting nearly 25% of total body length, bearing 4 pairs of swimming legs, first leg located at mid-level of trunk; second, third and fourth legs located posteriorly (Figure 3A). Two isolated setae present on surface of trunk posterior to leg 4, representing leg 5 (Figure 4D).

Urosome small (Figure 3C), consisting of genital double-somite and incompletely 3-segmented abdomen bearing caudal rami. Genital double-somite constituting nearly 60% of urosome length with paired slit-like genital apertures orientated longitudinally; row of spinules present ventrally on posterior margin (Figure 4A). First and second free abdominal somites fused dorsally, forming sclerotised double tergite (Figure 3B), but separate ventrally and each ornamented with ventral spinule row along posterior margin (Figure 4A). Anal somite deeply incised, with ventral spinule rows. Each caudal ramus armed with only 3 setae, however setae fragile and easily broken, so armature possibly incomplete.

Antennule 5-segmented (Figure 3E), tapering distally; first segment largest; setal formula as follows: 13: 5: 4+ae: 2: 7, probably incomplete.

Antenna 4-segmented with slightly curved terminal claw (Figure 3F). Coxobasis short, robust with minute inner seta; first endopodal segment robust, wider proximally, armed with strong spine medially. Second endopodal segment short, constituting less than 1/3 of first segment length; third endopodal segment vestigial, represented by minute sclerite (arrowed in Figure 3F). Claw robust, nearly 3 times longer than second endopodal segment.

Mouthparts small; mandible (Figure 4G) with anterior, middle and posterior blades. Maxillule (Figure 4F) small, with 2 setae and small medial process. Maxilla (Figure 4E) comprising large syncoxa and small spatulate basis, bearing small sharp teeth anteriorly.

Swimming legs 1-4 (Figure 4B-C, H) biramous, legs 1 to 3 with 3-segmented rami, leg 4 (Figure 4H) with 1-segmented exopod bearing only 4 setae, and 2-segmented endopod. Spine and seta formula of legs as follows:

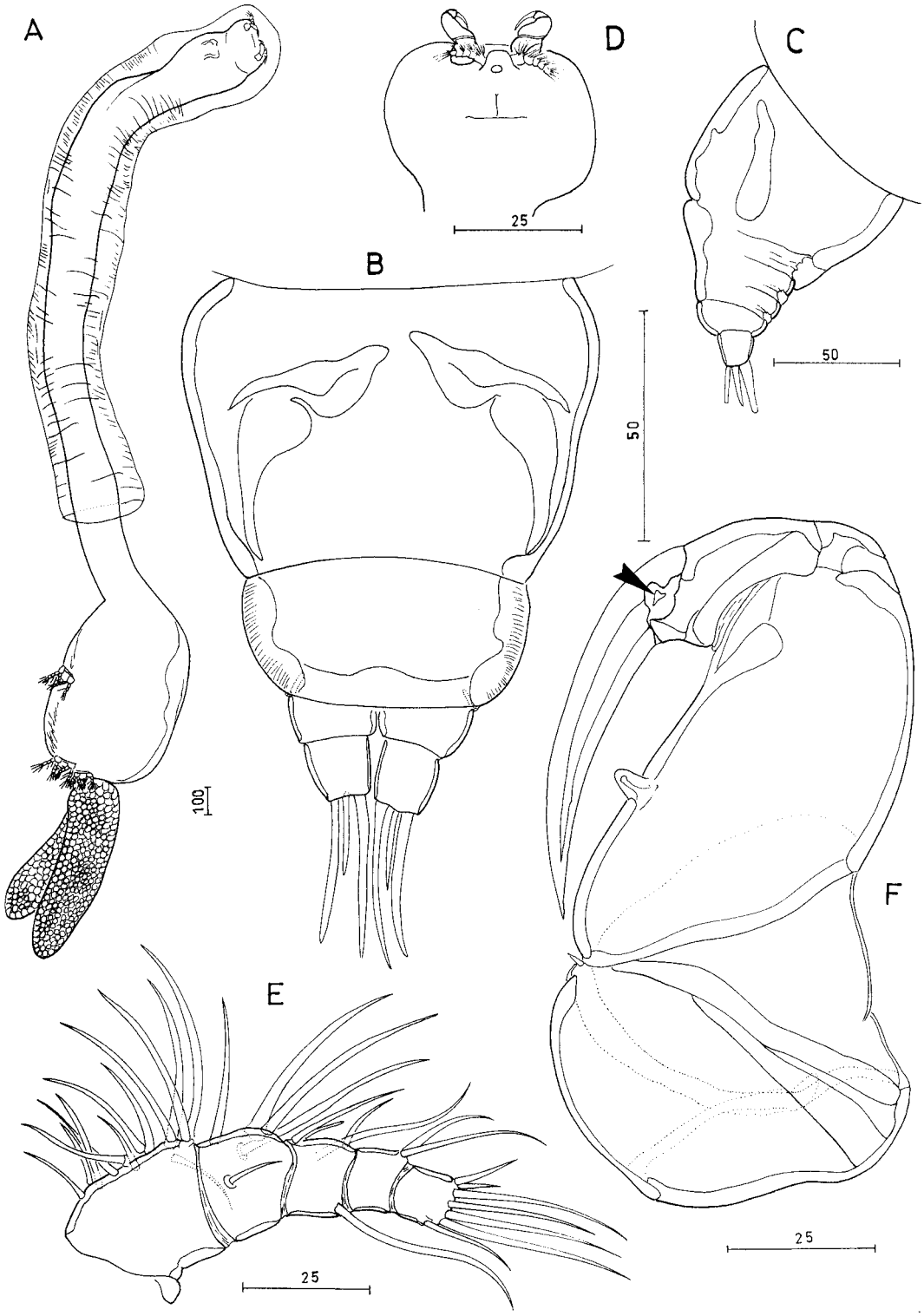

Figure 3. Paeonodes subviridis n. sp., adult female. A, lateral view; B, urosome, dorsal; C, urosome, lateral; D, head, dorsal; E, antennule, F, antenna, anterior with minute sclerite representing third endopodal segment arrowed. Scale-bars in micrometres.

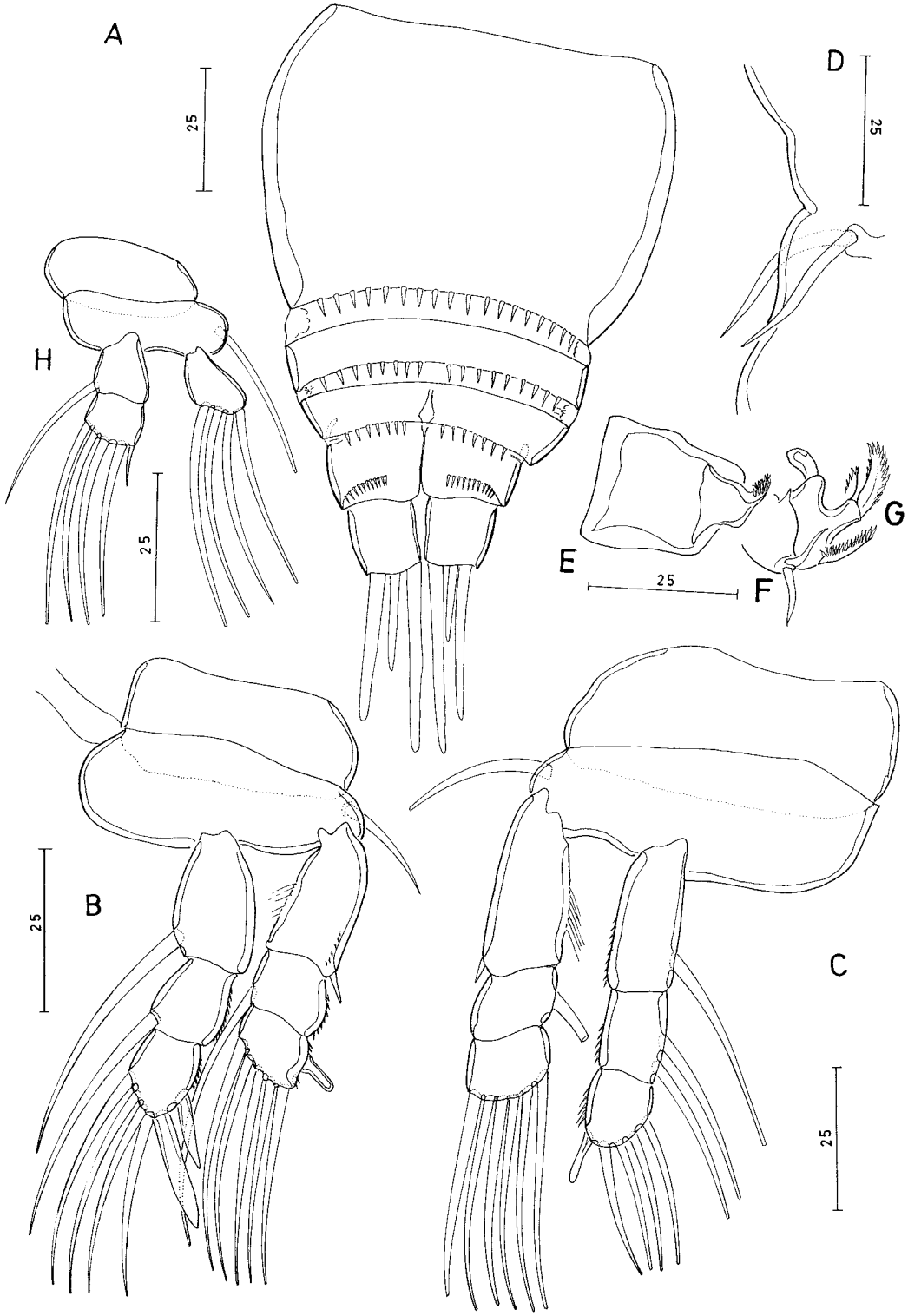

Figure 4. Paeonodes subviridis n. sp., adult female. A, urosome, ventral; B, first swimming leg, anterior; C, second swimming leg, anterior; D, fifth swimming leg, posterior; E, maxilla, ventral; F, maxillule, ventral; G, mandible; H, fourth swimming leg, anterior. Scale-bars in micrometres.

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

Setules present on inner margin of first exopodal segment of legs 1 to 3; other spinulation as figured (Figures 4B-C). Terminal exopodal segment of leg 1 with at least one outer spine; presence of second spine indicated by scar on segment could not be confirmed on material available.

Remarks

Three species of *Paeonodes* have been described: *P. exiguus*, found on an unknown host of the family Verillidae from an unknown locality (see Hewitt, 1969); *P. nemaformis* from the Haupiri River near Kopara, South Island, New Zealand (Hewitt, 1969) and *P. lagunaris* van Banning, 1974 from Saumo-Lagoon, Ghana (van Banning, 1974). The first species was inadequately described and, although the type-specimen was re-examined by Hewitt, it was in a poor condition and he was unable to give more detailed information about the swimming legs. An incomplete and unidentified specimen of *Paeonodes* was reported from an Australian mugilid *Aldrichetta forsteri* (Valenciennes) by El-Rashidy & Boxshall (1999).

The present species differs from *P. exiguus* and *P. nemaformis* in lacking cephalic lobes. It differs from *P. lagunaris* in the armature of the swimming legs. In addition, all three previously known species were described as having both rami of leg 4 only 1-segmented, whereas the new species leg 4 has 1-segmented exopod and 2-segmented endopod. Leg 4 is difficult to observe and the apparent 1-segmented endopod in the three previously described species requires verification. Leg 5 has not been reported before in any *Paeonodes* species: here it is represented by two separate setae located posterolaterally on the body surface at the trunk/urosome boundary. One seta represents the outer protopodal seta and the other, the exopod. The urosomites are not totally fused, as reported in the other species: three abdominal somites are defined ventrally, although the first and second free abdominal somites are fused dorsally.

Therodamas Krøyer, 1863

***Therodamas serrani* Krøyer, 1863** (Figure 5A-F)
Synonymy: Non *Therodamas serrani* of Thomsen (1949); non *Therodamas serrani* of Carvalho (1955)

Type-material: The "Type" vial in Zoologisk Museum, Copenhagen, contains 15 syntype metamorphosed adult females: 3 with heads, 1 with a damaged head, and 11 headless but with at least some neck plus an intact trunk. In addition the vial contained 5 incomplete trunks and 4 detached egg-sacs.
Type-locality: "Danish West Indies".
Type-host: *Serranus* sp.

Description of female

Cephalothorax (Figure 5A) modified, incorporating "neck" of entirely cephalic origin, constituting about 44.5% of body length and separating antennary and oral regions. Antennary region small, about 10.5% of body length, bearing antennules and antennae anteriorly; region produced into irregular posteroventrally directed lobes originating posterior to level of antennae (Figure 5A-B). Prominent rostrum and maxillae marking location of mouthparts (Figure 5A) at junction of "neck" and trunk. Trunk formed from postantennary cephalothorax, free pedigerous somites and urosome, comprising 45% of total length. Tergites of first to fifth pedigerous somites distributed along cylindrical, fleshy trunk (arrows 1 to 5 in Figure 5A). Urosome tapering from broad junction with prosomal part of trunk. Urosomites defined dorsally only by presence of tergites; urosomites not separated ventrally. Location of genital double-somite indicated by presence of paired longitudinal genital apertures. Three free tergites visible, presumably representing second and third abdominal somites and anal somite. Caudal rami defined at base, bearing 4 setae, inner longest (one seta missing from specimen shown in Figure 5C); spinule row present distally.

Antennule 5-segmented; setal formula not observed. Antenna 4-segmented; coxobasis massive, first endopodal segment robust, armed with spine medially; terminal claw strong (Figure 5D).

Swimming legs 1-4 damaged or incomplete in most syntypes but rami 3-segmented except 2-segmented endopod in leg 1 (Figure 5E) and 2-segmented exopod in leg 4. Interpodal sternites not observed. Spine and seta formula (based on syntype

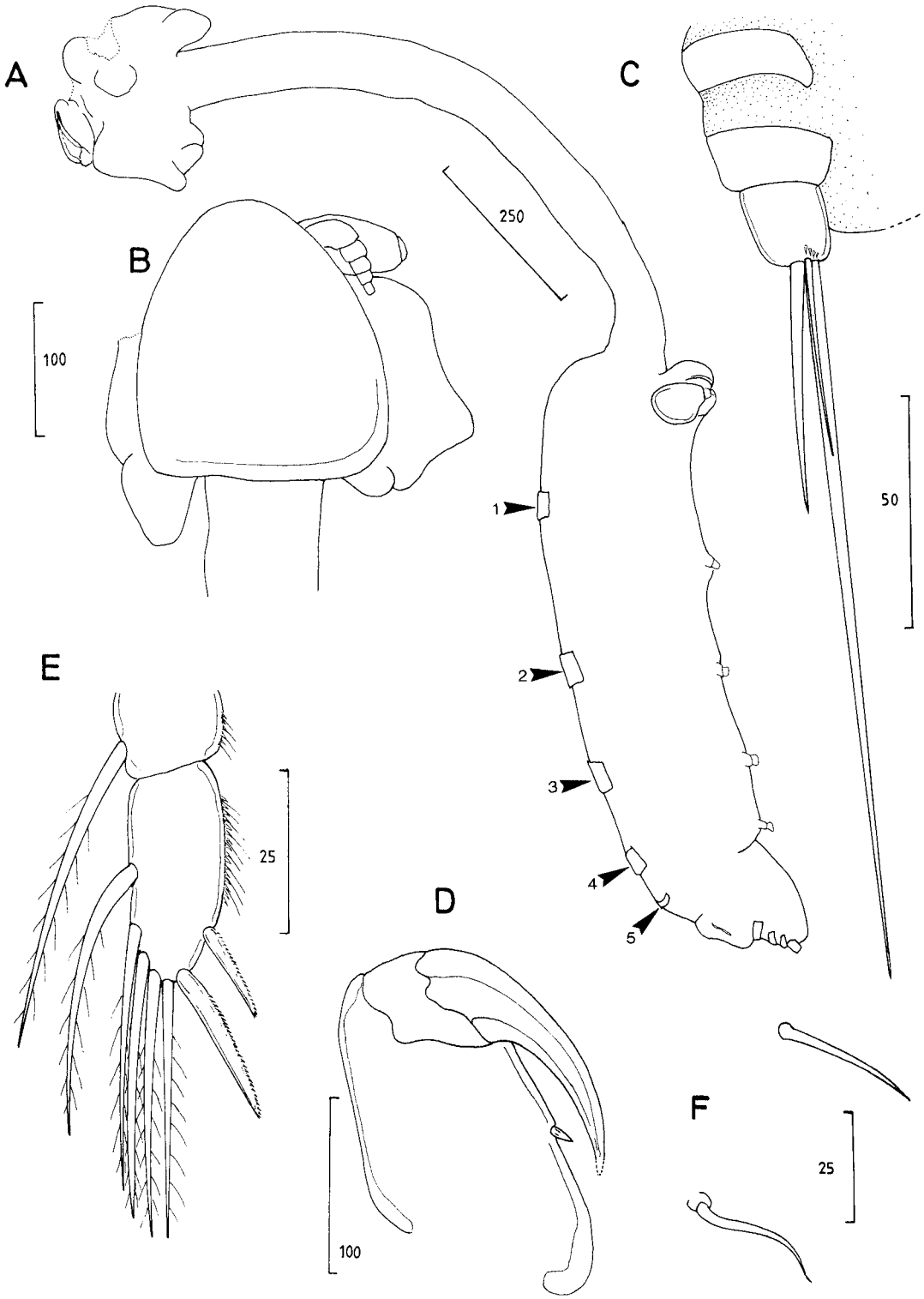

Figure 5. Therodamas serrani Krøyer, 1863, syntype females. A, habitus; B, antennary part of head, dorsal; C, posterior extremity of trunk showing anal somite and caudal rami; D, antenna, ventral in situ; E, endopod of leg 1; F, fifth swimming leg. Scale-bars in micrometres.

series) as follows:

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

Distal spines on endopod of leg 1 unequal, with outer 1.67 times longer than inner (Figure 5E). Fifth leg represented by 2 setae, each carried on separate papilla (Figure 5F).

Remarks

The original description of *T. serrani* by Krøyer (1863) is inadequate by modern standards and inaccurate. Both the redescription of *T. serrani* by Thomsen (1949), based on material collected from *Pimelodus barbus* (Lacepède) (as *Tachyurus barbus* (Lac.)) from the mouth of the Santo Lucía river in Uruguay, and the brief redescription of *T. serrani* by Carvalho (1955), from *Mugil* sp. off the coast of São Paulo State, are here treated as misidentifications of the new species, *T. frontalis*, described below. Fortunately Krøyer's type-material is safely deposited in the Zoologisk Museum, Copenhagen. Re-examination of this material has permitted the above supplementary description, based on the syntype series. It is unnecessary to designate a lectotype because there is no indication that the type-series contains a mixture of taxa.

A few additional details of the appendages were obtained by examining whole mounts only – the syntypes were not dissected. On some headless specimens the rami of some legs could be observed and the setal formula given above is based on observations of the syntype series. From one headless specimen drawings were made of the endopod of the first leg (Figure 5E), leg 5 (Figure 5F) and the caudal extremity of the urosome (Figure 5C). In the metamorphosed adult female the tergite of the second free abdominal somite, followed by the anal somite and the caudal rami (Figure 5C), resembles, in lateral view, the figure given by Thatcher (1986) of the posterior end of *T. elongatus* (Thatcher, 1986). Thatcher's interpretation of these structures as remnants of abdominal somites is confirmed here for *T. serrani*. The structure referred to by Thatcher as "a protrusible mouth tube" is identified here as formed by the labrum and maxillae.

Araujo & Boxshall (in press) described premetamorphic females of *Therodamas* taken from the plankton of the Piauí River estuary in Brazil. They attributed this material to *T. serrani* primarily on the basis of leg setation characters.

***Therodamas frontalis* n. sp.** (Figures 6A-E, 7A-C, 8A-D, 9A-D)
Synonymy: *Therodamas serrani* of Thomsen (1949); *T. serrani* of Carvalho (1955)

Type-material: Female holotype (BMNH Reg. No. 1999.1519); nine female paratypes (BMNH Reg. Nos. 1999.1520-1528).
Type-locality: Rio Grande do Sul, Brazil.
Type-host: *Mugil cephalus* (as *Mugil platanus*).
Etymology: The specific name refers to the anteriorly directed lobes on the head that distinguish this species.

Description of female

Cephalothorax (Figure 6A) modified, incorporating "neck" of entirely cephalic origin, constituting nearly 20% of body length and separating antennary and oral regions. Antennary region small, bearing antennules and antennae anteriorly; frontal part of cephalic shield small but well defined and ornamented with 2 circular markings dorsally. Antennary region bearing 2 anteroventral lobes originating posterior to antennae (Figure 6C,D). Trunk including 4 poorly-defined pedigerous somites, decreasing in width posteriorly. First pedigerous somite not separate from cephalothorax; first swimming leg located nearly at middle of trunk (Figure 6E). Tergites of incorporated pedigerous somites not defined on dorsal surface of trunk (Figure 6A). Urosome small, inflated (Figure 9B), comprising genital complex incorporating genital double-somite plus second abdominal somite, third abdominal somites and anal somite. Anal somite deeply incised and ornamented with 2 rows of spinules ventrolaterally. Caudal rami with spinules posteriorly and bearing 4 caudal setae; large medial seta spinulate.

Rostrum triangular (Figure 6B). Antennule 5-segmented (Figure 7A), tapering distally; first segment largest; setal formula: 11: 5+ae: 4: 2+ae: 7.

Antenna 4-segmented with curved terminal claw (Figure 7B). Coxobasis short, massive, with inner seta; first endopodal segment robust, broad proximally and tapering distally, armed with spine medially. Second endopodal segment short, constituting less than one-third length of first segment. Third endopodal segment vestigial, bearing minute seta anteriorly (Figure 7C). Claw robust, nearly 1.7 times longer than second endopodal segment.

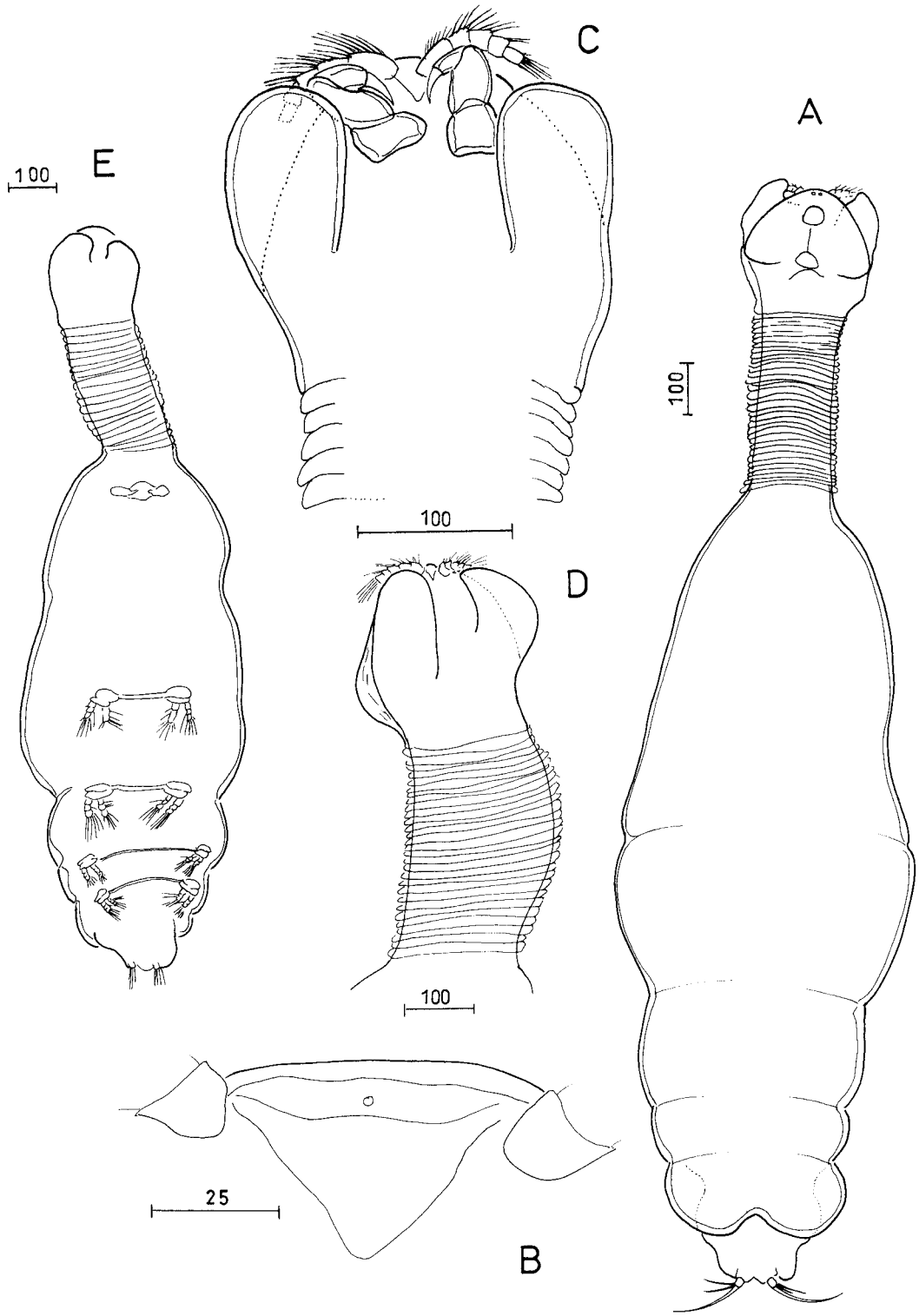

Figure 6. Therodamas frontalis n. sp., Holotype female. A, dorsal view; B, rostrum; C, head, ventral; D, head and neck, lateral; E, adult female, ventral view. Scale-bars in micrometres.

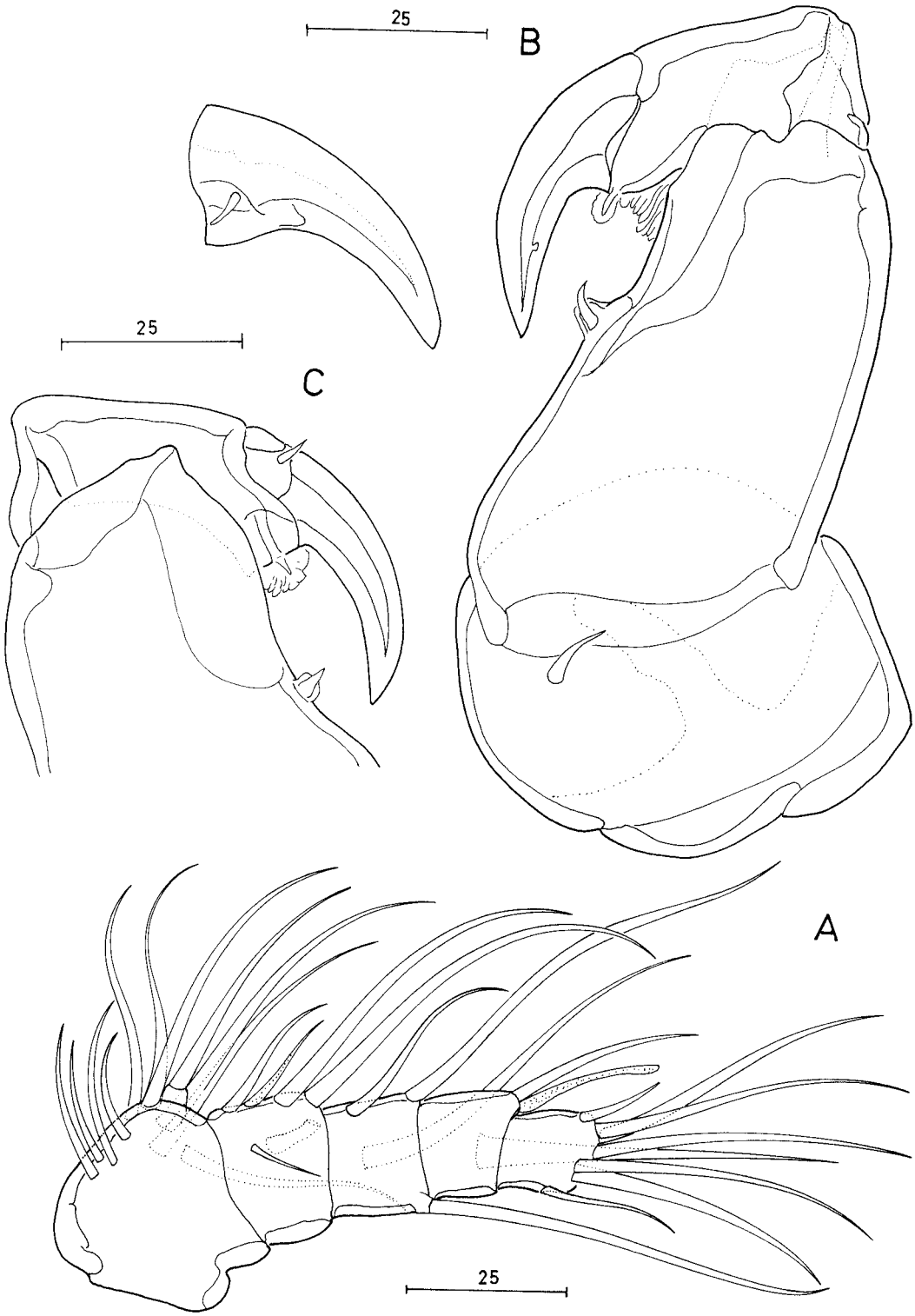

Figure 7. *Therodamas frontalis* n. sp., Holotype female. A, antennule; B, antenna, posterior; C, antenna, anterior. Scale-bars in micrometres.

Oral region located posterior to long neck region; mouth located ventrally (Figure 6E). Labrum small, ornamented with small denticles; mouthparts reduced, as figured (Figure 8A-B).

Swimming legs 1-4 (Figures 8C-D, 9A) with all rami 3-segmented, except 2-segmented endopod of leg 1 and exopod of leg 4. Posterior margins of interpodal sternites not ornamented. Spine and seta formula as follows:

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

Setules present on inner margin of first exopodal segment of each leg; other spinulation as figured (Figures 8C-D, 9A). Fifth leg represented by 2 setae, each carried on separate papilla (Figure 9C, D).

Remarks

The type-species *T. serrani*, as redescribed above, *T. fluviatilis* Paggi, 1796, *T. dawsoni* Cressey, 1972 and *T. sphyricephalus* Thomsen, 1949 are all characterised by the presence of lobate outgrowths around the posterior margin of the antennary region (preneck) of the head. Although somewhat variable, in all four species these lobes are posteriorly-directed. They are arranged around the dorsal, ventral and lateral surfaces (see Paggi, 1976; Cressey, 1972; Thomsen, 1949) or just ventrally and laterally (cf. Figure 5A,B). The developmental origin of these lobes was shown very clearly for *T. fluviatilis* by Paggi (1976: Fig. 1), who also demonstrated that the lobes extend onto the anterior part of the neck in this species. The new species lacks posteriorly-directed lobes but carries a pair of ventrally located and frontally directed lobes on the antennary region of the head (Figure 6C).

In contrast *T. elongatus* (Thatcher, 1986) and *T. tamarae* Motta Armado & Rocha, 1996 lack any lobes on the posterior margin of the antennary region of the head (Thatcher, 1986; Motta Amado & Rocha, 1996), but in both the anterior part of the neck is inflated, arched and separated by a constriction from the rest of the neck. Given that Thatcher's (1986) description is full of apparent errors and that *T. tamarae* occurs on the same host species as *T. elongatus* (the sciaenid *Plagioscion squamosissimus* (Heckel)), it is tentatively concluded here, on the basis of the similarities in body form, that *T. tamarae* is probably a synonym of *T. elongatus* and that the Motta Amado & Rocha description corrects many of the errors in Thatcher's original description. The difference in setation of the caudal rami between these two species, confirmed by Motta Amado & Rocha (1996), is regarded as not significant here, given the fragility of the caudal setae. The new species differs from *T. elongatus* in the presence of head lobes and in the presence of the outer spine on the first exopodal segment of leg 4 (absent in *T. elongatus* according to Motta Amado & Rocha, 1996, figure 12).

The form of the antennary region lobes is the main character justifying the establishment of the new species. This arrangement of lobes has been reported before, in the *Therodamas* material from *Pimelodus barbus* (as *Tachyurus barbus* (Lac.)), misidentified as *T. serrani* by Thomsen (1949, Lámina XI, figure 3) and in the material collected from *Mugil* sp. taken off the coast of São Paulo State and briefly described under the name *T. serrani* by Carvalho (1955). This material is here treated as belonging to *T. frontalis* n. sp. and the numerous differences in detail are regarded as due to observational error and not discussed further.

Biogeographical distribution and host utilisation

Therodamas occurs in the Neotropical region only (Figure 10). Species have been reported from six different host families: *T. fluviatilis* on Characidae from Argentina (Paggi, 1976); *T. dawsoni* on Dactyloscopidae from Panama (Cressey, 1972); *T. elongatus* on Sciaenidae from Brazil (Thatcher, 1986; Motta Amado & Rocha, 1996); *T. sphyricephalus* on Carangidae from Uruguay (Thomsen, 1949); *T. serrani* on Serranidae from the Caribbean (Krøyer, 1863); *T. frontalis* n. sp. on Carangidae from Uruguay (Thomsen, 1949, as *T. serrani*) and Mugilidae from Brazil (Carvalho, 1955, as *T. serrani*; present account). The utilisation of hosts representing six different families indicates a low level of host-specificity at generic level.

Three of the four *Mugilicola* species are recorded from hosts belonging to the Mugilidae. In India, *M. bulbosus* occurred on *Liza subviridis* from Bombay (present work), on *L. parsia* (Hamilton Buchanan) and *L. tade* (Forsskål) (Tripathi, 1960), and on *Mugil cephalus* at Trivandrum (Pillai & Jayasree, 1978, as *Paeonodes mugilis*). *M. kabatai* was found on *Liza abu* from Iraq (Ho et al., 1996) and *M. smithae* was recorded on four species of mugilids, *Liza alata* (Steindachner), *L. macrolepis* (Smith), *Myxus capensis* (Valenciennes) and *Valamugil seheli* (Forsskål) in

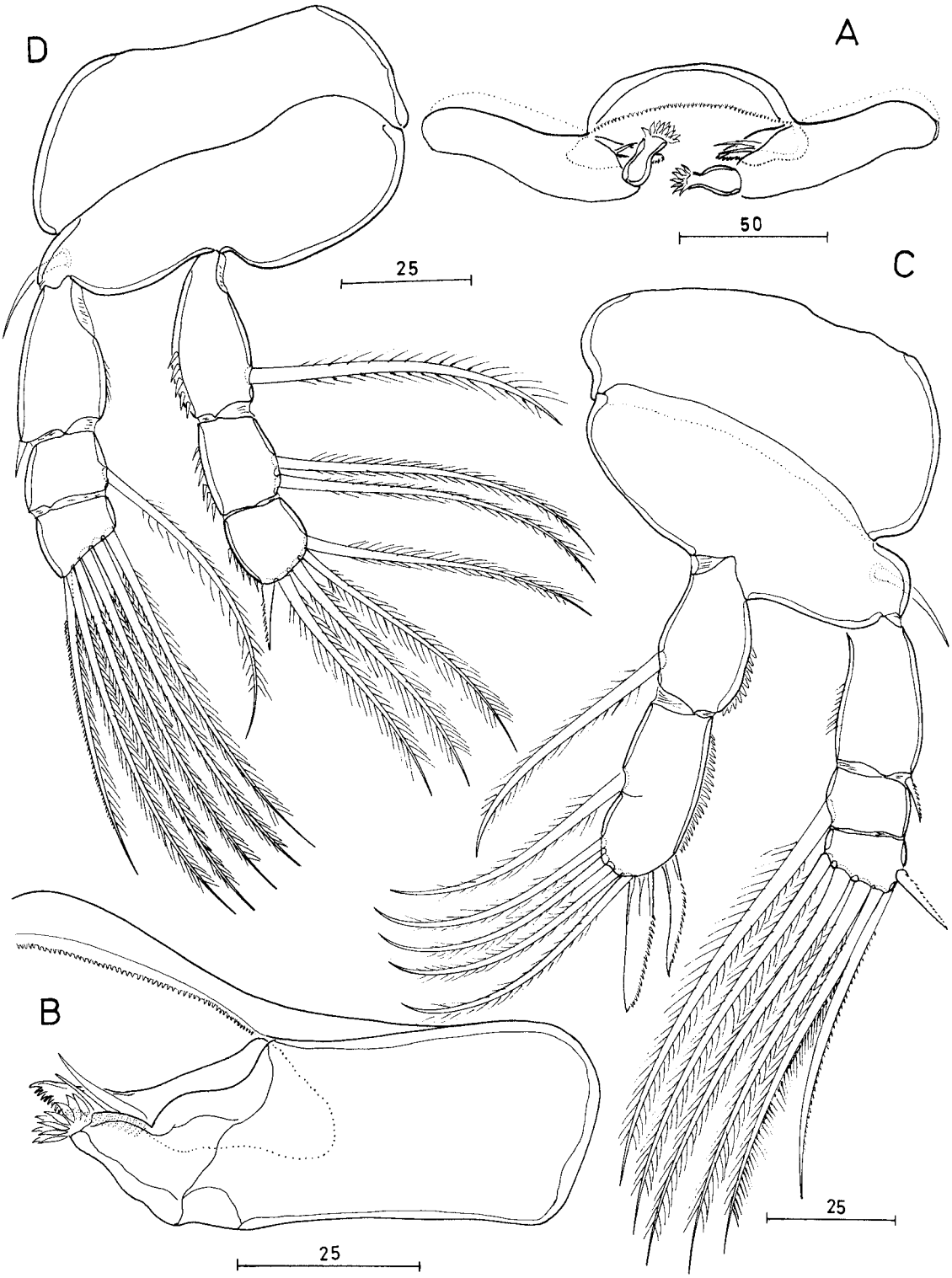

Figure 8. Therodamas frontalis n. sp., Holotype female. A, B, labrum and mouthparts; C, first swimming leg, anterior; D, second swimming leg, anterior. Scale-bars in micrometres.

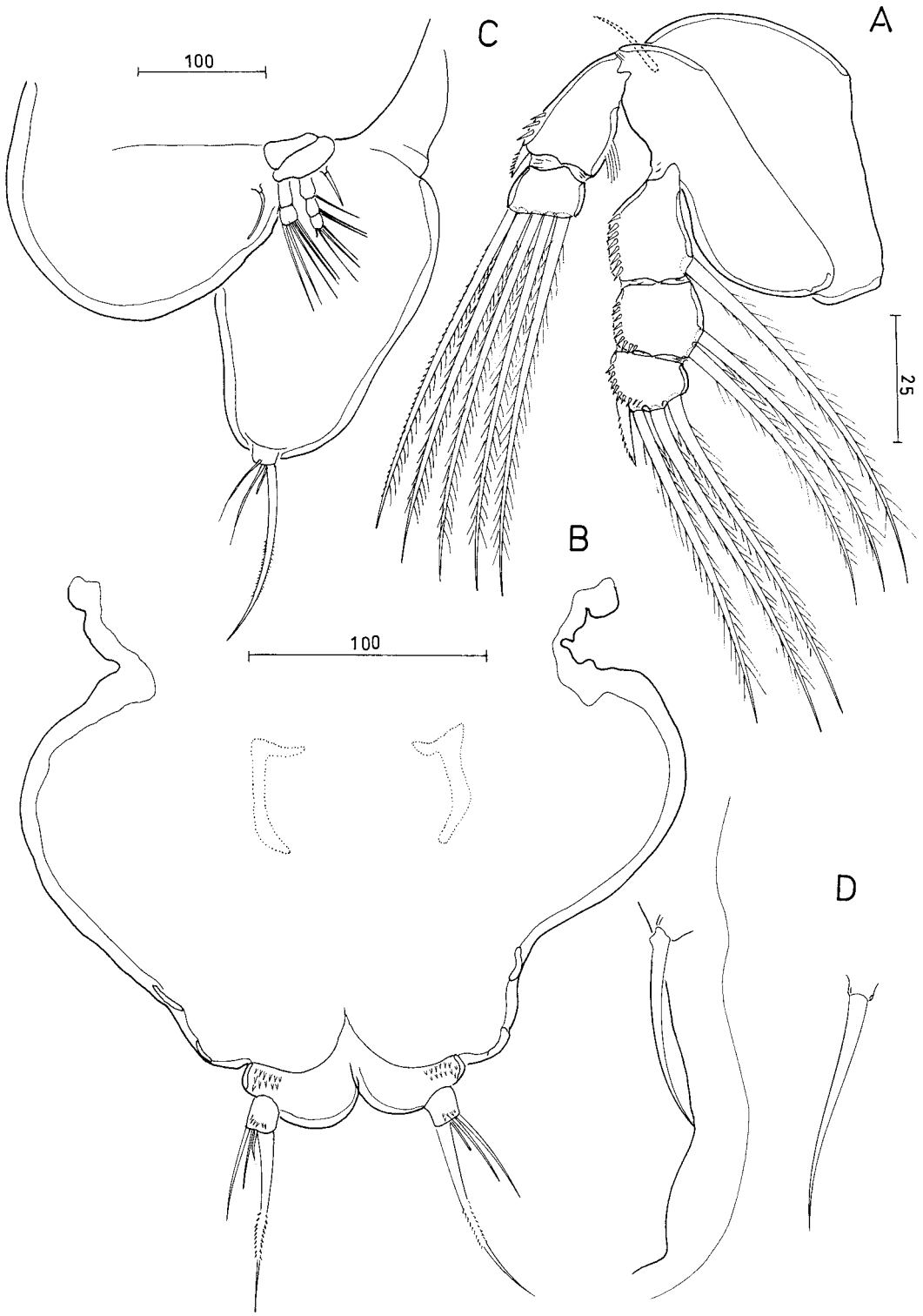

Figure 9. Therodamas frontalis n. sp., Holotype female. A, fourth swimming leg, anterior; B, urosome, ventral; C, lateral view showing fourth and fifth pedigerous somites; D, fifth swimming leg. Scale-bars in micrometres.

Table 1. Character matrix for phylogenetic analysis of relationships between species of *Mugilicola, Paeonodes, Therodamas* and *Teredophilus*.

Character number *Taxon name*	1	2	3	4	5	6	7	8	9	10	11	12
M. bulbosus	1	1	1	1	1	0	0	0	0	2	3	0
M. smithae	1	1	1	1	1	0	0	0	1	2	3	0
M. australiensis	1	1	1	1	1	0	0	0	0	2	3	0
M. kabatai	1	1	1	1	1	0	0	0	0	2	3	0
P. exiguus	1	1	1	1	1	0	1	0	1	1	?	0
P. nemaformis	1	1	1	1	1	0	1	0	1	1	2	0
P. lagunaris	1	1	1	1	1	0	1	0	0	1	2	0
P. subviridis	1	1	1	1	1	0	0	0	0	1	1	0
T. serrani	0	0	0	0	0	1	1	0	0	0	0	1
T. sphyricephalus	0	0	0	0	0	1	1	0	0	0	0	1
T. fluviatilis	0	0	0	0	0	1	1	1	0	0	0	1
T. dawsoni	0	0	0	0	0	1	1	1	0	0	0	1
T. elongatus	0	0	0	0	0	1	1	1	0	0	0	0
T. frontalis	0	0	0	0	0	1	1	1	0	0	0	0
Teredophilus	0	0	0	0	0	0	0	0	0	0	0	0

South Africa (Kruger et al., 1997, 1998), in addition to *Anguilla mossambica* Peters (Anguillidae) (Jones & Hine, 1978). *M. australiensis* was recorded from *Sillago ciliata* Cuvier & Valenciennes, a member of the Sillaginidae, in Australia (Boxshall, 1986). Although *Mugilicola* occurs on hosts representing three families, it is most closely associated with the Mugilidae, parasitising nine species in four genera of the Mugilidae in the Ethiopian, Oriental and Australasian regions. The close association with Mugilidae reflects a high level of host specificity to the Mugilidae as a family, but relatively low specificity at the generic and specific levels.

Paeonodes is distributed through the Ethiopian and Australasian regions (Figure 10), and occurs on several host families. *P. subviridis* n. sp. was discovered on *Liza subviridis* from Guam, *P. nemaformis* on brown trout, *Salmo trutta* Linnaeus (family Salmonidae), from New Zealand (Hewitt, 1969), *P. lagunaris* on *Tilapia melanotheron* Rüppel (family Cichlidae) from Ghana (van Banning, 1974) and *P. exiguus* on a unknown member of the family Verillidae (Wilson, 1944). The genus *Paeonodes* shows low host specificity at the host family level.

Phylogenetic relationships of the mesoparasitic Ergasilidae

A phylogenetic analysis was performed using PAUP 3.1.1. The data-matrix (Table 1) comprises 15 species representing the three mesoparasitic genera and the monotypic genus *Teredophilus* and 12 morphological characters (Table 2). The type and only species of *Teredophilus, T. renicola* Rancurel, 1954, was chosen as the outgroup, since the analysis of Motta Amado et al. (1995) identified these four genera as forming a monophyletic group (Clade IV of Motta Amado et al., 1995), with *Teredophilus* as the first offshoot.

The PAUP options employed were BRANCH AND BOUND, with character setting IRREVERSIBLE-UP. The analysis generated two trees with length = 18, CI = 0.833, and f value = 48. The strict consensus tree was computed (Figure 11). *Therodamas* is a monophyletic group defined by the presence of pre-oral neck, by the failure of expression of the articulation between second and third endopodal segments of leg 1, and by the fused abdominal somites forming a unit (Figure 11: 1). *Paeonodes* and *Mugilicola* together form a single clade defined by the apomorphies of the fused pedigerous somites to cephalothorax and the presence of post-oral neck (Figure 11: 2). According to this preliminary analysis, *Mugilicola* is defined from *Paeonodes* only by the loss of leg 4, leaving *Paeonodes* as a paraphyletic group. The validity of

Table 2. Character set and character states of *Mugilicola, Paeonodes, Therodamas* and *Teredophilus*.

No	Character	States
1	Second pedigerous somite	0 = not fused to cephalothorax, 1 = fused
2	Third pedigerous somite	0 = not fused to cephalothorax, 1 = fused
3	Fourth pedigerous somite	0 = not fused to cephalothorax, 1 = fused
4	Articulation between fourth and fifth pedigerous somites	0 = expressed, 1 = not expressed
5	Post-oral elongation forming a neck	0 = not present, 1 = present
6	Pre-oral elongation forming a neck	0 = not present, 1 = present
7	Free abdominal somites	0 = not fused, 1 = fused dorsally and ventrally to form a unit
8	Articulation between second and third endopodal segments of leg 1	0 = expressed, 1 = not expressed
9	Posterior margin of cephalothorax	0 = without lobes, 1 = with lobes
10	Exopod of leg 4	0 = 2-segmented, 1 = 1-segmented, 2 = absent
11	Endopod of leg 4	0 = 3-segmented, 1 = 2-segmented, 2 = 1-segmented, 3 = absent
12	Posterior margin of antennary region of cephalothorax	0 = without lobes, 1 = with posteriorly-directed lobes

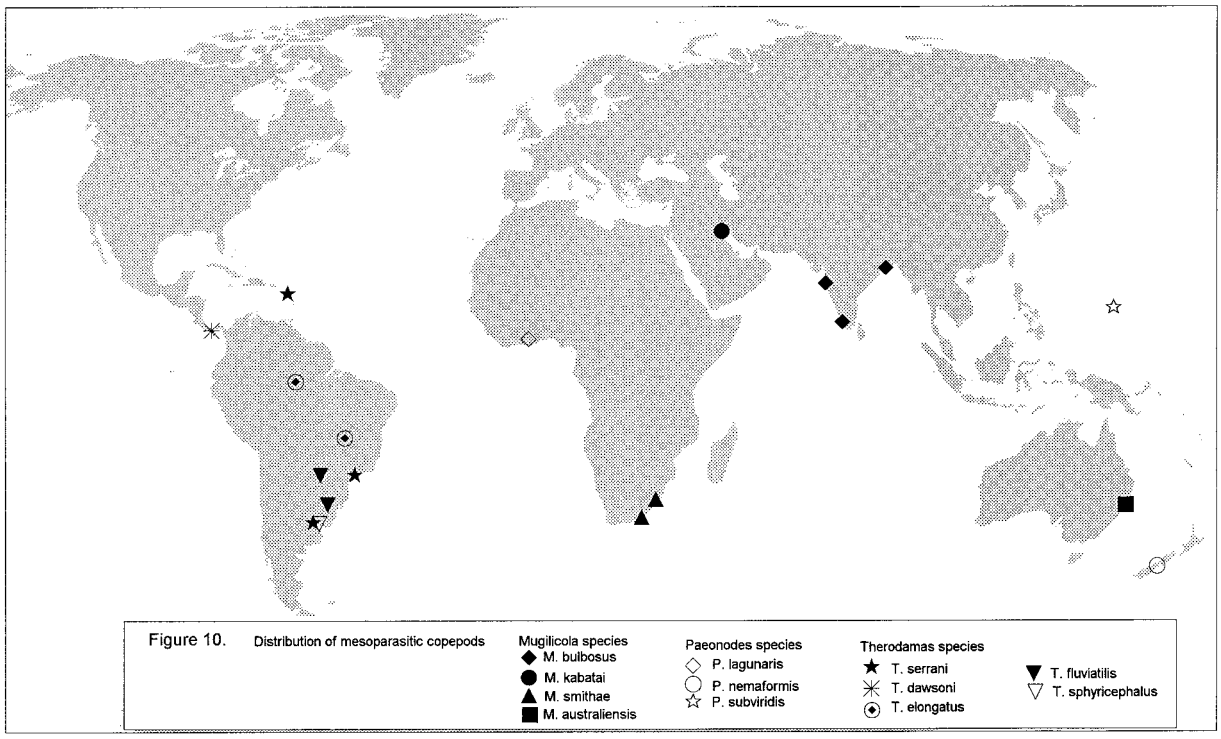

Figure 10. The geographical distribution of the mesoparasitic ergasilid copepods.

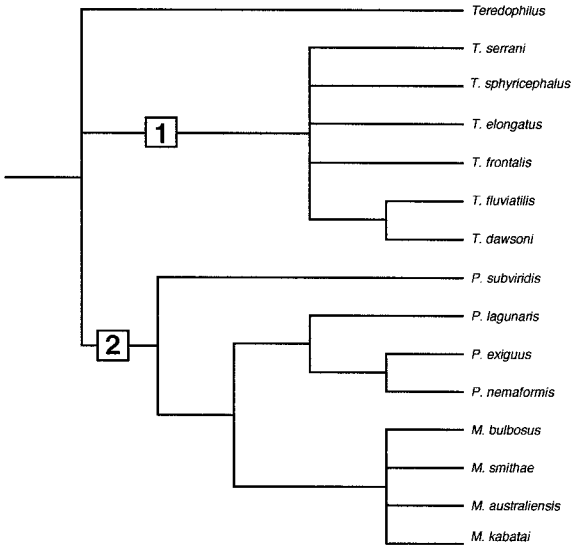

Figure 11. The inferred phylogenetic relationships of *Therodamas, Mugilicola, Paeonodes* and *Teredophilus*. 1 = cephalic neck formed anterior to mandible, 2 = postcephalic neck.

these genera is in question, but can only be tested in the context of a full generic level revision of the entire family Ergasilidae. No changes in generic status will be proposed here, until that comprehensive revision is completed.

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