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On the discovery of the male of *Mormonilla* Giesbrecht, 1891 (Copepoda: Mormonilloida)

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CONTENTS

SYNOPSIS. Males of the two known species of *Mormonilla* Giesbrecht are described in detail for the first time. They have reduced or vestigial mouthparts and are probably non-feeding. Males have a single testis and produce a single spermatophore. Male antennules are geniculate. A system of probable segmental homologies for the antennulary segments is proposed and the supporting evidence for this system discussed. Females carrying egg sacs are reported and figured for the first time. *Mormonilla* is unusual amongst copepods in producing paired egg sacs from a common medial genital aperture.

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INTRODUCTION

The order Mormonilloida was established by Boxshall in 1979 to accommodate the family Mormonillidae which consists of a single genus, *Mormonilla*, containing two species, *M.phasma* Giesbrecht, 1891 and *M.minor* Giesbrecht, 1891 (Boxshall, 1979). Both species have a very widespread distribution in the midwater oceanic plankton, especially at depths between 400 and 1000m. The skeletomusculature and external morphology of the feeding apparatus of adult females of *Mormonilla* indicate that they are small particle feeders (Boxshall, 1985). In a brief review of their biology Boxshall (1986) noted that no males of *Mormonilla*, or females carrying egg sacs have ever been reported, although he had observed a single female with a spermatophore attached to its median genital aperture.

Mormonilla is relatively common in the Arabian Sea, in the deep eastern Indian Ocean, and in the Gulf of Aden; in the Red Sea its occurrence is restricted to the southernmost parts only (Beckmann, 1984; Böttger-Schnack, unpubl.). In zooplankton samples collected using a very fine mesh net (0.055 mm) several males were found, in addition to numerous females bearing egg sacs or spermatophores and some copepodid stages. The males of both species are described below in detail and short notes are presented on the reproductive biology of the genus.

MATERIALS AND METHODS

The specimens of *Mormonilla* were collected during cruises of the German Research Vessel *Meteor* using a multiple opening-closing net (Weikert & John, 1981) of mesh size 0.055 mm hauled vertically. The majority of the material was taken in the Arabian Sea and in the Strait of Bab el Mandab, the southern entrance of the Red Sea, during *Meteor* cruise 5/3a+b and 5/5 respectively (see Table 1). A single ovigerous

Table 1. *Mormonilla* specimens from the Arabian Sea, the Red Sea, the Mediterranean Sea and the eastern Indian Ocean.

Station	Position	Date	Depth	Number of specimens
Arabian Sea				
347	20°44′N 59°40′E	5.4.87	1250–1450m	1 ♀ *M.phasma* (ovigerous) 2 ♂ *M.phasma*
347	"	5.4.87	1450–1650m	42 ♀ *M.phasma* (2 ovigerous) 1 ♀ *M.phasma* (+ spermatophore) 1 ♂ *M.phasma* 57 copepodid stages 34 ♀ *M.minor* (2 ovigerous)
347	"	5.4.87	1650–1850m	1 ♀ *M.phasma* (ovigerous) 1 ♀ *M.minor* (+ spermatophore)
496	18°00′N 66°25′E	12.5.87	1650–1850m	2 ♀ *M.phasma* (ovigerous) 1 ♀ *M.phasma* (+ spermatophore) 2 ♀ *M.minor* (ovigerous)
Bab el Mandab, Red Sea				
717	12°2′N 43°24.5′E	6.8.87	125–150m	7 ♂ *M.minor*
Eastern Mediterranean Sea				
34/35	34°25′N 26°14′E	20.1.87	100–150m	2 ♀ *M.minor* 1 ♂ *M.minor* 2 copepodid stages
34/35	34°25′N 26°4′E	20.1.87	600–750m	1 ♀ *M.minor* (ovigerous) 1 ♂ *M.minor*
Eastern Indian Ocean				
11	04°47′S 87°14′E	24.1.77	200m	1 ♂ *M.minor*
11	"	24.1.77	600m	2 ♂ *M.phasma*
11	"	24.1.77	800m	2 ♂ *M.phasma*
11	"	24.1.77	1000m	2 ♂ *M.phasma*

female of *M.phasma* was also found in zooplankton samples collected during *Meteor* cruise 64 at a depth of 550–650 m in the upwelling area of the N.W. African coast in spring of 1983 using a multiple opening-closing net of 0.3 mm mesh size.

The specimens were dissected in lactic acid and examined as temporary mounts in lactophenol. All drawings were prepared using a camera lucida on a Leitz Dialux 20 interference microscope. All appendage segments and setation elements are named and numbered using the system established by Huys & Boxshall (1991). The material is stored in the collections of The Natural History Museum, London, BM(NH) Reg.Nos. 1992.38–81.

DESCRIPTION OF MALE *Mormonilla phasma*

Body slender, cyclopiform (Fig. 1A–B). Body length of figured specimen 1.42 mm; range 0.90 to 1.42 mm (based on 7 specimens). Prosome 5-segmented, comprising cephalosome and 4 free pedigerous somites; urosome 5-segmented, comprising fifth pedigerous, genital and 3 free abdominal somites. Genital somite with functional genital aperture on left side only. Anal somite about 1.67 times longer than wide; ornamented with patches of fine spinules on ventral surface (Fig. 6A). Rostral region poorly developed, with pair of sensilla (Fig. 2A). Caudal rami elongate, about 18 times longer than wide (Fig. 5C); armed with 6 setae; seta I lacking, seta II located 34% of distance along ramus, setae III to VI postioned around distal margin, seta VII located dorsally, just anterior to rear margin. Ramus ornamented with fine denticles.

Antennule indistinctly 8-segmented (Fig. 2A); with well developed geniculation separating segments 7 and 8. Part proximal to geniculation comprising long proximal segment armed with 1 long and 6 short naked setae and 1 large aesthetasc, a middle section consisting of 5 poorly separated segments bearing 2, 2, 2 + 1 aesthetasc, 2 and 2 elements, and a long distal segment armed with 1 long and 2 short setae and 1 aesthetasc proximally, 2 hirsute setae at midlength (Fig. 2B) and a curved subapical seta. Apical segment slender, bearing 3 subapical setae, one of which with biarticulate base.

Antenna biramous (Fig. 2C) with partly fused coxa and basis, both unarmed. Endopod 2-segmented; proximal segment indistinctly separated from basis, unarmed; distal segment representing fused second and third endopodal segments, armed with 11 setae around apex. Exopod 9-segmented, setal formula 1,0,0,0,0,1,1,1,3. Seta on first exopodal segment plumose, setae on distal part of ramus sparsely spinulate.

Labrum (Fig. 3A) a simple rounded lobe. Paragnaths small, ridge-like lobes.

Mandible (Fig. 4A) biramous; coxal gnathobase extremely reduced with poorly developed blades on margin (Fig. 4B); basis unarmed; endopod 2-segmented, first segment unarmed, second segment with 5 plumose setae; exopod 4-segmented with 2,1,1,2 setal formula (Fig. 4C).

Maxillule biramous (Fig. 3B); praecoxa with weakly developed arthrite (Fig. 3C); coxa and basis fused, bearing single

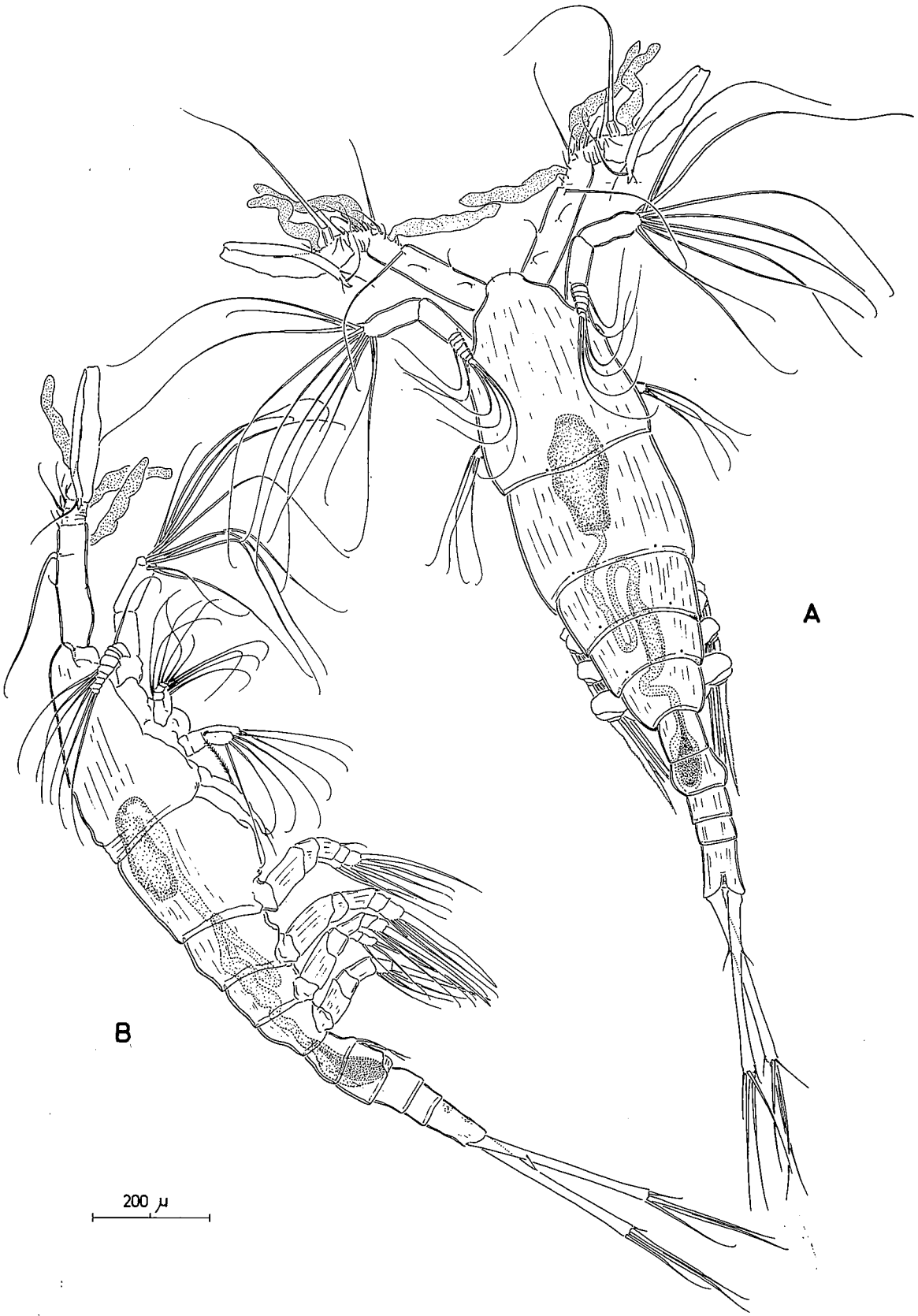

Fig. 1 *Mormonilla phasma* male. A, Entire, dorsal; B, Entire, lateral.

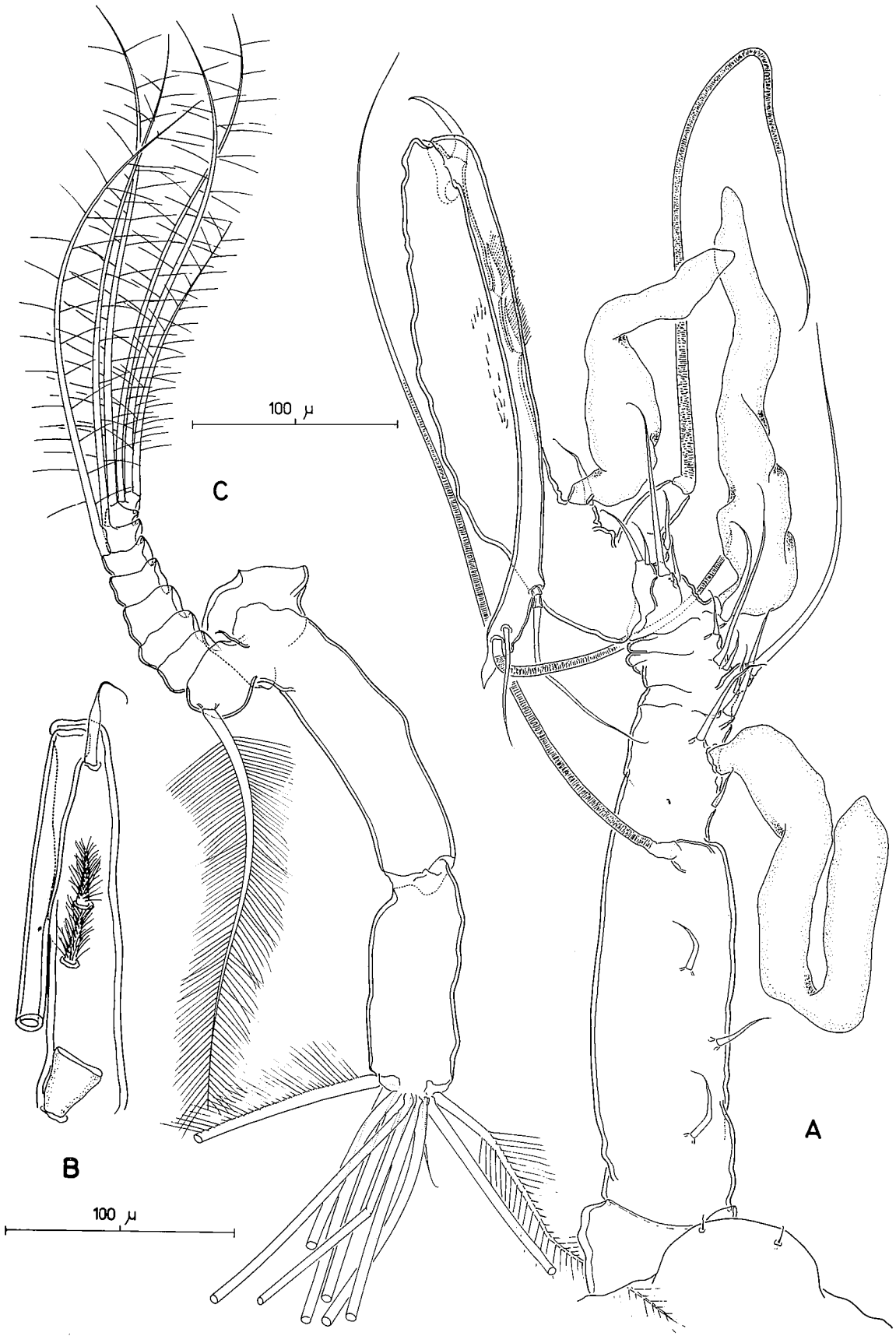

Fig. 2 *Mormonilla phasma* male. A, Antennule, dorsal; B, Detail, showing compound segment proximal to geniculation, anterior; C, Antenna, anterior.

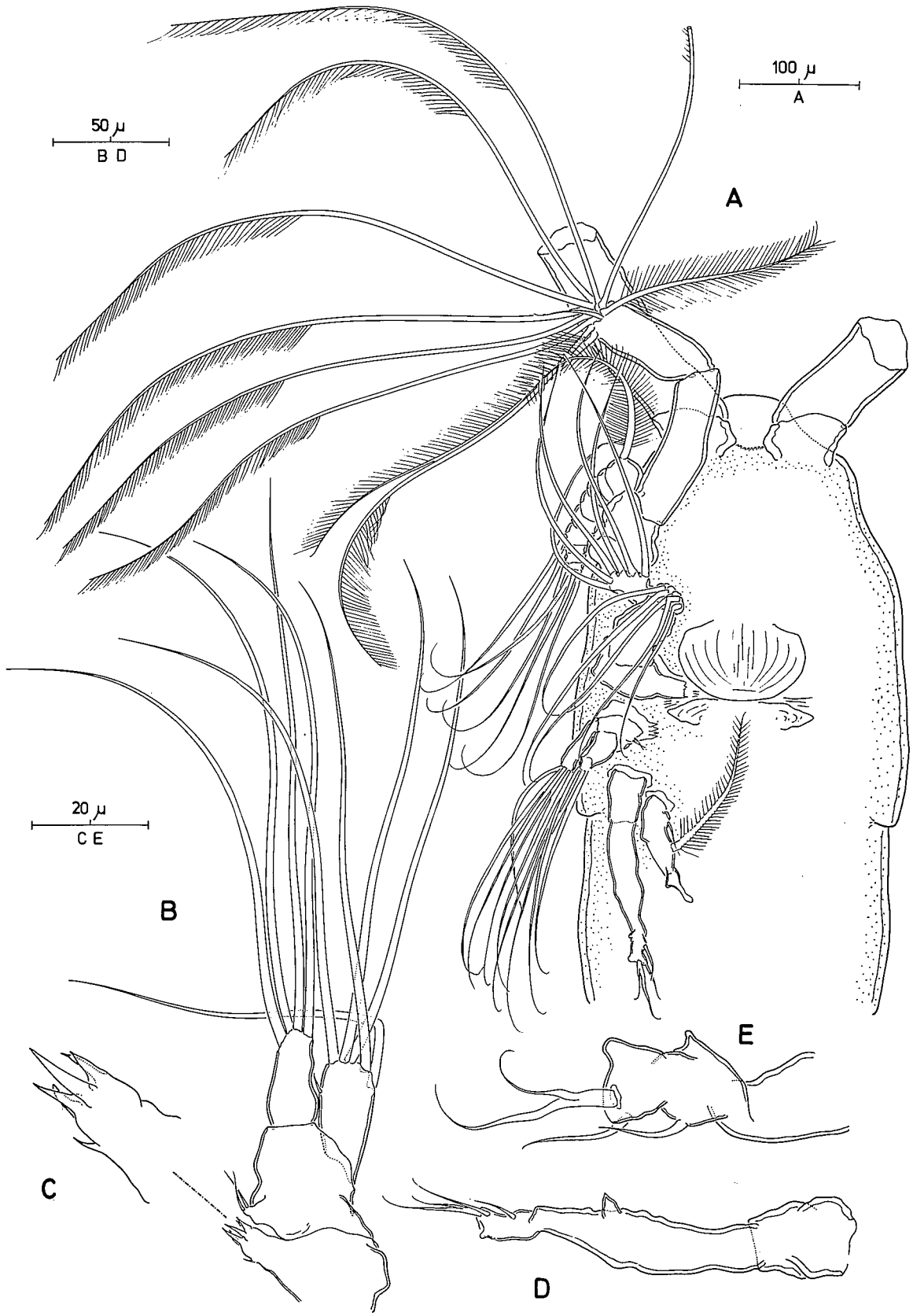

Fig. 3 *Mormonilla phasma* male. A, Cephalosome, ventral view showing cephalosomatic appendages on right side only; B, Maxillule, posterior; C, Detail of praecoxal arthrite of maxillule; D, Maxilla, anterior; E, Maxilla, lateral.

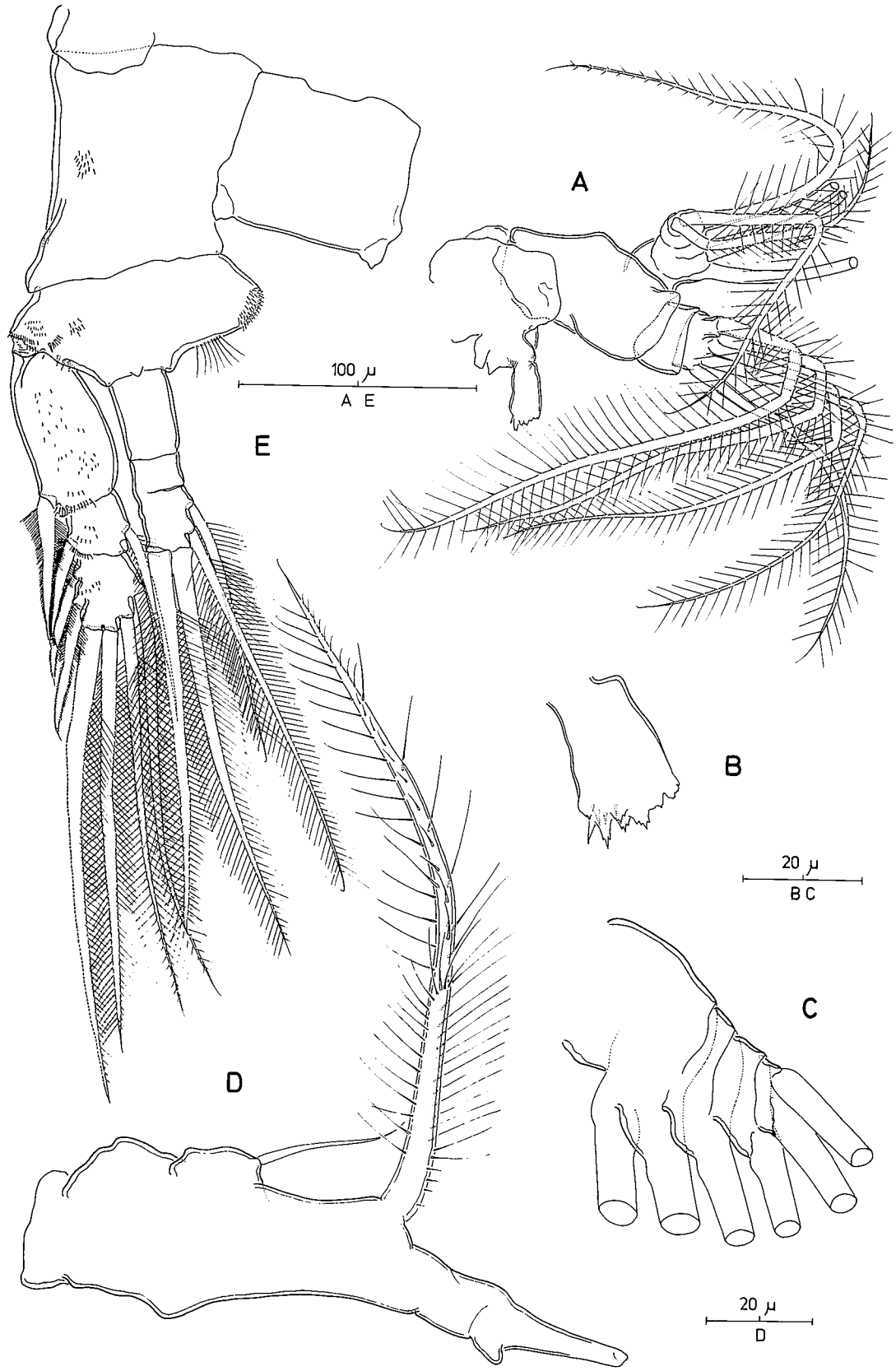

Fig. 4 *Mormonilla phasma* male. A, Mandible, anterior; B, Detail of mandibular gnathobase; C, Detail of mandibular exopod; D, Maxilliped, anterior; E, First leg, anterior.

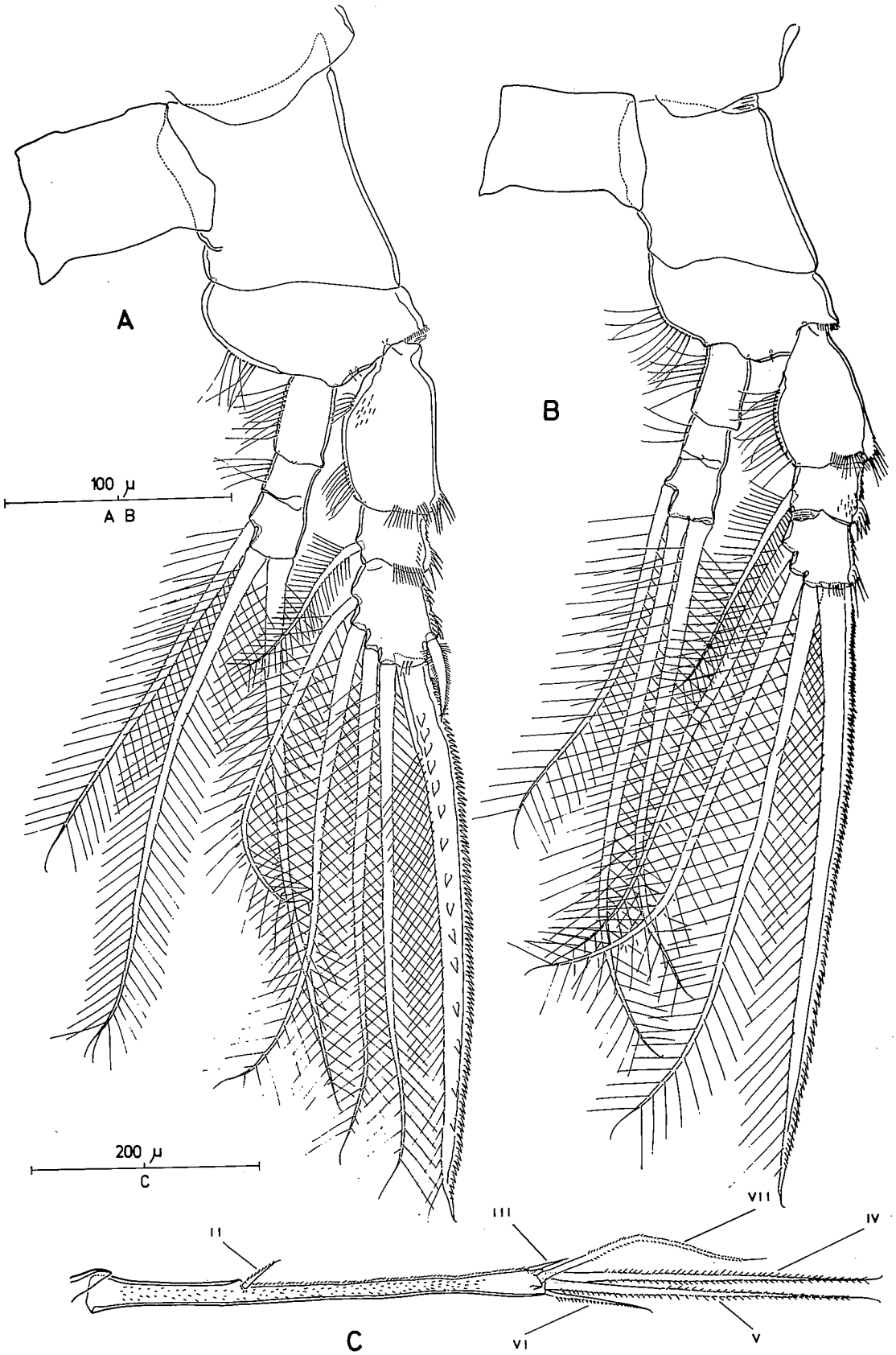

Fig. 5 *Mormonilla phasma* male. A, Second leg, anterior; B, Third leg, anterior; C, Caudal ramus, dorsal.

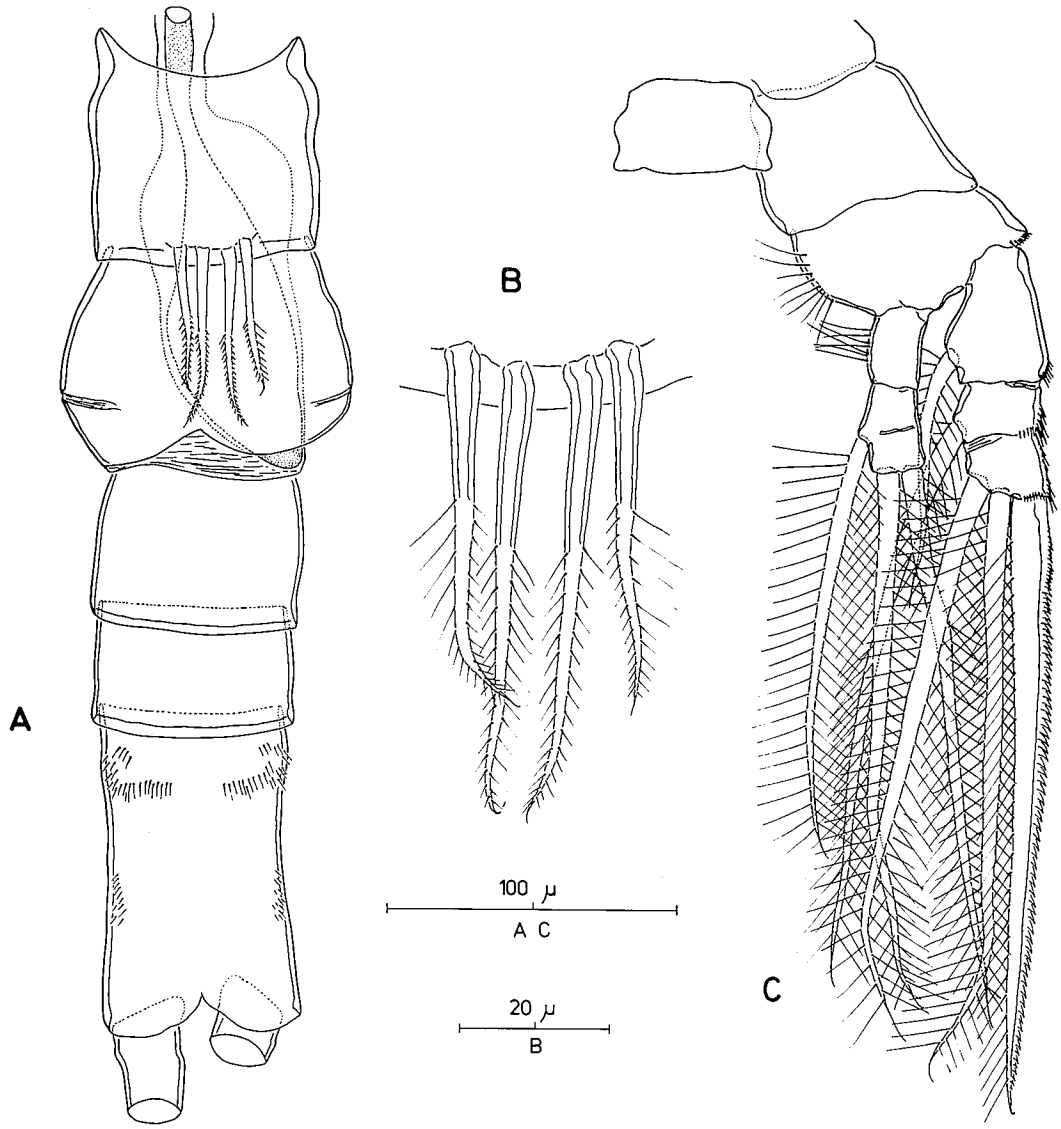

Fig. 6 *Mormonilla phasma* male. A, Urosome, ventral view showing single spermatophore present inside vas deferens on left side; B, Fifth leg, ventral; C, Fourth leg, anterior.

proximal endite with 2 setae; endopod 1-segmented with 4 distal setae; exopod 1-segmented with 5 distal setae.

Maxilla vestigial (Fig. 3D-E); reduced to indistinctly 2-segmented lobe bearing 1 bifid and 2 naked, simple setae distally and a spinous process at midlength. Maxilliped vestigial (Fig. 4D), reduced to unsegmented, tapering lobe bearing a short naked seta and 1 large plumose seta.

Swimming legs 1 to 4 biramous (Figs. 4E, 5A-B, 6C) with 3-segmented exopods and indistinctly 3-segmented endopods. Endopodal segments 2 and 3 partly fused in all legs. Spine and setal formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	0–0	I–0;I–1;II,I,3	0–0;0–0;0,2,2
Leg 2	0–0	0–0	0–0;0–1;I,I,4	0–0;0–0;0,2,1
Leg 3	0–0	0–0	0–0;0–1;0,I,3	0–0;0–0;0,2,1
Leg 4	0–0	0–0	0–1;0–1;0,I,2	0–0;0–0;0,2,1

Rows of pinnules present on inner margins of basis of legs 1 to 4 and on unarmed inner margin of first exopodal segment of legs 2 and 3. Slender spinules present on unarmed outer margins of exopodal segments of legs 2 to 4. Other fine ornamentation as shown in figures. Intercoxal sclerites present in legs 1 to 4.

Fifth legs reduced, represented by 2 pairs of sparsely plumose setae originating on mid ventral surface of somite, near posterior margin (Fig. 6A-B). Sixth legs represented by unarmed opercula closing off genital apertures (Fig. 6A).

DESCRIPTION OF MALE *Mormonilla minor*

Body slender, cyclopiform (Fig. 7A-B); prosomal and urosomal segmentation as in *M.phasma*. Body length of figured specimen 0.83 mm; range 0.75 to 0.84 mm (based on 3 specimens). Two pairs somitic sensilla present near posterior margin of dorsal cephalic shield; single pair present dorsally on pedigerous somites 2 to 5 and on genital somite. Rostral region with pair of sensilla as in *M.phasma*. Caudal rami (Fig. 7C) elongate, about 14 times longer than wide; armed with 6 setae; seta I lacking, seta II located 25% of distance along ramus, setae III–VI positioned around distal margin, seta VII located dorsally on rear margin. Ramus ornamented with fine denticles medially.

Antennules and maxillipeds exactly as in *M.phasma*. Differences in other cephalosomatic appendages as follows: exopod of antenna (Fig. 10B) 8-segmented, with an additional distal fusion between ancestral segments IX and X. Setation formula 1,0,0,0,0,1,1,4. Mandible (Fig. 8A) with similarly reduced coxal gnathobase lacking any distal blades; segmentation and setation formula of rami as in *M.phasma* but with 2 setae on apex of exopod much smaller. Maxillule (Fig. 10C) with very reduced praecoxal arthrite; fused coxa and basis bearing only single seta; endopod with 3 distal setae and lateral setae on exopod smaller than in *M.phasma*. Maxilla (Fig. 10D) with setiform element at middle of medial margin rather than spinous process as in *M.phasma*.

Swimming legs 1 to 4 (Figs. 8C, 9A-D) with basic segmentation as in *M.phasma*. Coxa and basis partly fused in legs 2 to 4. Spine and setal formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	0–0	I–0;I–1;II,I,3	0–0;0–0;0,2,1
Leg 2	0–0	0–0	0–0;0–1;I,I,3	0–0;0–0;0,2,1
Leg 3	0–0	0–0	0–0;0–1;0,I,3	0–0;0–0;0,2,1
Leg 4	0–0	0–0	0–1;0–1;0,I,2	0–0;0–1;0,2,1

Outer margin spine on third exopodal segment of leg 2 (Fig. 9D) fused to segment basally. Ornamentation sparse; basis without inner rows of pinnules; pinnules present on inner margins of first exopodal segment of legs 2 and 3. Other fine ornamentation as shown in figures. Intercoxal sclerites present, unarmed. Fifth legs (Fig. 8B) represented by 4 setae but setae naked and relatively longer than in *M.phasma*. Sixth legs (Fig. 8B) unarmed, ornamented with 4 short rows of fine spinules.

REPRODUCTIVE BIOLOGY OF *Mormonilla*

Mormonilla females have paired ovaries and paired oviducts, both of which open via the single median genital aperture on the genital double somite. They produce a pair of small egg sacs, each containing 2 eggs arranged antero-posteriorly. Both sacs emerge from the common median aperture, presumably one from each oviduct. Males have a single testis located medially in the prosome about at the boundary between cephalosome and first pedigerous somite (stippled in Fig. 1A-B). The single vas deferens forms a loop in the second and third pedigerous somites, then passes into the urosome to open on the left side of the genital somite. The vas deferens is not highly differentiated into specialised regions. The extruded spermatophore (Fig. 10E) is ovoid, has a slender neck and, after being placed on the female during copulation, discharges directly into the copulatory pore located within the median genital aperture.

DISCUSSION

Mormonilla displays extreme sexual dimorphism. The dimorphism in urosome segmentation, with the male possessing separate genital and first abdominal somites, and in antennule structure, with the male having geniculate antennules, is typical of podoplean copepods. The use by the male of geniculate antennules to grasp the female during mating is a primitive attribute of calanoids and podoplean copepods, although it has been secondarily lost in the Poecilostomatoida and in some representatives of other orders.

The male antennules are described above as indistinctly 8-segmented and even these few segments are poorly differentiated. The best defined articulation is the geniculation that separates the slender distal segment from the rest of the limb. Since the presence of the geniculation between ancestral segments XX and XXI of the male antennule is an apomorphy of the Neocopepoda we believe that it is reasonable to assume that the well defined geniculation in *Mormonilla* is homologous with the neocopepodan geniculation. On the basis of this assumption the distal segment is treated as homologous with ancestral segments XXI to XXVIII. A compound segment formed by the fusion of these same ancestral segments is present in males of the order Monstrilloida. The precise location of aesthetascs on antennules provides reference points that have proved very useful in determining segmental homologies in copepods (Huys & Boxshall, 1991). The 3 aesthetascs on the part of the male antennule proximal to the geniculation were tentatively identified as those derived from segments VII, XI and XVI, by Huys & Boxshall (1991). The aesthetascs on these particular segments are very conservative in podoplean copepods. For example, the male of the misophrioid *Archimisophria discoveryi* Boxshall retains only 4 aesthetascs on the part of the antennule proximal to the geniculation, on segments III, VII, XI and XVI. The males of harpacticoids retain a maximum of 2 aesthetascs on the proximal part of the antennule, on segments XI and XVI. In the male of the primitive siphonostomatoid *Ecbathyrion prolixicauda* aesthetascs are retained on segments I to IV, VII, IX, XI, XIV, XVI and XVIII in the proximal part. Even in gymnoplean copepods, which typically retain aesthetascs on many segments, it is possible to find examples with few aesthetascs remaining in males, such as *Stephos lucayensis* Fosshagen which retains aesthetascs only on segments III, VII, XI, XVI and XX in the proximal part of the male antennule.

The conservative nature of the aesthetascs on segments VII, XI and XVI in a wide range of copepod taxa supports the interpretation of the aesthetasc-bearing segments as the same 3 segments in *Mormonilla* males. This is reinforced by careful examination of the relative lengths of setae on the antennulary segments. Primitively the antennules of the Neocopepoda show an ancestral pattern of long and short setae arranged on particular segments. The basic pattern is best retained in modern calanoids. In *Ridgewayia wilsonae* Fosshagen, for example, a long seta is present on segments V,

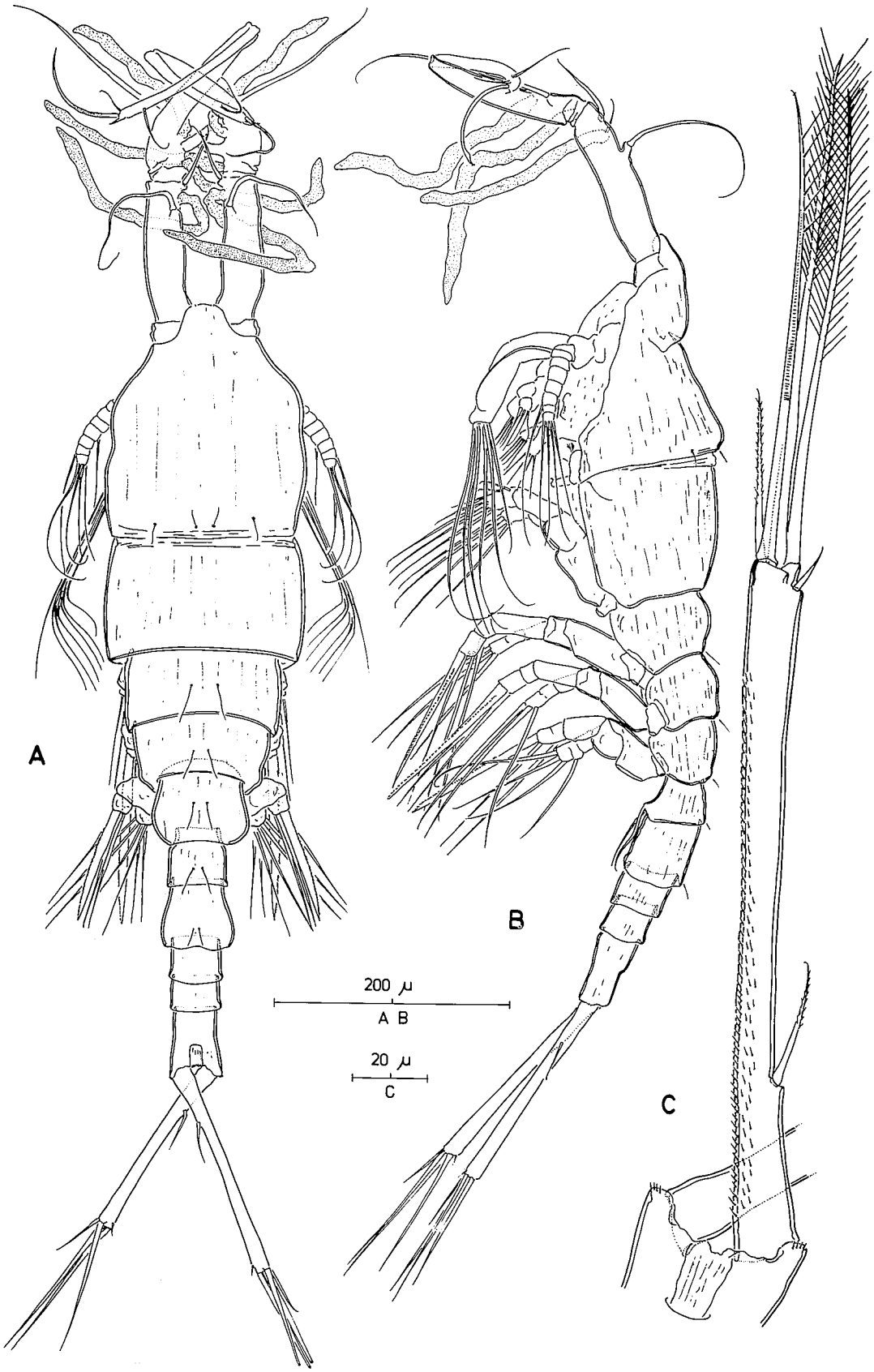

Fig. 7 *Mormonilla minor* male. A, Entire, dorsal; B, Entire, lateral; C, Caudal ramus, dorsal.

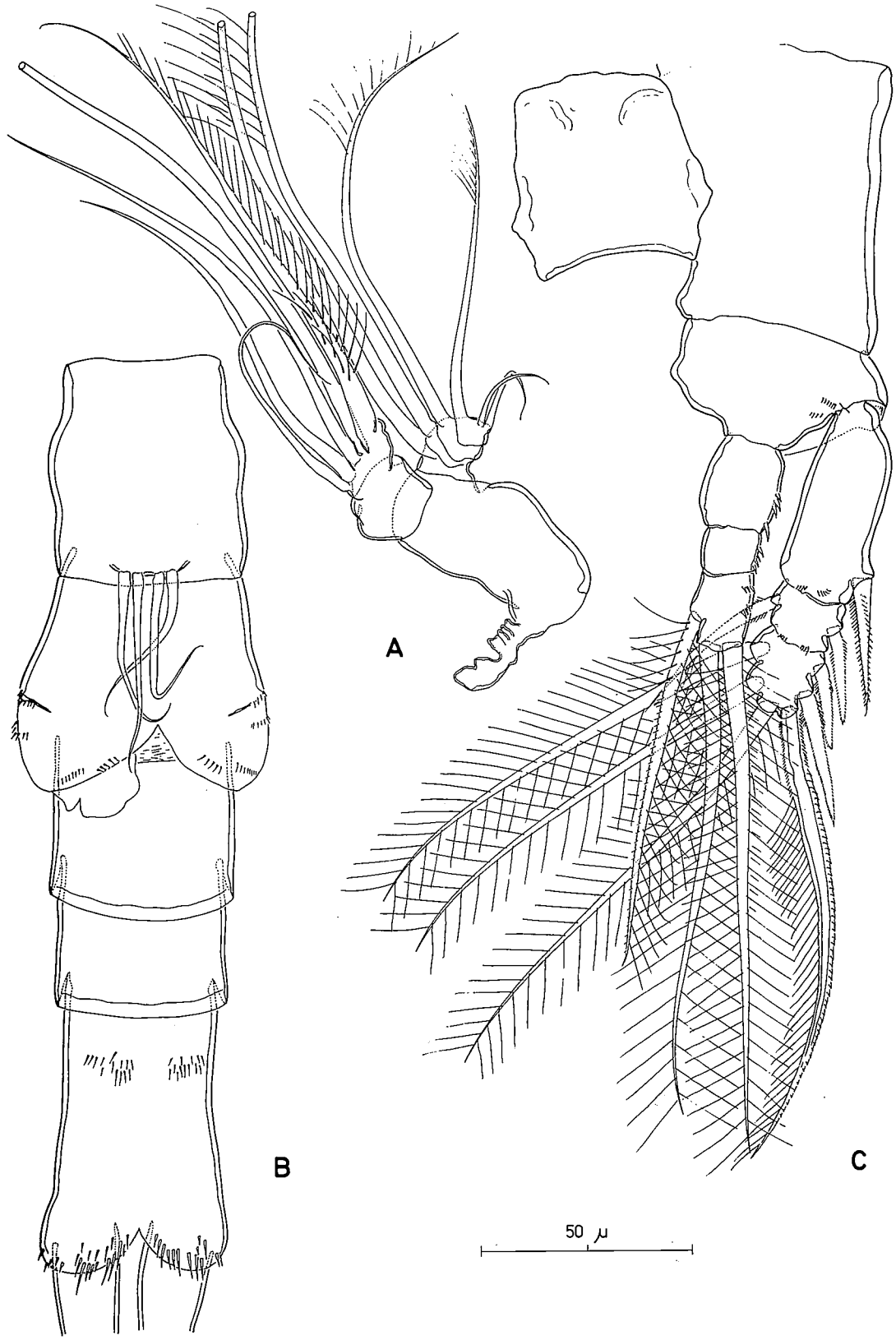

Fig. 8 *Mormonilla minor* male. A, Mandible, anterior; B, Urosome, ventral; C, First leg, anterior.

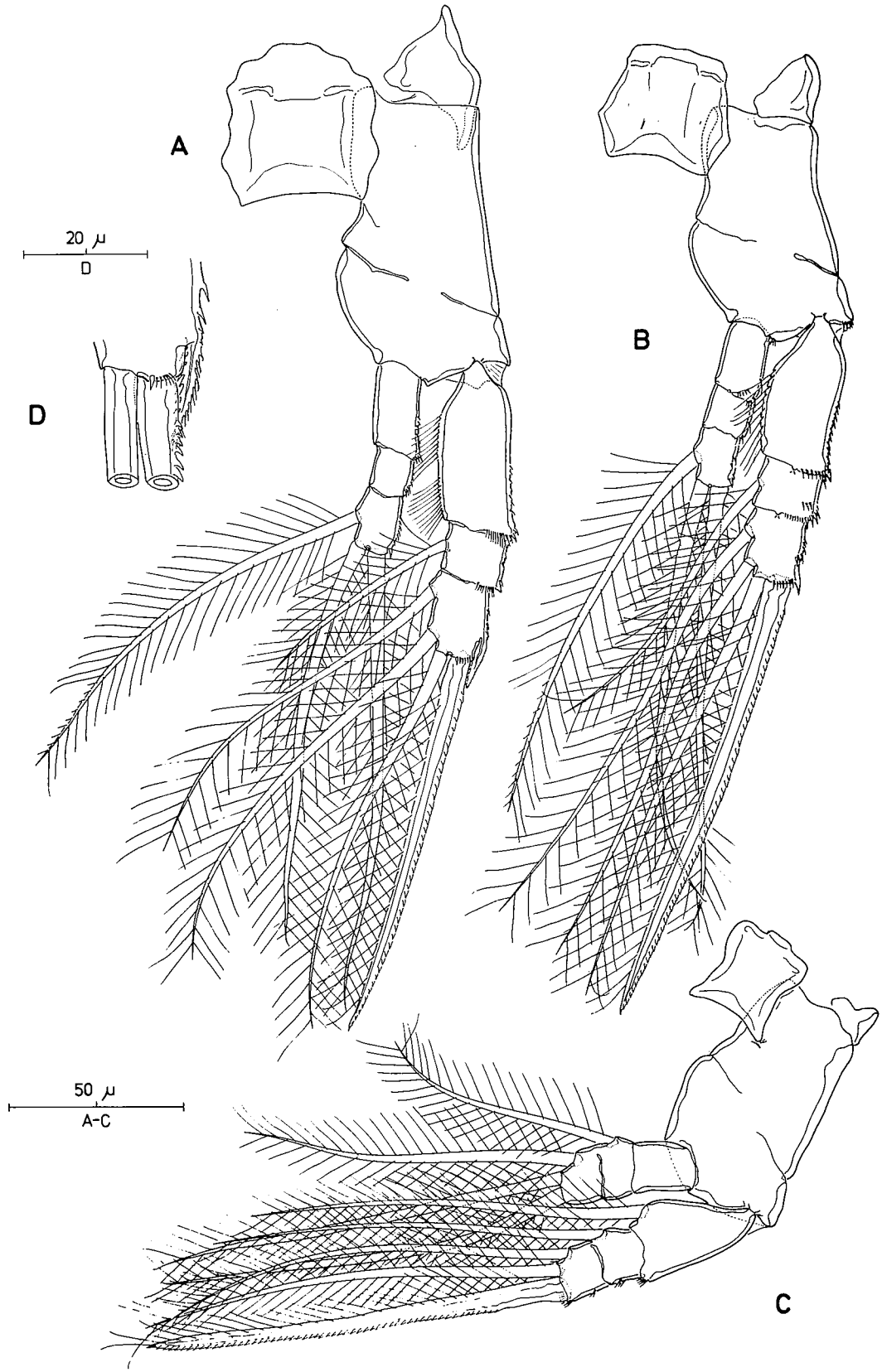

Fig. 9 *Mormonilla minor* male. A, Second leg, anterior; B, Third leg, anterior; C, Fourth leg, anterior; D, Detail of outer distal margin of exopod of second leg, anterior.

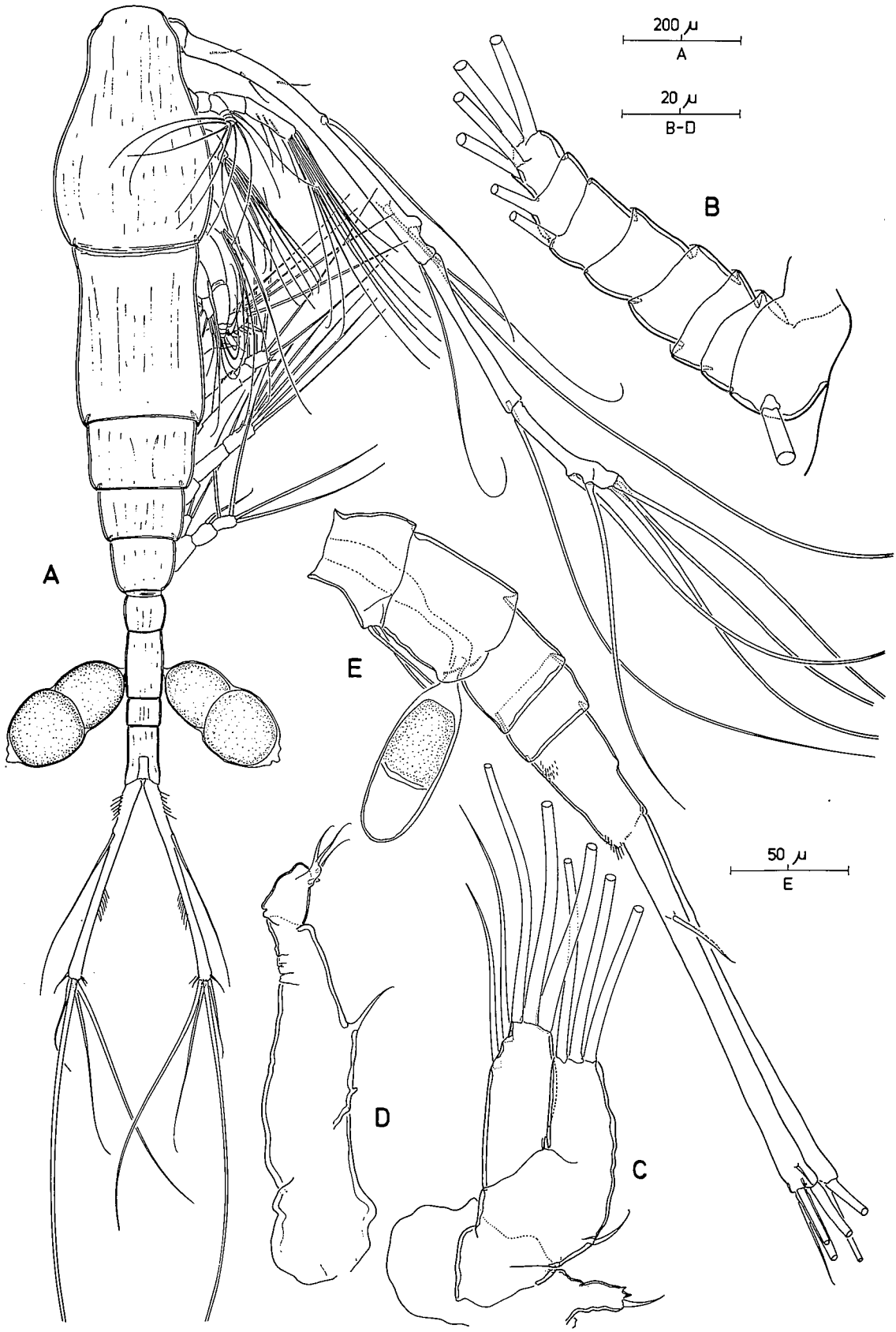

Fig. 10 *Mormonilla*. A, Ovigerous female *M.phasma*, dorsal. *M.minor* male. B, Antennary exopod, anterior; C, Maxillule, posterior; D, Maxilla, anterior; E, Urosome of male showing freshly extruded spermatophore, lateral.

IX, XI, XIV and XX, in the proximal part of the antennule (Huys & Boxshall, 1991: Fig. 2.2.2B). On the antennules of male *Mormonilla* there are 3 long setae present (Fig. 2A). If the identification of the aesthetasc-bearing segments is correct then the segments bearing long setae correspond well with ancestral segments V, IX and XIV. In our opinion this provides additional evidence in support of the interpretation of the segmental fusion pattern of the antennules of male *Mormonilla* as follows: I–VIII, IX, X, XI, XII, XIII, XIV–XX, XXI–XXVIII.

The sexual dimorphism in the other cephalosomatic appendages is very pronounced, especially in the more posterior limbs, i.e. the maxilla and maxilliped. The antenna of the male differs from that of the female primarily in the retention of separate first and second exopodal segments (these segments are fused in the female) and in the complete fusion of endopodal segments 2 and 3 (which are incompletely fused in the female). In addition a considerable number of setation elements present in the female are lost in the male. Differences in the mandible and maxillule are the gross reduction of the coxal gnathobase of the former and praecoxal arthrite of the latter. The palps of both appendages also show reductions in either segment numbers or setation. Both the maxilla and maxillipeds are reduced to tapering lobate structures bearing a few weak setae, except for a single well developed seta on the maxilliped.

All the postantennary mouthparts are very reduced in the male and the parts of the limbs most closely associated with processing food particles in the female are relatively more reduced than other parts. For example, the coxal gnathobase of the mandible is more reduced than the mandibular palp. Collectively these reductions can be interpreted as evidence that the adult male is a non-feeding stage. Functions performed by these limbs in the female that are not directly related to the particle-handling aspect of feeding, such as slow swimming movements, may still be carried out by them in the adult males.

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