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New Tetragonicipitidae (Copepoda, Harpacticoida) from the Indo-Pacific

Frank Fiers[1,*] & Marleen De Troch[2]
[1]*Royal Belgian Institute of Natural Sciences, Invertebrate Section, Vautierstraat 29, B-1000 Brussels, Belgium*
[2]*University of Ghent, Marine Biology Section, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium*
*(*Author for correspondence)*

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Abstract

During an intensive study of the copepod associations living on the seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson in Gazi Bay (Kenya), three representatives of the harpacticoid family Tetragonicipitidae Lang, 1944 were found. *Diagoniceps laevis* Willey, 1930 previously reported from Bermuda (type locality) and the Bahamas, was found in Gazi Bay. Comparison with the Atlantic material revealed only minor differences. *Odaginiceps immanis* n. sp. is the fourth species of the genus, which was known until now from three species described from the Central Atlantic. The new genus *Mwania* is defined for *M. phytocola* n. sp. which, with its three-segmented endopodite of the P1 bearing only two terminal appendages, appears to represent a stem taxon in the clade leading to*Aigondiceps* Fiers, 1995 and *Godianiceps* Fiers, 1995. The description of this species is amended with observations on its copepodid development. A second new taxon *Neogoniceps* n. gen. is defined for *N. martinezi* n. sp., a species found in a sublittoral sediment sample off the coast of Peru. This taxon, belonging to the same clade as *Mwania*, shares with the latter the primitive body shape and the large endopodal rami of the swimming legs, but displays an advanced P1 endopodite (two-segmented) and an advanced spine formula on the distal exopodal segments of the swimming legs (2.2.2). The description of this species is extended with some observations on its latest (CIV and CV) copepodids. In addition, presence and homology of sexual dimorphic features in the natatorial legs of the Tetragonicipitidae are discussed. Based on these amendments, the generic definition of the genus *Paraschizopera* Wells, 1981 is discussed.

Introduction

To get a better idea of the structure and composition of tropical benthic communities, a research project on the East African coast was initiated in 1992 in cooperation with the Kenya Marine Fisheries Research Institute (KMFRI, Mombasa). A second project started in 1996 on 'Causal factors of biodiversity: community structure, phylogeny and biogeography. A comparative research of fauna of tropical and subtropical estuarine and lagoon systems' (FWO-Flanders, Belgium).

In the frame of this project, a sampling campaign in Gazi Bay (Kenya) was organized in July 1996. Gazi Bay (also called Maftaha Bay) is situated 50 km north to the Tanzanian border and 60 km south to Mombasa. The bay is 1.75–3.5 km wide and 3.25 km long, and covers an area of approximately 15 km^2.

Meiofauna (epiphytic and benthic) was sampled in two transects in an intertidal seagrass bed. Seagrass species belonging to the circumtropical *Thalassia* association (as defined by Brazier, 1975) were sampled: *Thalassia hemprichii* (Ehrenberg) Ascherson, *Halophila ovalis* (Braun) Hooker, *Halophila stipulacea* (Forsskål) Ascherson, *Halodule wrightii* Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy. The harpacticoid copepod associates were identified to species level. Approximately 100 different species were found, a large percentage being new to science.

In the present contribution, three harpacticoid species collected from the *Thalassia hemprichii* collected in Kenya and one species found in a sediment sample from the Peruvian coast are described. The description of two species is complemented with observations on their copepodid development. Finally, some

comments about occurrence of secondary dimorphic features in the setal complement in the natatorial legs of the Tetragonicipitidae are given. Based on these observations, the generic diagnosis of *Paraschizopera* Wells, 1981 is discussed.

Materials and methods

abbreviations: Aesth – aesthetasc; Exo – exopodite; End – endopodite; P1–P6 – legs 1 to 6; Cop I-V – first to fifth copepodid; setal ornamentation of the adult legs follows the notation of Lang, 1948.

Epiphytic copepods from the roots of *Thalassia hemprichii* (Ehrenberg) Ascherson (Angiospermophyta) in Gazi Bay (Kenya) were collected using a 3.6 cm diameter meiocorer (sample surface 10 cm^2), drawn 10 cm deep in the sediment, after carefully removing the aboveground parts (stem and leaves) of the seagrass plant. Samples were fixed in a sea water-formaldehyde solution (final concentration 4%). The animals were separated from the sediment both by decantation and centrifugation in a Ludox gradient. Those retained on a 38 μm sieve, were picked out and stored in 75% ethanol prior to examination.

All series are deposited in the invertebrate collections of the Royal Belgian Institute of Natural Sciences (catalogued: COP #). Dissected parts of the specimens are mounted in glycerine with sealed coverglasses and preserved specimens are stored in denaturated ethanol of 75%. Observations were made at magnifications of 625× and 1250× on a Leitz Diaplan lightmicroscope equipped with phase-contrast and a drawing tube.

Taxonomical account

Family Tetragonicipitidae Lang, 1944

Genus Diagoniceps Willey, 1930

Diagoniceps laevis Willey, 1930
Figure 1A–C

Material: (1) Kenya, Gazi Bay (Gazi village: 4° 25′ S, 39° 30′ E, south to Mombasa): intertidal root samples of *Thalassia hemprichii* (Ehrenberg) Ascherson, 2 hours before and after low tide. Leg. M. De Troch, July 17, 1996. Materials:1 ♀, labeled COP 4249A-E and 1 ♂, labeled COP 4248A-B dissected; preserved: 2♀♀ and 1♂, labeled COP 4250 and COP 4251.

(2) Mexico, Quintana Roo state, Bioreserve Sian Ka=an, Laguna Ascension. Subtidal sediments between *Thalassia testudinum* Banks *ex.* König seagrass beds, at 0.5 m depth (t. 32.4 °C, sal. 37.9 ppm). Leg. F. Fiers, July 20, 1997 (field nr. MEX 87-012). Material: 1 ♀ (ovigerous), preserved in ethanol, COP 4369.

Comparison

Detailed comparison of the Kenyan specimens with those studied in Fiers (1995: from the Bahamas and Bermuda) and with the female specimen found along the Caribbean coast of Mexico, revealed only minor differences:

(1) the Kenyan animals are maximum 510 μm long, thus 150 to 180 μm shorter than the specimens from the Central Atlantic (660–685 μm) and the Caribbean (690 μm);
(2) the inner pectinate seta on the first endopodal segment of the P1 is slightly shorter in the Kenyan animals than in the Atlantic specimens: only reaching to the distal third of the second segment in the former, but extending up to the distal end of the second segment in the latter;
(3) the distal margin of the P3 endopodite reaches the implantation of the inner spiniform seta on the second exopodal segment in the Kenyan specimens, whereas the Atlantic specimens display a quite shorter endopodite, reaching to the middle of the second exopodal segment, at the most;
(4) on the female P5 exopodite, the outer proximal seta extends to nearly the apex of the segment in the Kenyan material (Figure 1B), but does not quite reach the implantation of the inner subdistal seta in the Atlantic specimens;
(5) the two apical setae on the endopodal P5 lobe of the Kenyan females display quite different proportional lengths from those observed in the Atlantic females. Kenyan specimens have the outer seta only half as long as the inner one (Figure 1C) whereas this seta equals 4/5 of the outer seta in the Atlantic specimens. Curiously, the proportional lengths of the P5 endopodal lobe in the Mexican specimen resembles those of the Kenyan specimens.

At last, it should be noted that the illustration of the female P6 vestiges in Fiers (1995: Figure 7a) is

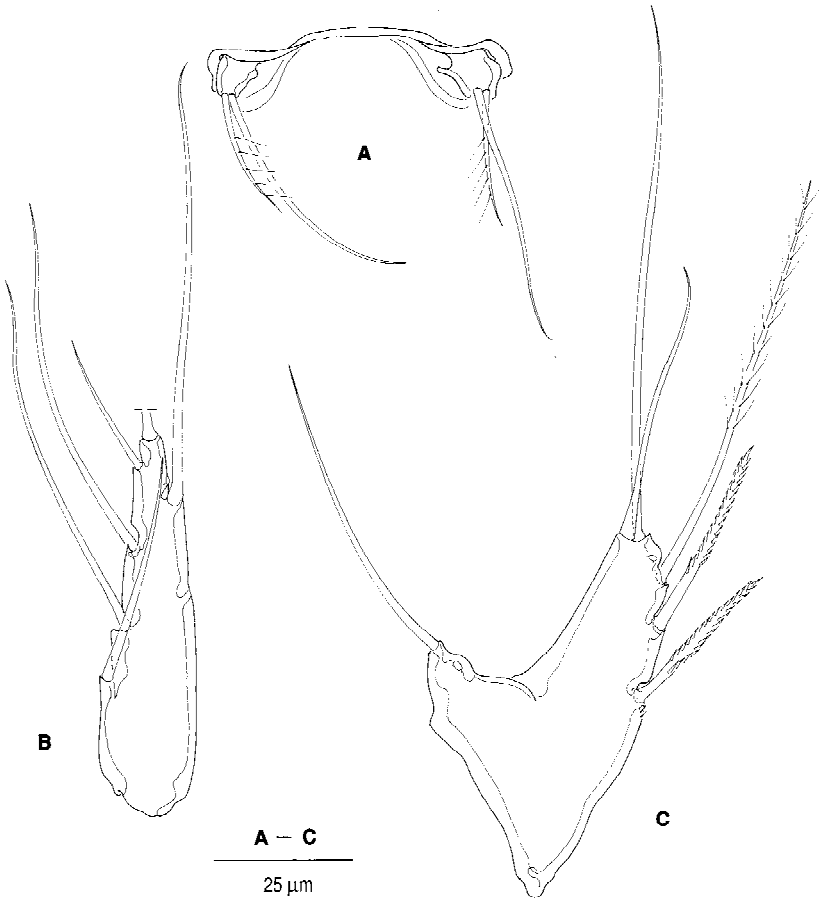

Figure 1. *Diagoniceps laevis* Willey, 1930: (A) female P6 vestiges; (B) female P5 exopodite; (C) female P5 baseoendopodite.

erroneous as it shows three elements on each vestige. Re-examination of the specimens clearly proved that only two appendages (a plumed and a smooth one) are present. The correct setation as illustrated here (Figure 1A) is drawn from the dissected Kenyan female specimen (COP 4249). Also, the P6 vestiges of the females of *D. mexicana* Fiers, 1995 bear only two elements instead of three as was illustrated previously (Fiers, 1995).

Discussion

Thus far, *D. laevis* was known only from two localities in the central western Atlantic: Bermuda (Wiley, 1930; Yeatman, 1980), and the Bahamas (Fiers, 1995). At first, we wanted to attribute the Kenyan specimens to a separate species. We refrain, however, to define a new species solely on the five differences listed above. Although these features seem to be constant within a population, we need more information on the variability of them from more populations within the Indo-Pacific area to reach to a conclusion.

Genus Odaginiceps Fiers, 1995

Odaginiceps immanis spec. nov.
Figures 2–6

Type-material: Holotype female, dissected on 7 slides, labeled COP 4379 A-G; allotype male, dissected on 4 slides, COP 4380 A-D; paratypes: 1 ♀, 2♂♂, and 1 damaged cop V♀, preserved in alcohol, COP 4378 and 4247.

Type-locality: Kenya, Gazi Bay (Gazi village: 4° 25′ S 39° 30′ E, south to Mombasa), intertidal root samples of *Thalassia hemprichii* (Ehrenberg) Ascher-

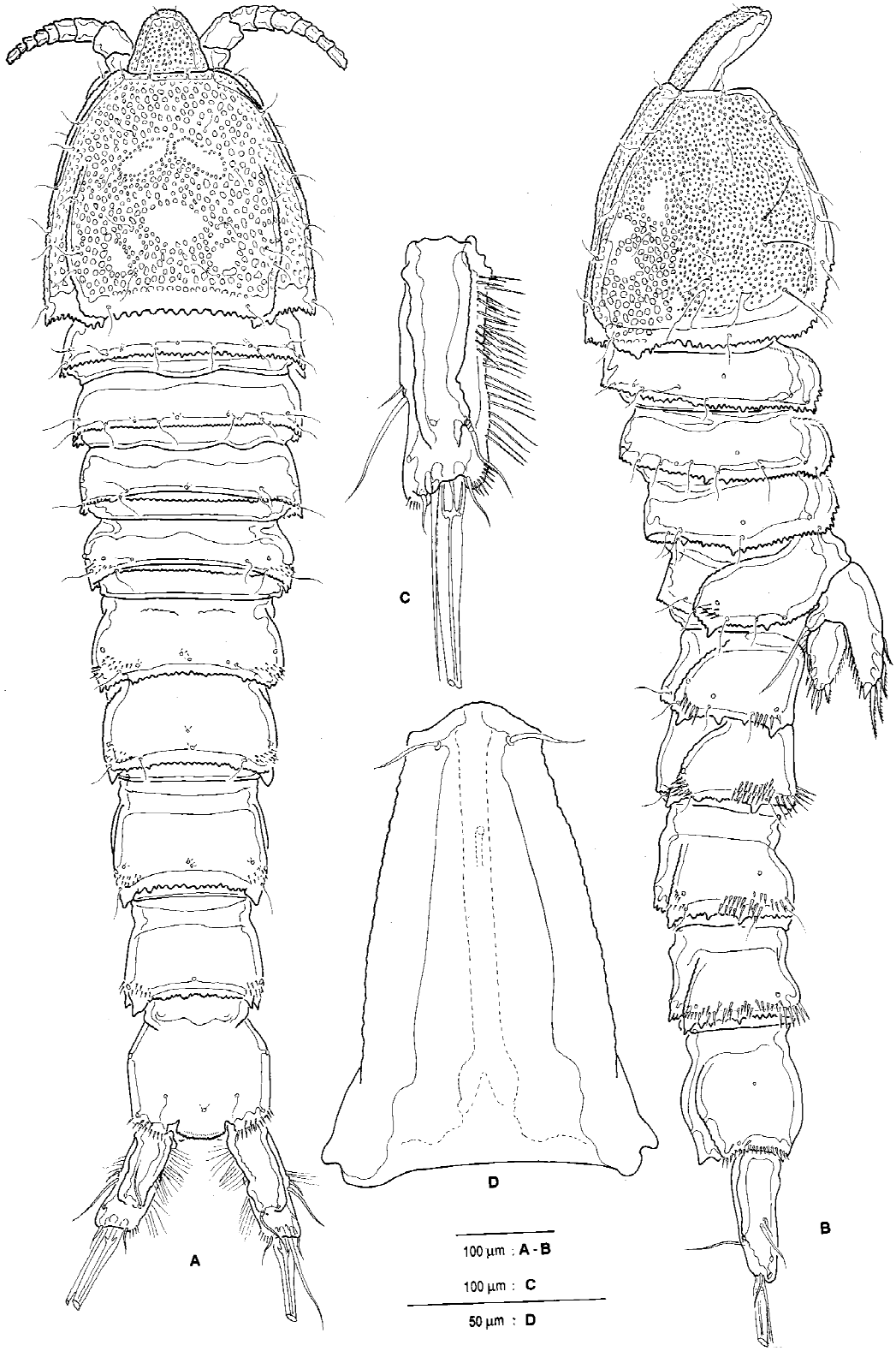

Figure 2. Odaginiceps immanis n. spec: (A) female habitus, dorsal view; (B) female habitus, lateral view; (C) female left caudal ramus, dorsal view; (D) female rostrum, dorsal view.

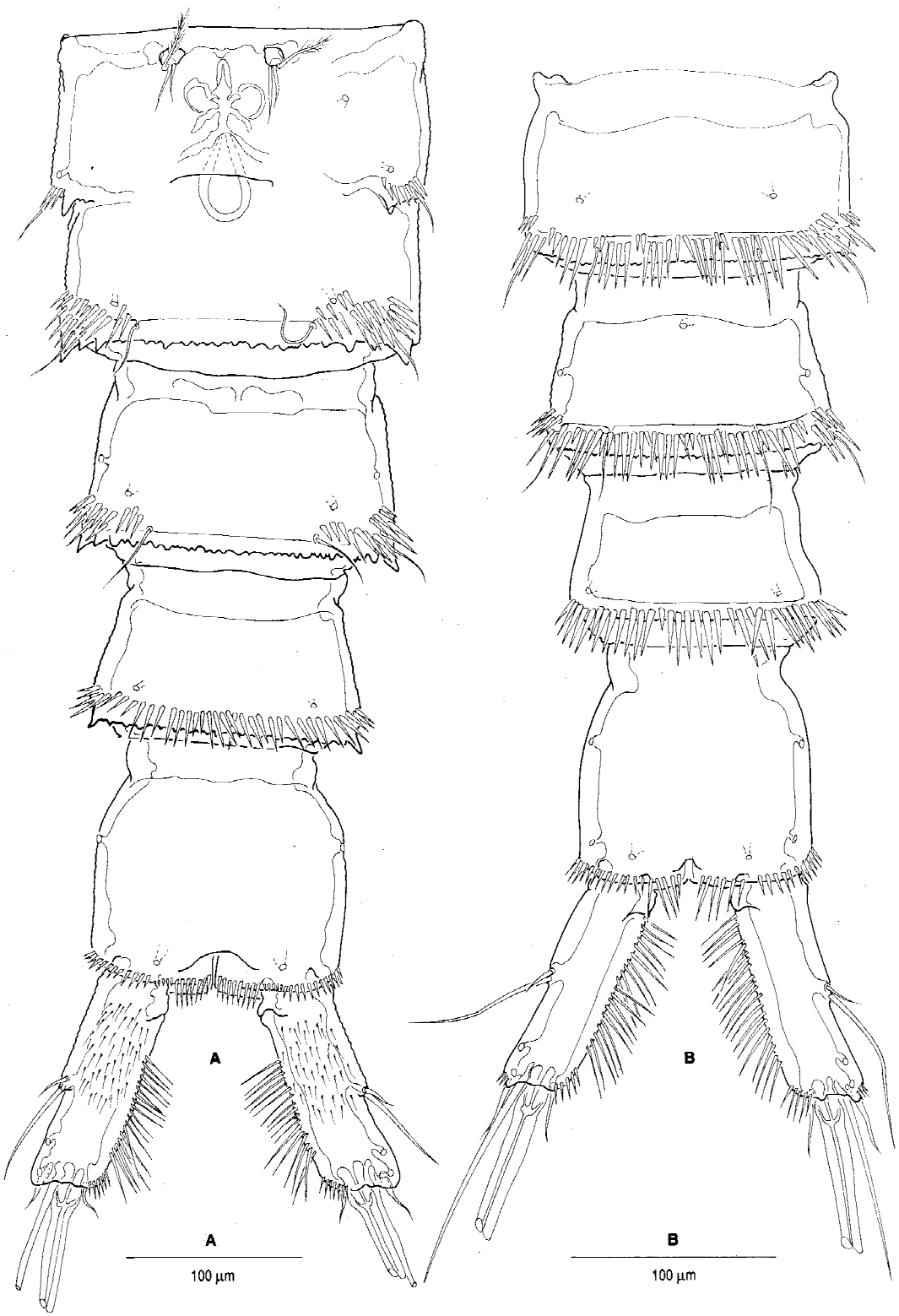

Figure 3. Odaginiceps immanis n. spec: (A) female urosome, in ventral view; (B) male urosome (P6 bearing somite omitted), in ventral view (A of holotype, B of allotype).

Figure 4. Odaginiceps immanis n. spec: (A) P1, posterior view; (B) coxa and basis of P1, frontal view; (C) P2, frontal view (A–C, female).

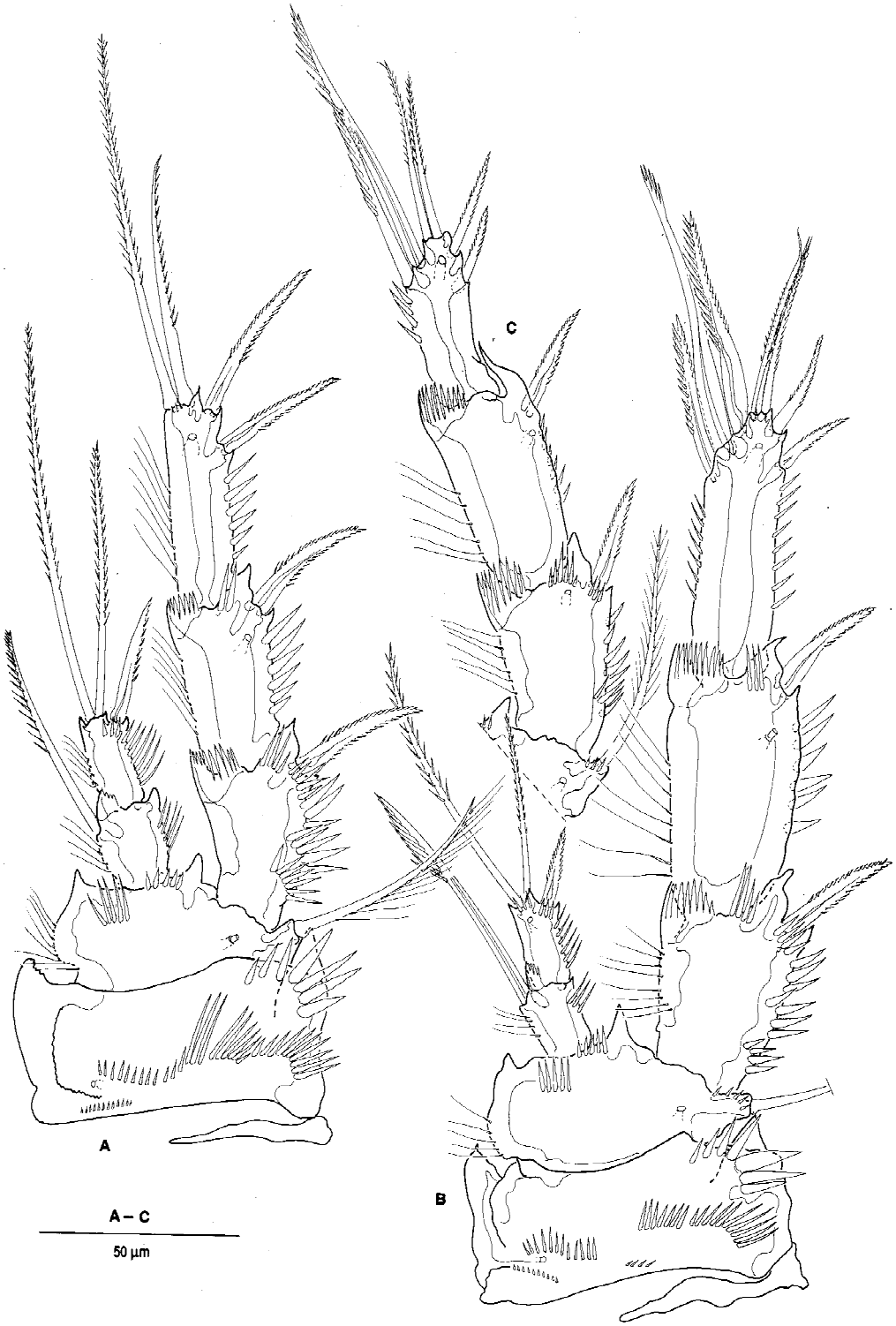

Figure 5. Odaginiceps immanis n. spec: (A) P3, frontal view; (B) P4, in frontal view; (C) exopodite and distal outer edge of basis of P4 (A–B, female; C, male).

Figure 6. Odaginiceps immanis n. spec: (A), female P5, anterior view; (B) male P5, anterior view (exopodite detached); (C) endopodite of male P2, posterior view; (D) endopodite of male P3, posterior view.

son, 2 h before and after low tide. Leg. M. De Troch, 17 July 1996.

Etymology: The specific name, *immanis* (Latin for huge, frightful or fierce) refers to largeand heavely sclerotized body.

Description of female: Habitus (Figure 2A, B) fusiform, robust and large (1250 μm long, including rostrum and caudal rami). Body slowly tapering towards anal somite, the latter bearing divergent caudal rami. Head with compact appearance, bell-shaped, with two dorsolateral carinae in posterior half. Posterior margin of head crenate, of succeeding somites irregularly serrate. Dorsolateral and ventrolateral posterior edges of urosomites acute. Anal somite with crescentic anal operculum. The latter with a finely serrate posterior margin.

Integument of somites and all appendages rigidly sclerotised. Integument of head pitted, except for a dorsal symmetrical pattern of ovate smooth areas, and its smooth margins. All other somites with pitted integument (not illustrated) dorsally and laterally. Median ventral surface of genital double-somite and following urosomites smooth. Additionally, each urosomite with one or more short rows of spinules on lateral surface. Posteroventral margin of penultimate somite with a complete row of spinules.

Caudal rami (Figure 2C) semi-cylindrical, slightly more than 3 times as long as wide. Distal outer margin rounded and somewhat protruded. Anterior lateral setae located just beyond middle of outer margin. Posterior lateral seta located somewhat beyond implantation of terminal setae, very short and slightly bulbous proximally. Biarticulate dorsal seta arising in distal fourth of dorsal surface, close to inner margin. Principal terminal setae not fused at base: with outer one slender and short (as long as ramus), and inner one robust at base (entire length not observed). Inner terminal seta very short and slender. Dorsal surface with two longitudinal, irregular, carinae, extending from articulation with anal somite to slightly further than implantation of dorsal seta. Inner margin and inner and outer distal edge spinulose. Ventral surface (Figure 3A) furnished with fine hairs in anterior half.

Rostrum (Figure 2D) large and broad, slowly tapering in anterior direction, with a arcuate anterior margin. Subdistal pair sensillae arising dorsally, ventral pore situated in distal fifth on a longitudinal crest. Dorsal integument densely pitted.

Antennule, antenna and mouthparts exactly the same as in *O. clarkae* Fiers, 1995, type species of the genus.

P1 (Figure 4A) with large, unornamented, praecoxal structure. Coxa furnished with robust spinules on posterior and anterior surface. Median region of frontal surface with a dense field of minute spinules (Figure 4B). Basis smooth posteriorly, ornamented with spinules below implantation of medial spine, and along distal rim. Outer and medial basal spine strong and spinulose. Exopodite 3-segmented with robust outer spines on proximal and median segment. Outer spines of terminal segment rather slender, spinulose along one side of the stem. Distal elements of third exopodal segment geniculate, and plumose near median knick. Endopodite two-segmented, with first segment slightly shorter than exopodite, and second segment about half as long as proximal segment. Inner element of proximal endopodal segment bipinnate along major part of the stem, slightly pectinate near tip. Terminal elements of distal endopodal segment: inner one smooth and short, median one geniculate, and outer one spinulose along outer side of stem.

P2 (Figure 4C) – P3 (Figure 5A) both with robust general appearance. Praecoxal element, smooth, and slender. Coxa heavely ornamented with spinules on anterior surface. Inner and outer distal corner of coxa protruded in a sharp extension. Basis with spinules along medial and mediodistal margin. Outer basal seta unipinnate. Exopodite 3 segmented with robust outer spines, and two finely spinulose terminal setae on distal segment. Endopodite two-segmented without (P2) or with an inner (P3) element, and reaching to just below articulation between second and third exopodal segment (P2), or just beyond articulation between first and second exopodal segment (P3). Terminal setae finely spinulose, outer sub-distal spine long and spinulose. Chaetotaxy in Table 1. Intercoxal plate rigid, with concave distal rim, and smooth surface.

P4 (Figure 5B) with praecoxa, coxa and basis resembling the preceeding legs. Three-segmented exopodite very robust, with broad first and median segments. Endopodite two-segmented just reaching articulation between first and second exopodal segments. Outer exopodal spines robust on first and second segments, more slender on distal segment. Terminal exopodal elements finely spinulose, and inner elements with swollen proximal half and pectinate distal part. Inner element on first endopodal segment pectinate.

P5 (Figure 6A) having a compact appearance. Exopodite with ovate shape, articulating with baseoendo-

Table 1. Setal complement of the legs in *Odaginiceps immanis* n. sp.

	EXO	END
P1	0-0-0.2.2	1-0.2.1
P2	0-0-0.2.3	0-0.2.1
P3	0-0-0.2.2	1-0.2.1
P4♀	0-0-3.2.2	1-0.2.1
P4♂	0-0-2.2.2	1-0.2.1

podite, and not reaching apical margin of endopodal lobe. Six exopodal elements: outer and apical ones smooth, slightly thickened near implantation, inner subdistal one spiniform. Endopodal lobe broad ovate, bearing 5 spiniform elements. Outer apical one pear-shaped, short and armed with some minute spinules along distal part of outer margin. Outer and inner margin of endopodal lobe and exopodal segment furnished with slender spinules. Surface of the rami marbled anteriorly, smooth posteriorly.

P6 vestiges (Figure 3A) individual, each with three short setae: outer one plumose, median and inner one smooth. Genital field rather large, with wide and straight gonopore, situated close to the middle of the ventral surface of the genital double-somite.

Description of male: Habitus as in the female, only slightly shorter (1210 μm, including rostrum and caudal rami), and having separated genital somites. Integument of somites ornamented as in female, except for posteroventral margins of third and fourth urosomites having a complete transversal row of spinules (Figure 3B), and the smooth ventral surface of the caudal rami.

Antennule as in *O. clarkae* Fiers, 1995. Antenna, mouthparts and P1 as in female.

P2 and P3 with protopodal segments and exopodite as in the female. Endopodite P2 (Figure 6C) with typically modified elements on second segment: inner one short, spinulose; median one smooth, thickened in proximal half; outer one fused with segment, slightly shorter than median one. Endopodite P3 (Figure 6D) having a strong pectinated element on proximal segment. Subdistal outer spine modified: globulous proximally, serrate along slender distal half. Edges of second segment slightly more prominent than in female.

P4 protopodal and endopodal segments as in female. Exopodite with a sinusoid extended outer distal corner of median segment. Terminal exopodal segment narrower than in female, bearing only two pectinate inner elements instead of three (Figure 5C).

P5 (Figure 6B) with medially fused opposite baseoendopodites. The latter with rigid integument, and furnished with several spinule rows and spinule fields on anterior surface. Inner endopodal spine robust and pectinate; both distal spines equally long. Exopodite less or more rectangular, having 3 smooth outer setae, serrate distal and sub-distal element, and a pectinate inner proximal spine.

Right P6 vestige articulating with somite, left one fused to somite. Each bearing three sub-equal elements: outer one spinulose, median and inner one smooth.

Comparison

The present species is assigned to the genus *Odaginiceps* because of the following features: the large, prominent rostrum, the antennule with short second segment, the presence of pinnate setae on the antennular segments II and III, and the two-segmented P1 endopodite with three appendages on the second segment.

Thus far, three species are attributed to the genus *Odaginiceps*: *O. clarkae* Fiers, 1995, *O. xamaneki* Fiers, 1995, and *O. elegantissima* Fiers, 1995, known, respectively, from the Mexican Caribbean coast, the southern bight of the Gulf of Mexico, and Bermuda.

The here described species is easily distinghuishable from its congeners in several aspects: the body length (1.250 mm versus 974 μm in *O. elegantissima*, the largest of the three known species), the chaetotaxy of the endopodite in P3 bearing an inner seta on the proximal segment, the unique spine formula of the distal exopodal segments of P2–P4 with 3, 2, 2 outer spines, respectively, and, not at least, the compact and robust shape of the rami and setae in the female P5.

Genus Mwania gen. nov.

Diagnosis: Tetragonicipitidae with a nonfoliaceous fifth leg in the female, and a short first antennular segment, without ornaments. Rostrum minute, not sexually dimorph. Body fusiform, with slightly dimorphic caudal rami. Principal terminal setae on caudal rami not fused at base. Antennule 9-segmented. Second segment twice as long as first one. Setae smooth. Segment II with 8, segment III with 9 setae, and segment IV with 4 setae and principal aesthetasc. Male

Table 2. Setal complement of the legs in *Mwania phytocola* n. gen., n. sp.

	EXO	END
P1	0-0-0.2.2	1-0-0.1.1
P2	1-1-0.2.3	1-1.2.1
P3	1-1-1.2.3	1-1.2.1
P4♀	1-1-3.2.3	1-1.2.1
P4♂	1-1-2.2.3	1-1.2.1

antennule 12-segmented with principal aesthetasc on segment V. No large expanded elements on inner margin of segments forming palm. Antenna with seta on first endopodal segment, and one-segmented exopodite bearing 2 lateral and 1 terminal setae. Mandible with one-segmented endopodite and 3-segmented exopodite. Maxilliped with two setae on basis, and two additional setae near claw. P1 with 3-segmented endopodite, bearing two terminal elements on distal segment. Third exopodal segment of P1 with subdistal and outer distal elements comb-like. Exopodites P2–P4 3-segmented, endopodites 2-segmented with setal complement in Table 2. Endopodites of P2 and P3 reaching towards distal exopodal segment, having no pectinate inner seta on proximal segment. P4 with pectinate seta on proximal segment of endopodite. Distal endopodal segment shorter than proximal one. Exopodite of P5 articulating with baseoendopodite, bearing 6 setae (4 outer ones, 1 apical, 1 sub-apical inner one). Endopodal lobe of P5 with 5 elements: 3 inner ones, 2 apical ones. P6 vestiges with 3 setae. Sexual dimorphism in urosome and antennule. Appendages of P2 and P3 endopodite typically modified. Outer distal edge of median exopodal segment of P4 resembling closely that of female. P5 with both exopodites or only one 2-segmented, bearing 6 elements: inner subdistal and apical one robust and spiniform, other slender. Endopodal lobe with 3 equal spiniform elements. P6 with 3 long appendages.

Type species: *Mwania phytocola* spec. nov., by monotypy.

Etymology: The generic *Mwani* is Kishwahili, the language spoken in Kenya, for seagrasses. The gender is masculine.

Justification: The here described *Mwania phytocola* spec. nov. is an intriguing tetragonicipitid species because of its three-segmented endopodite of the first leg. Thus far, only the genera *Paraschizopera* Wells, 1981 and *Pteropsyllus* Scott, 1906 are defined to have a three-segmented endopodite in the P1. However, *Mwania* cannot be considered as closely related to *Pteropsyllus* as this genus with its prolonged first antennular segment and its foliaceous female fifth leg belongs to the lineage including *Phyllopodopsyllus*, *Laophontella* and *Oniscopsis*.

The first leg of *Mwania* differs from that of *Paraschizopera* in two aspects: 1. there are only two terminal elements on the third segment (3 in *Paraschizopera*) and 2. the subdistal and outer distal setae of the third exopodal segment have a comb-like appearance (ordinary spinulose in *Paraschizopera*). *Mwania* shares these two (apomorphic) features with the genera *Aigondiceps* and *Godianiceps* which indicate the close relationship between these taxa.

Mwania differs from these two taxa in the body shape. Whereas the two sister taxa have a body with a distinct prosomal and urosomal body region, the present genus still posses a fusiform body type in which, in dorsal view, the somites gently tapering towards the anal somite. Such body shape reminds closely that of *Diagoniceps* and of *Paraschizopera trifida*.

Apparently, the here defined genus, *Mwania*, represents an early branch within the clade assembling *Aigondiceps*, *Godianiceps* and *Neogoniceps* gen. nov. (described below). Body shape, three-segmented endopodite of the first leg, complete chaetotaxy of the endopodites in the legs, undifferentiated setae on the proximal endopodal segments of the female P2 and P3, and large endopodites in both legs reaching towards the terminal exopodal segments, are plesiomorphic characterstates belonging to the ground pattern of the Tetragonicipitidae. The reduced chaetotaxy of the terminal exopodal segments of the P2 (023) and P3 (123) is, however, a unique setal complement within the above mentioned clade and among the other tetragonicipitid taxa without a foliaceous female fifth leg. Secondly, the amazing shortness of the distal segment of the P4 endopodite, being distinctly shorter than the proximal segment is unique. Among those tetragonicipitid genera with a non-foliaceous fifth leg in the female, non has such remarkable short second endopodal segment. Instead, reduction of the endopodal size seems invariablely archieved by the reduction of the proximal segment.

Mwania phytocola spec. nov.
Figures 7–20.

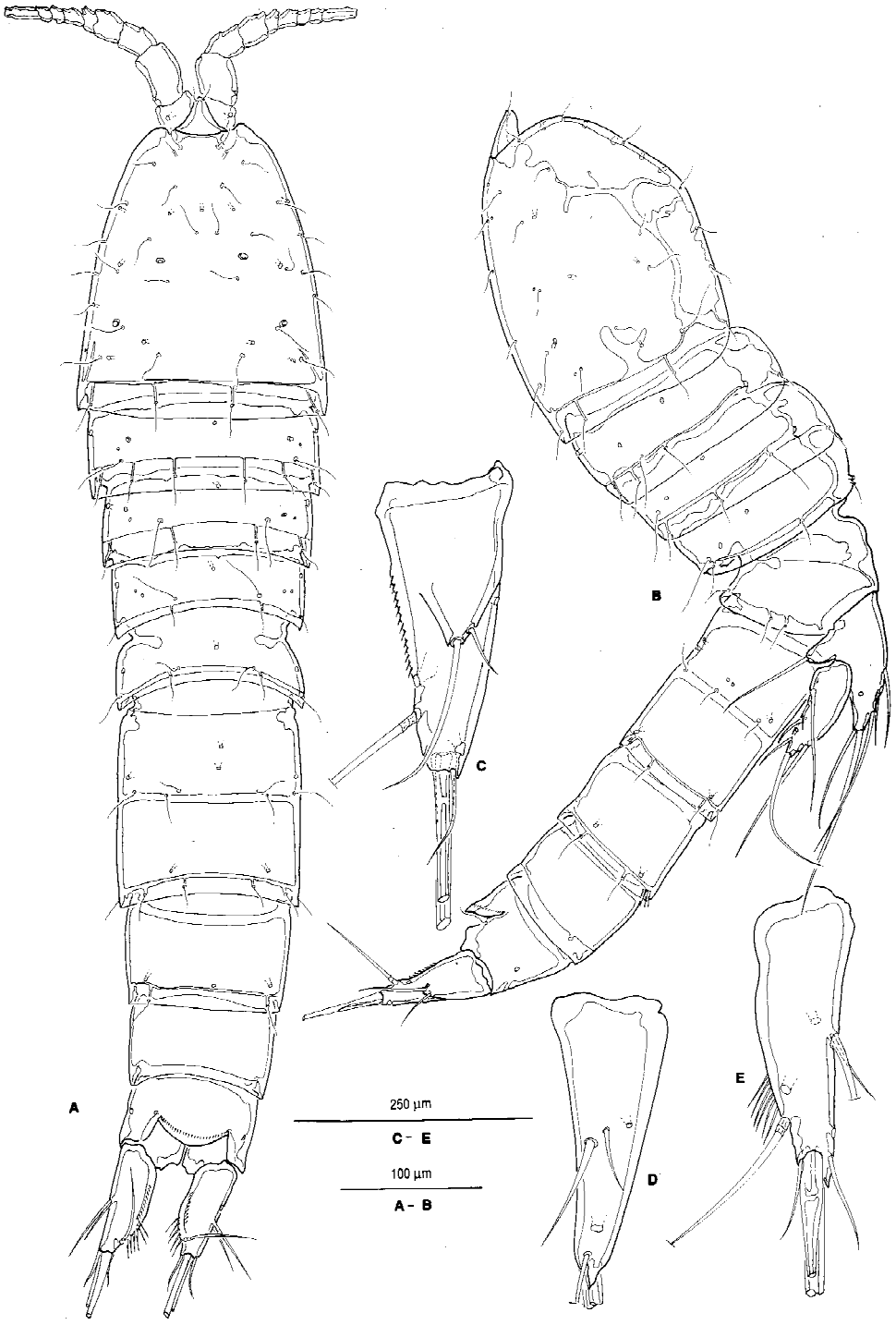

Figure 7. Mwania phytocola n. gen., n. spec.: (A) female habitus, in dorsal view; (B) idem, in lateral view; (C) right caudal ramus of female, in lateral view; (D) right caudal ramus of male, in lateral view; (E) idem, in dorsal view.

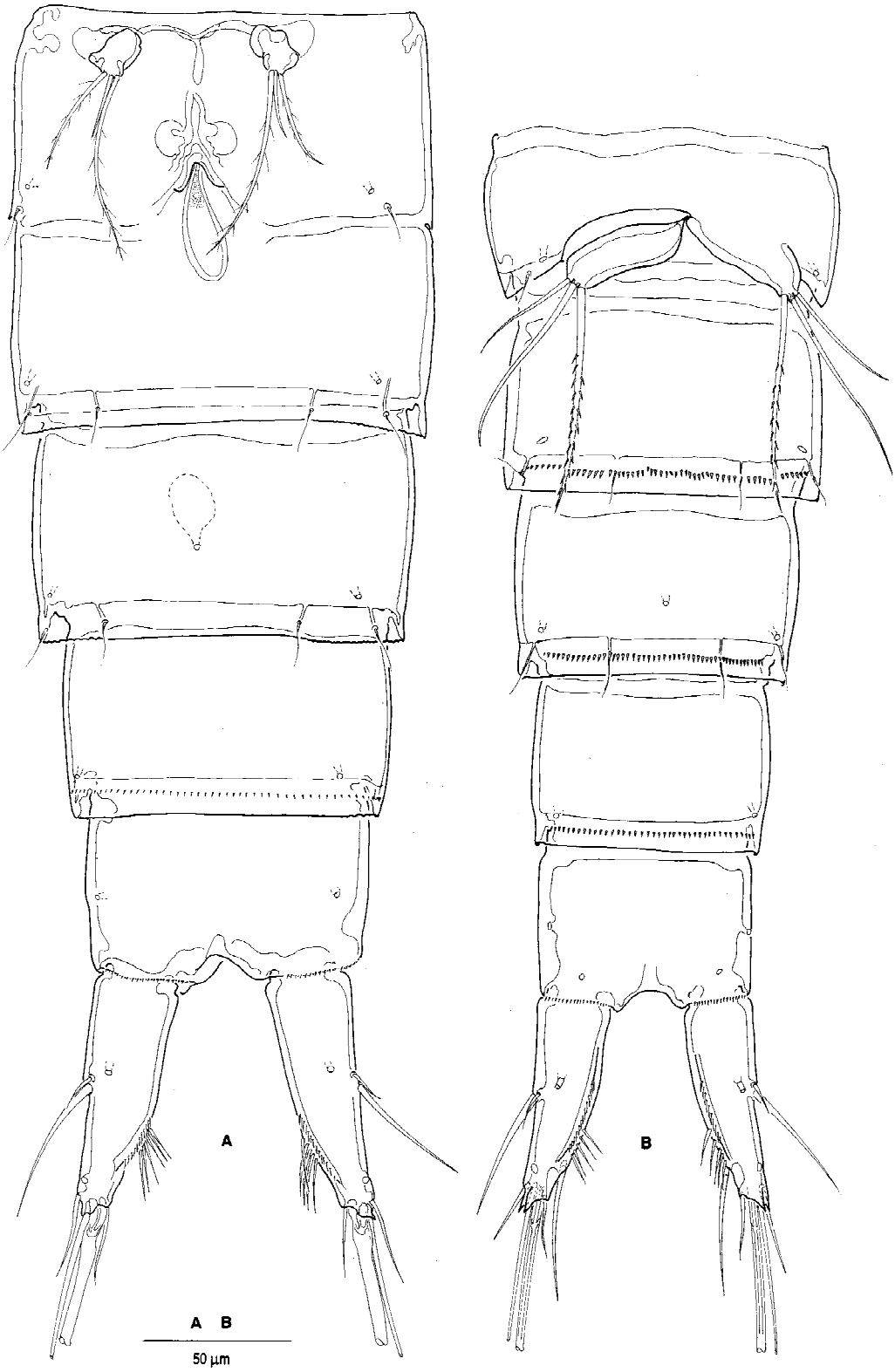

Figure 8. *Mwania phytocola* n. gen., n. spec.: (A) female urosome, ventral view; (B) male urosome, in ventral view.

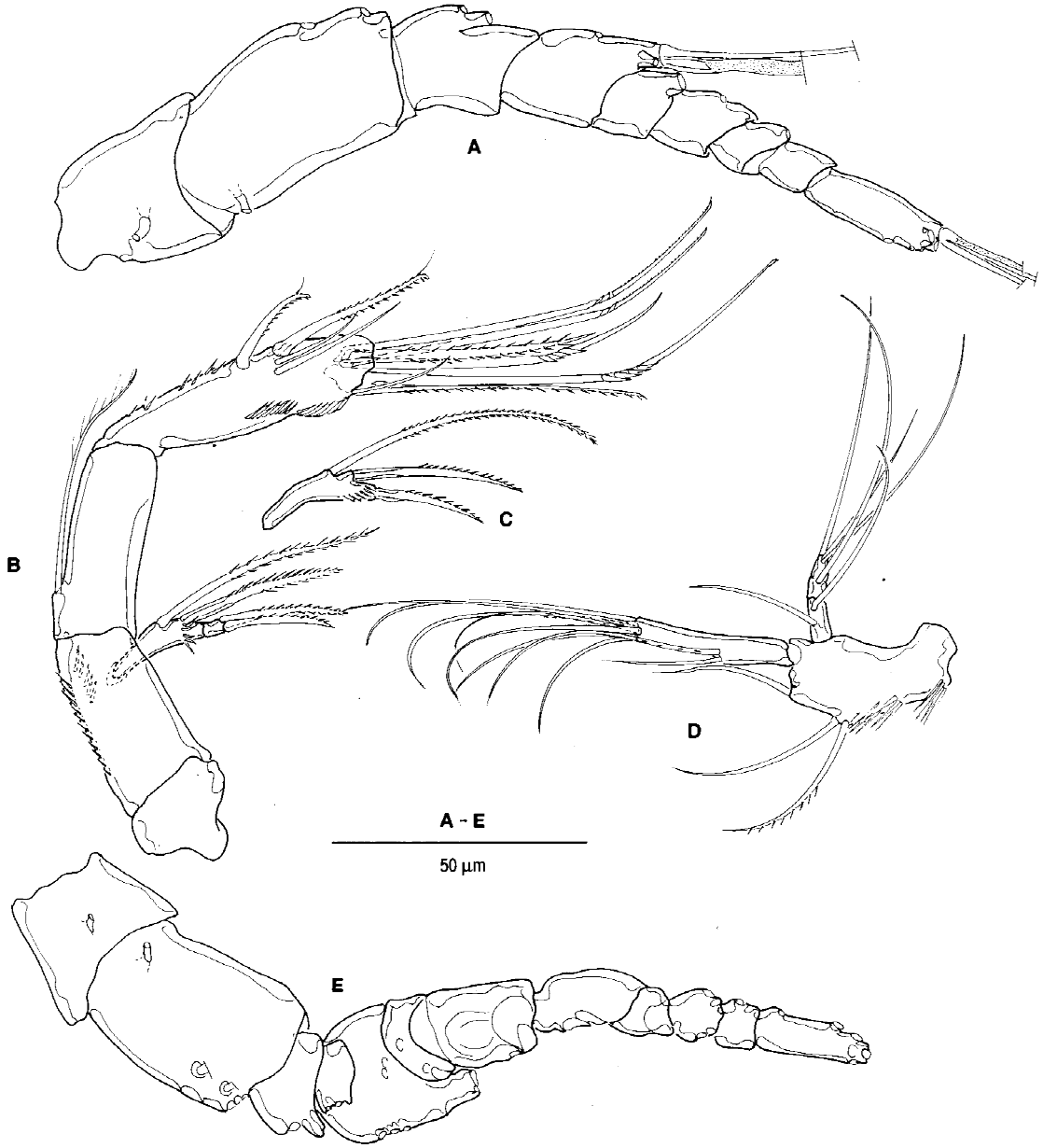

Figure 9. Mwania phytocola n. gen., n. spec.: (A) contour of female antennule, dorsal view; (B) antenna (aberrant); (C) normal antennal exopodite; (D) mandibular palp; (E) contour of male antennule, dorsal view.

Type material: Holotype female, dissected, mounted on 6 slides, labeled 4253 A–F; allotype male, dissected and mounted on 3 slides, COP 4381 A–C; preserved paratypes: 15 ovigerous ♀♀, 5 non-ovigerous ♀♀, 28 ♂♂, 3 Cop 1, 2 Cop II, 3 Cop III, 1 Cop IV ♀ and 1 Cop V♀ (COP 4252); dissected paratypes: 1♂, mounted on 2 slides, COP 4254 A–B; 1♂ dissected on 3 slides, COP 43 77A–C, 1 Cop I (COP 4382), 1 Cop II (COP 4383), 1 Cop III (COP 4384), 1 Cop IV ♀ (COP 4385) and 1 Cop V ♀ (COP 4386).

Type locality: Kenya, Gazi Bay (4° 03′ S, south to Mombasa): intertidal root samples of *Thalassia hemprichii* (Ehrenberg) Ascherson, 2 hours before and after low tide. Leg. M. De Troch, July 17, 1996.

Etymology: The specific name is derived from the words *phyton* (Greek: plant) and *cola* (Latin:

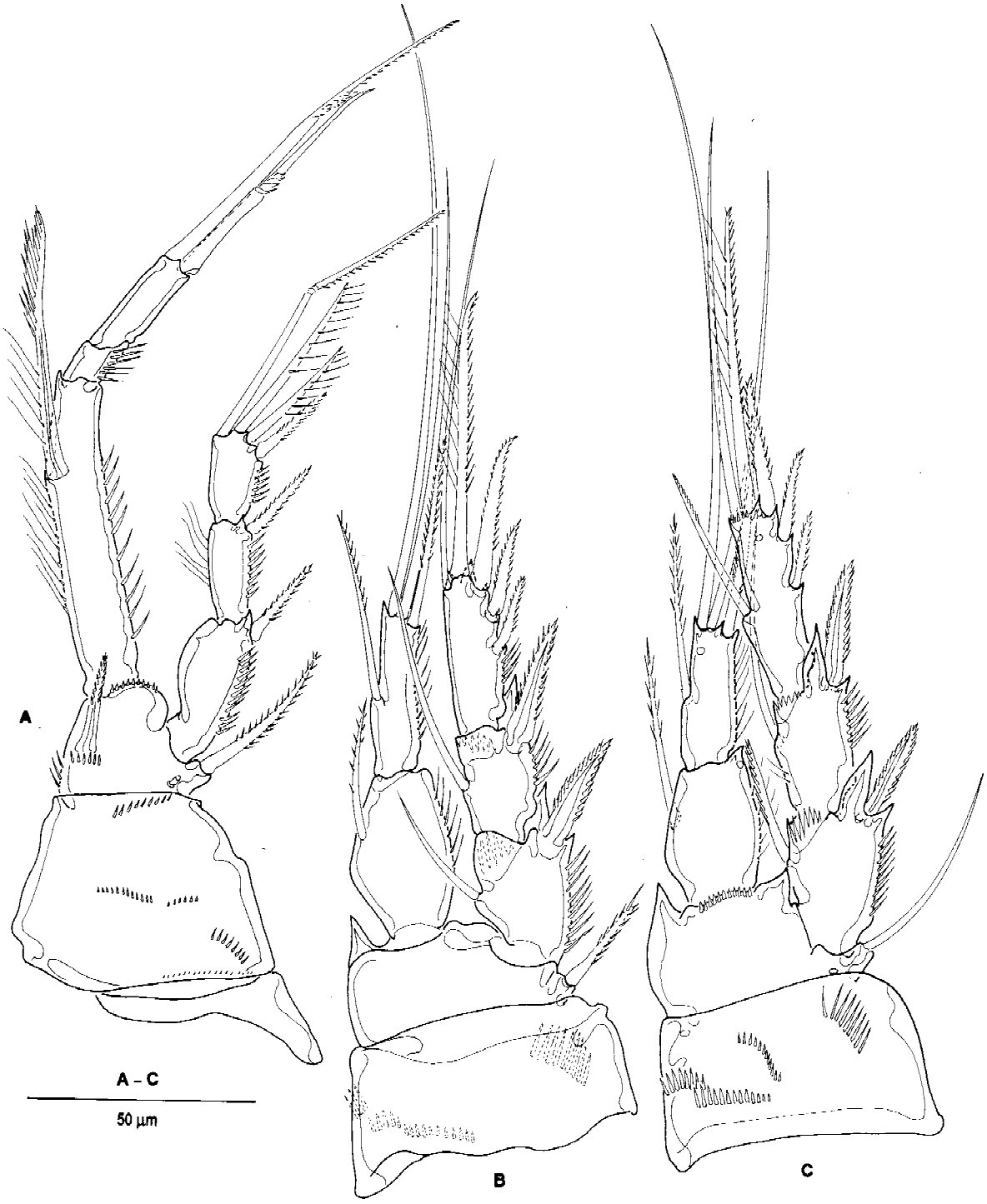

Figure 10. Mwania phytocola n. gen., n. spec.: (A) female P1, anterior view; (B) female P2, posterior view; (C) female P3, anterior view.

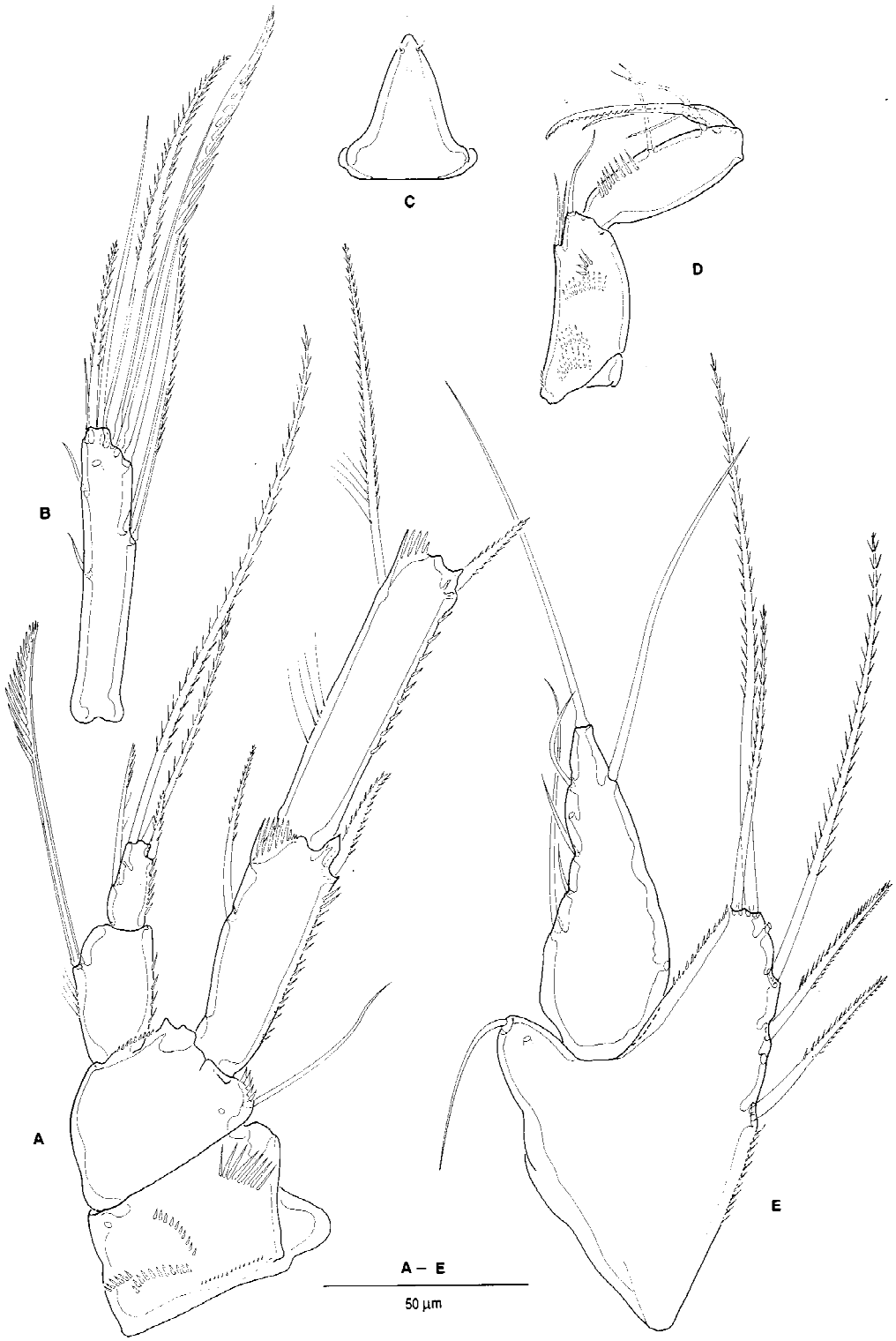

Figure 11. *Mwania phytocola* n. gen., n. spec.: (A), right female P4, anterior view (third exopodal segment broken); (B) third exopodal segment of female P4 (opposite ramus); (C) female rostrum, dorsal view; (D) maxilliped; (E) female P5, anterior view.

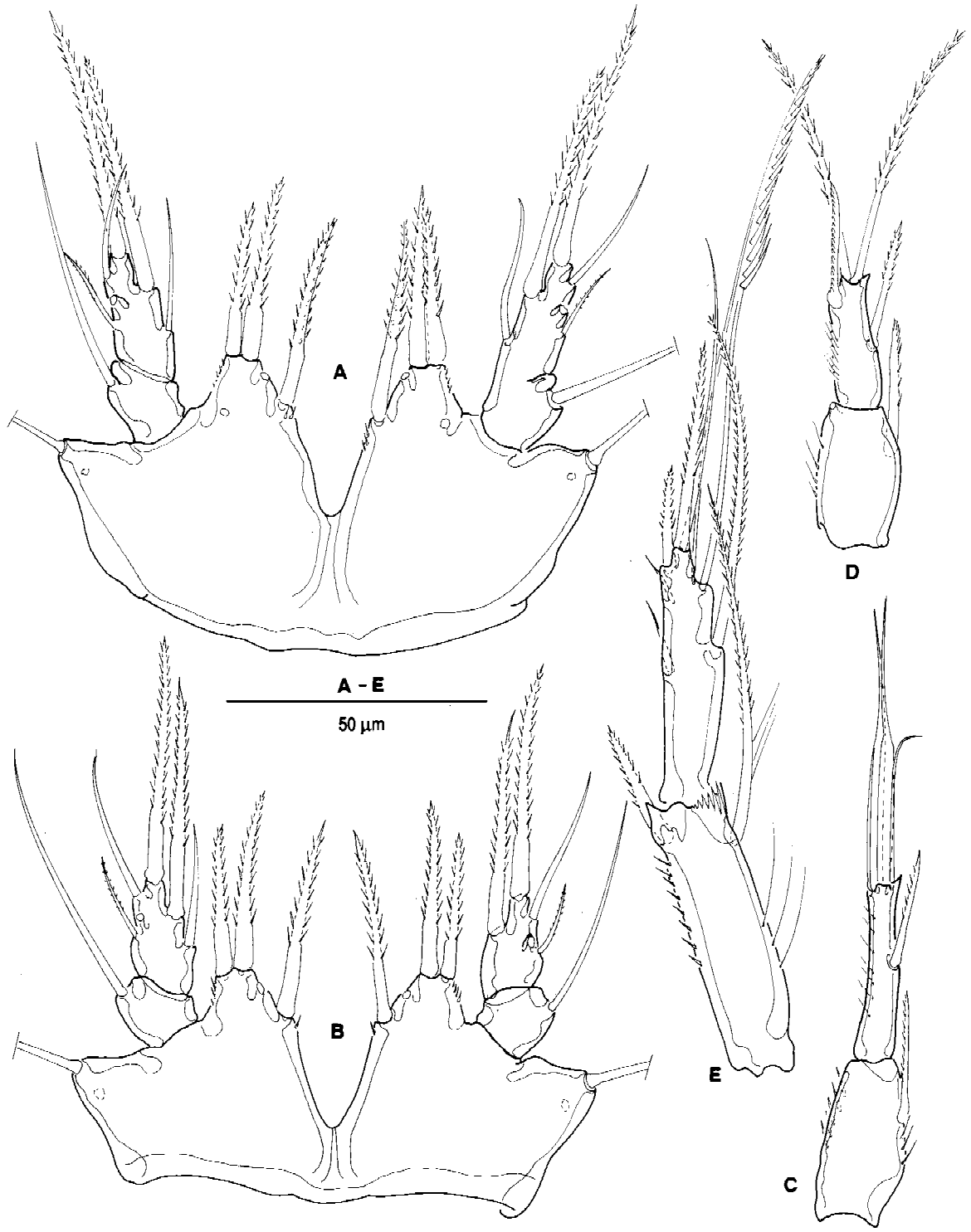

Figure 12. Mwania phytocola n. gen., n. spec.: (A) male P5, anterior view; (B) aberrant male P5, posterior view; (C) endopodite of male P2; (D) endopodite of male P3; (E) middle and distal segment of male P4 exopodite.

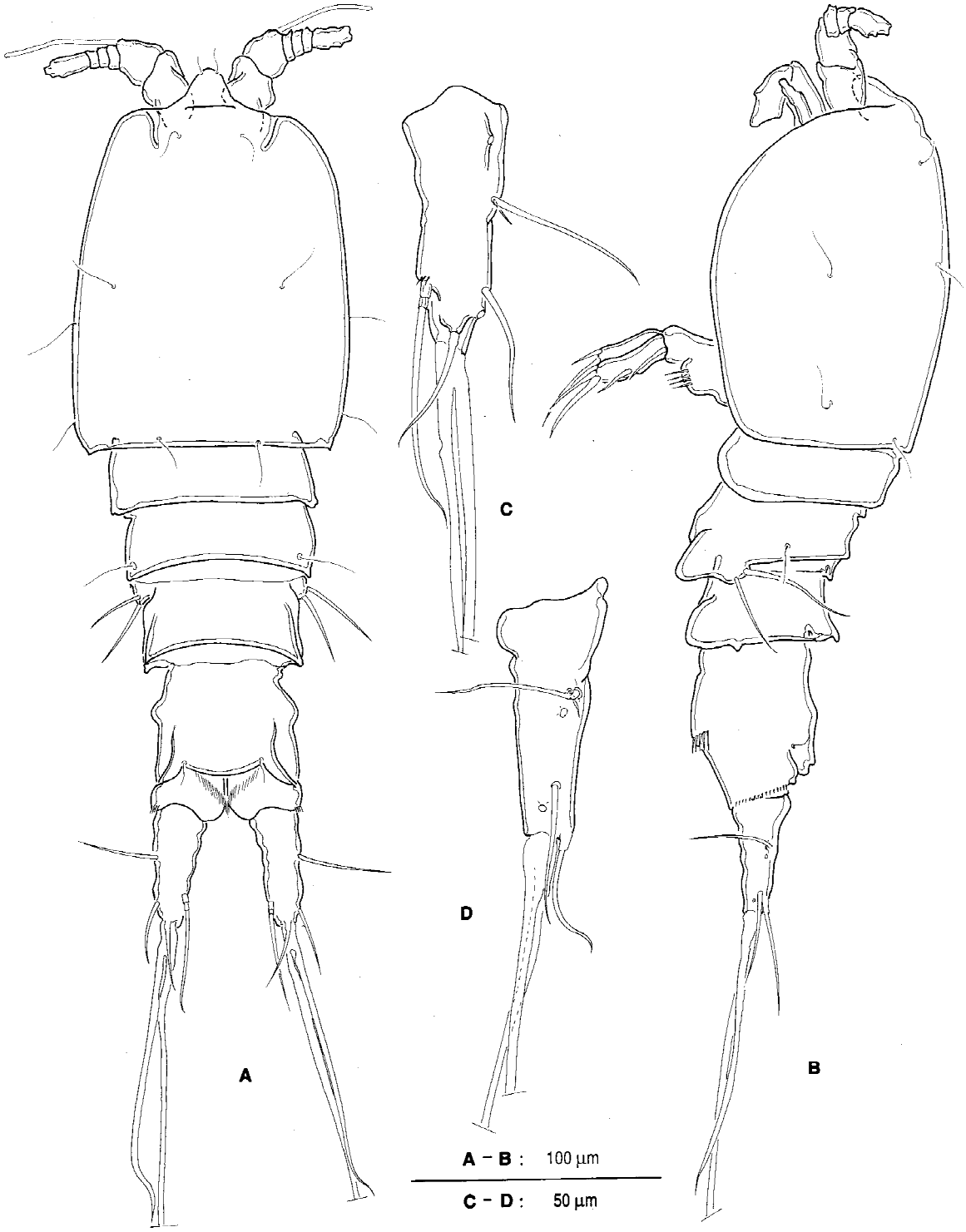

Figure 13. Mwania phytocola n. gen., n. spec.: (A) first copepodid, dorsal view; (B) idem, lateral view; (C) caudal ramus of CI, in dorsal view; (D) idem, in lateral view.

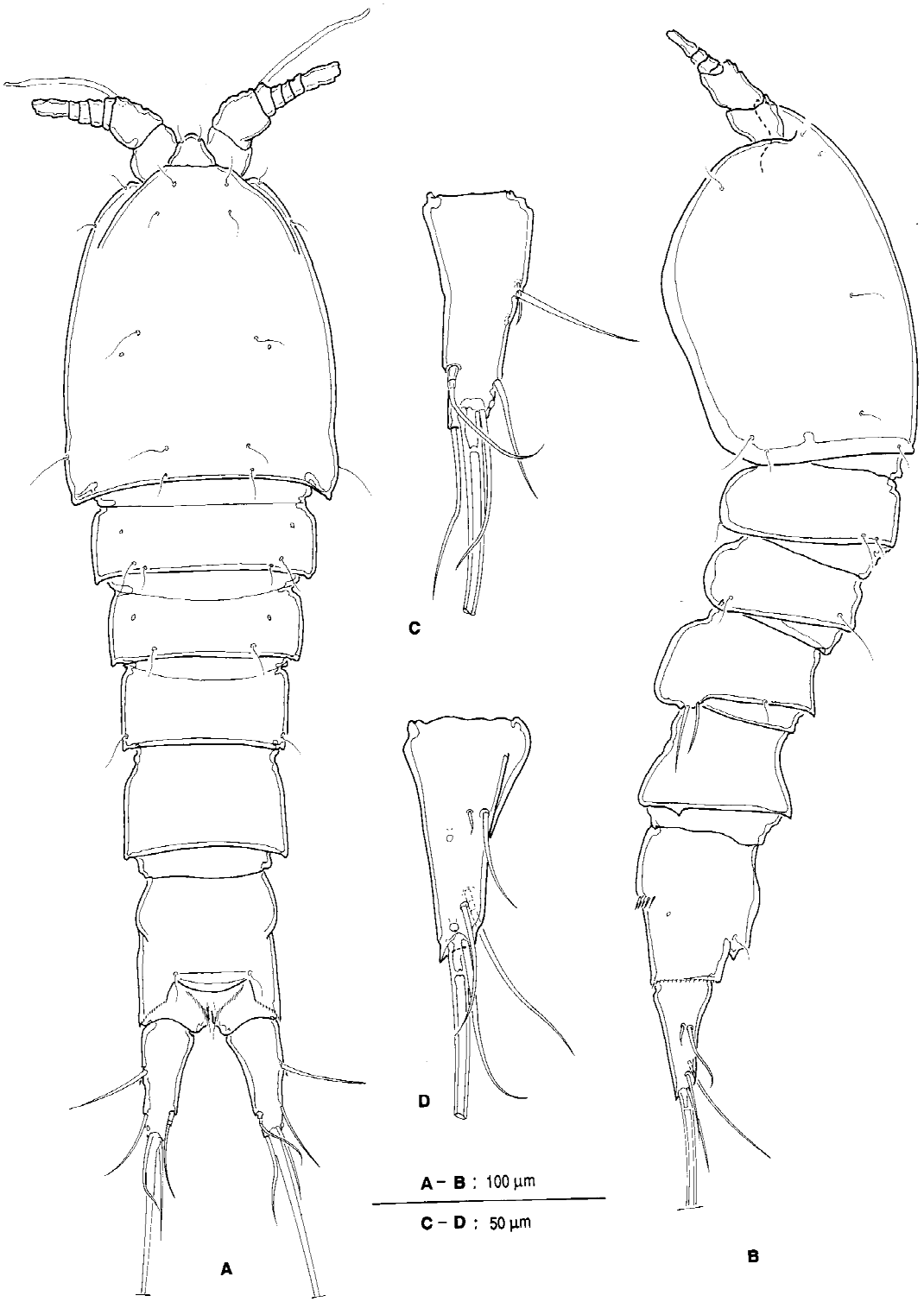

Figure 14. Mwania phytocola n. gen., n. spec.: (A) second copepodid, dorsal view; (B) idem, lateral view; (C) caudal ramus of CII, in dorsal view; (D) idem, in lateral view.

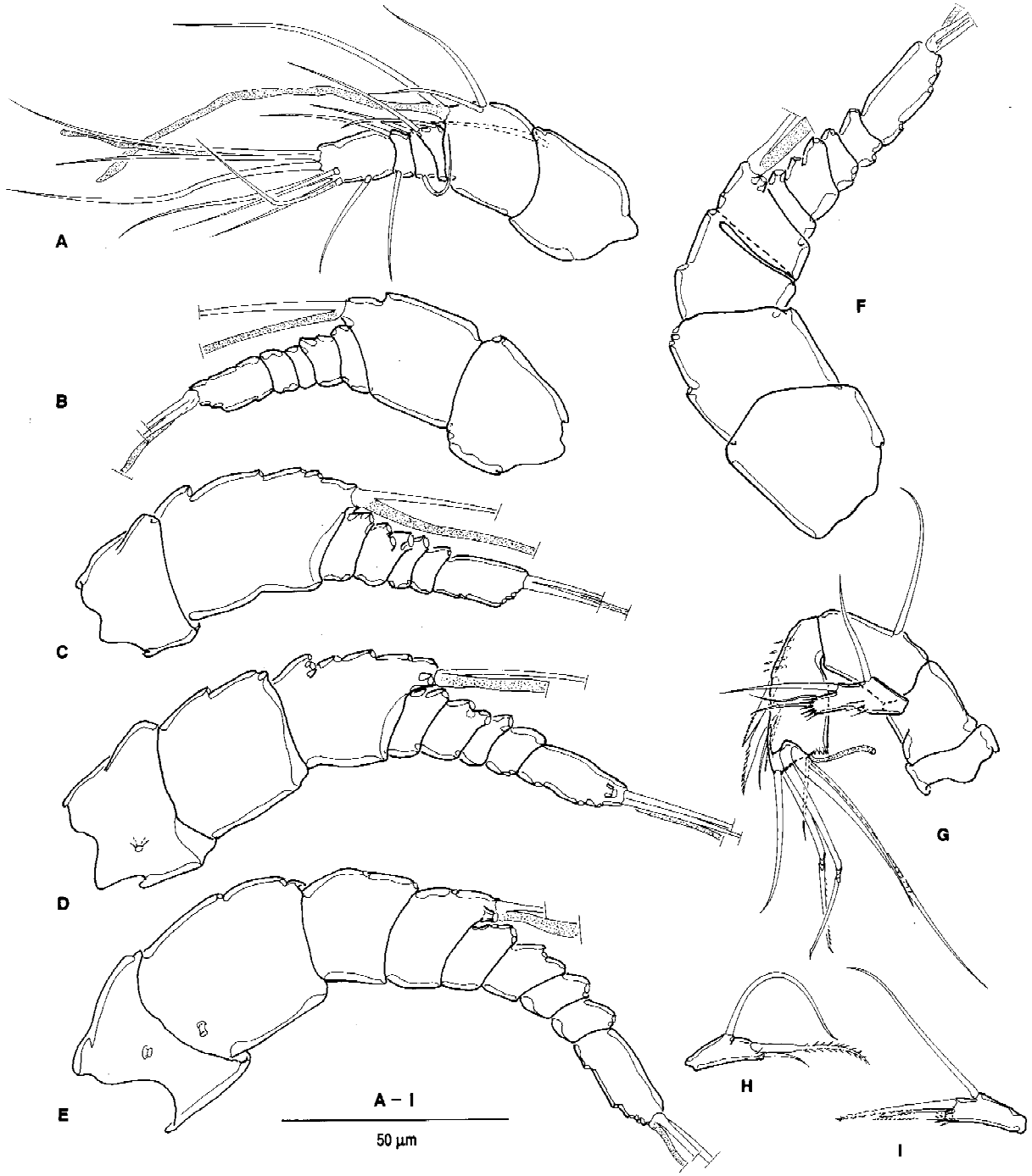

Figure 15. Mwania phytocola n. gen., n. spec.: (A) antennule, copepodid I; (B) idem, copepodid II; (C) idem, copepodid III; (D) idem, copepodid IV; (E) idem, copepodid V; (F) idem, copepodid IV, aberrant; (G) antenna, copepodid I; (H) antennal exopodite, copepodid II; (I) idem, copepodid III.

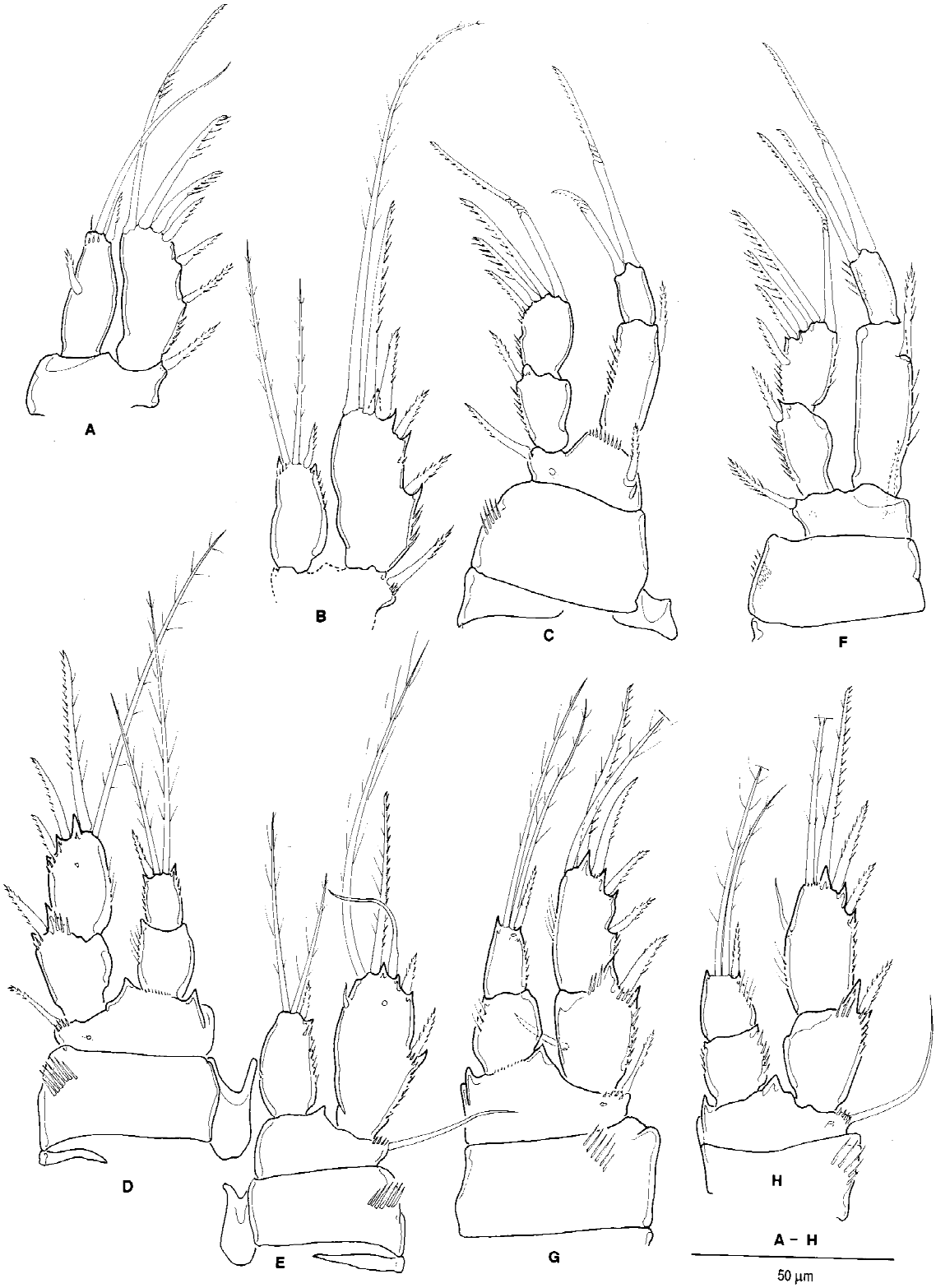

Figure 16. Mwania phytocola n. gen., n. spec.: Copepodid I: (A) P1 (protopodite broken); (B) P2 (protopodite broken); Copepodid II: (C) P1, anterior; (D) P2, anterior; (E) P3, anterior; Copepodid III: (F) P1, posterior; (G) P2, anterior; (H) P3, anterior (setal ornamentation of terminal setae omitted).

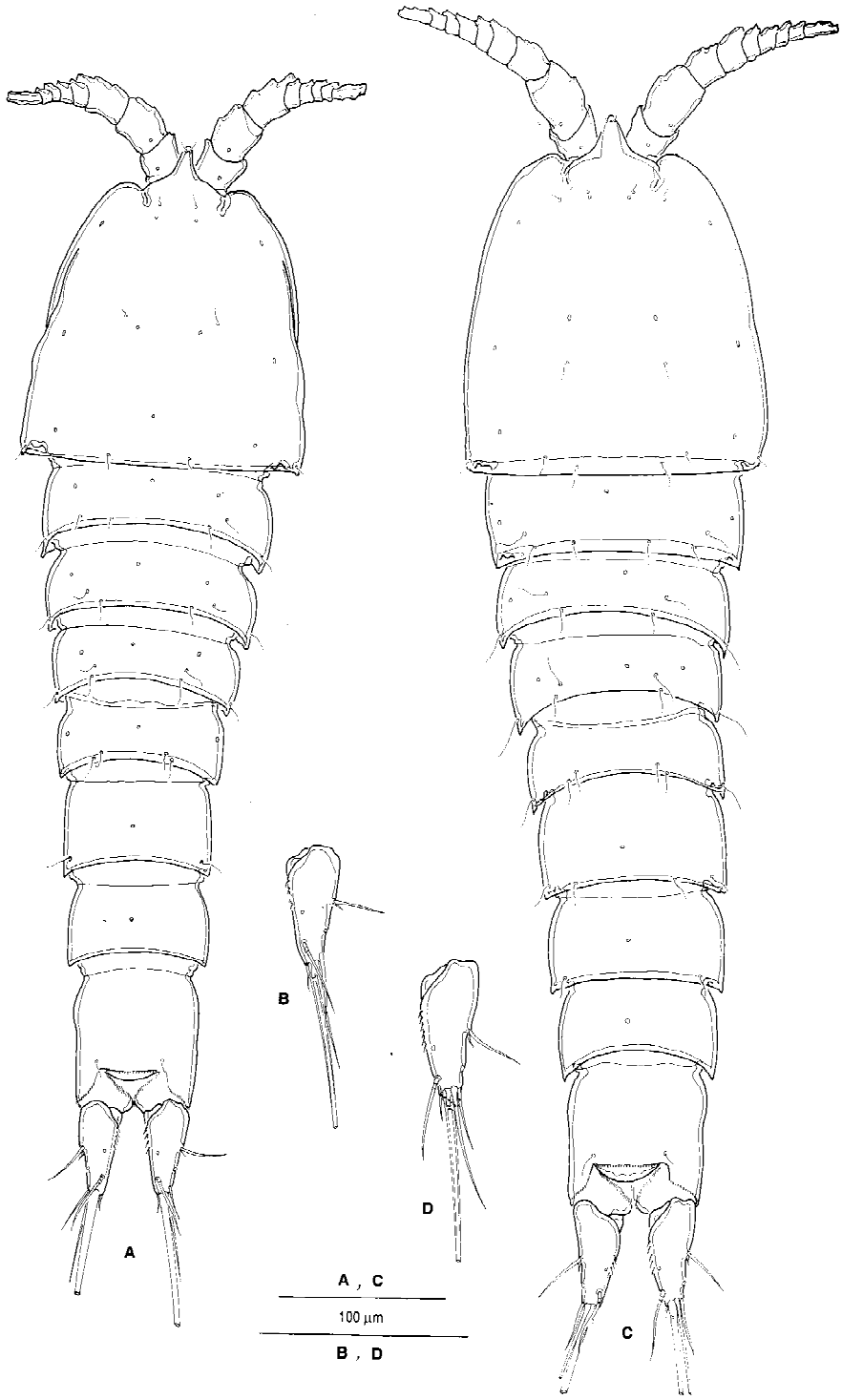

Figure 17. Mwania phytocola n. gen., n. spec.: (A) female fourth copepodid, dorsal view; (B) caudal ramus of CIV, in dorsal view; (C) female fifth copepodid, in dorsal view; (D) caudal ramus of CV, in dorsal view.

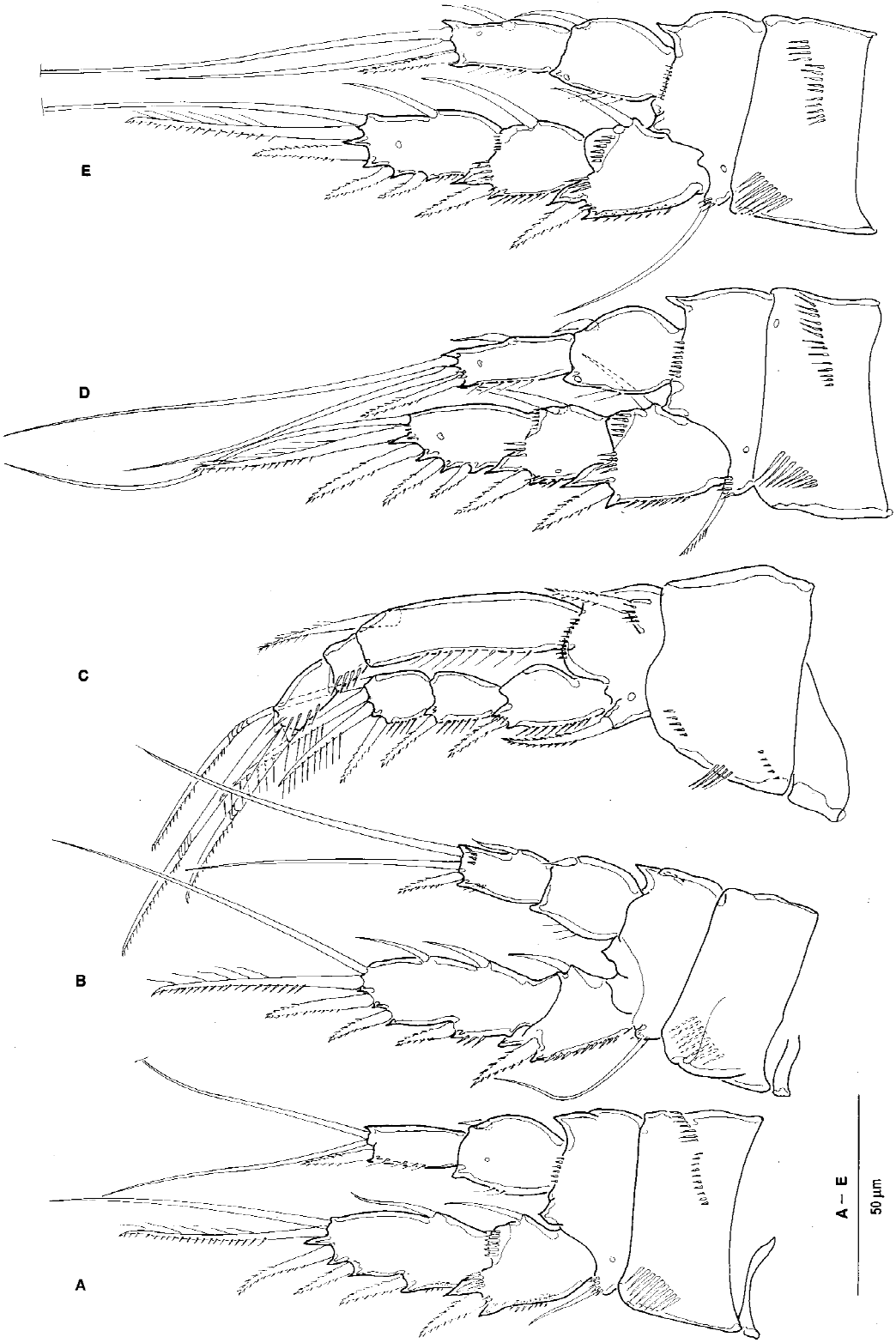

Figure 18. Mwania phytocola n. gen., n. spec.: Copepodid IV: (A) P2, anterior; (B) P3, posterior; Copepodid V: (C) P1, anterior; (D) P2, anterior; (E) P3, anterior.

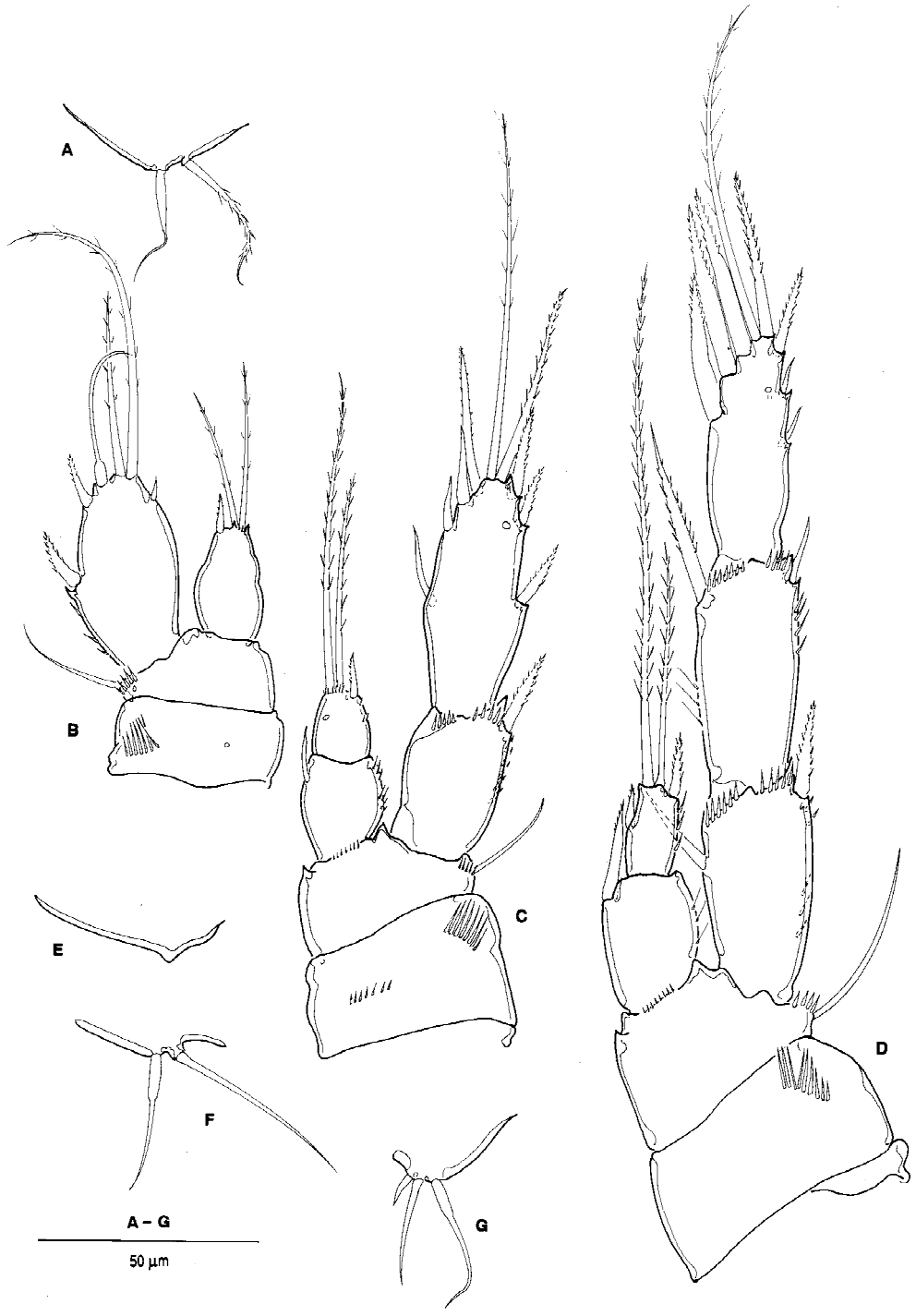

Figure 19. Mwania phytocola n. gen., n. spec.: (A) P4 of copepodid II; (B) P4 of copepodid III; (C) P4 of copepodid IV; (D) P4 of copepodid V; (E) precursor of P6 in copepodid III; (F) P6 in copepodid IV; (G) P6 in copepodid V.

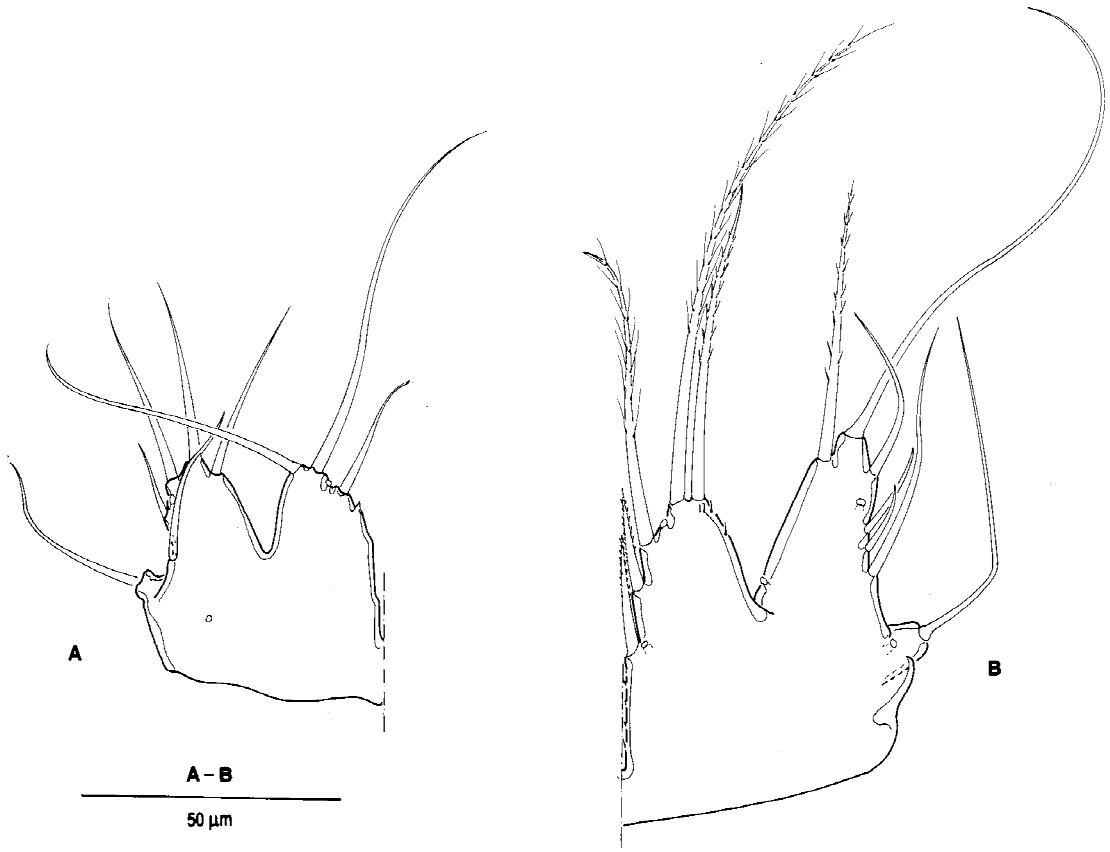

Figure 20. Mwania phytocola n. gen., n. spec.: (A) P5 in copepodid IV, anterior; (B) P5 in copepodid V, anterior.

inhabitant), and refers to the association of this species with the roots of seagrasses.

The adults

Description of Female: Habitus (Figure 7A, B) fusiform, with body somites smoothly tapering towards anal somite. Length, including rostrum and caudal rami, 845 μm. Head about 1/4 of total length. Posterior hyaline fringes of all somites straight. Somites completely devoid of integumental structures, exept for a transversal row of minute spinules along posteroventral margin of penultimate somite, near implantation of caudal rami (Figure 8A) and on anal operculum. Anal operculum cresentic.

Caudal rami (Figure 7C) with straight outer margin, and arcuate inner margin. General appearance conical, twice as long as wide. Both anterior lateral setae located in middle of outer margin, arising from a strong rim. Biarticulate dorsal seta located subapically, on inner margin. Principal terminal setae not modified and not fused near base. outer lateral and inner terminal seta shorter than rami. Inner margin furnished with two rows of spinules: a dorsal median one with minute spinules, and a distal ventral one with long and slender spinules (Figure 8A).

Rostrum (Figure 11C) small, separated from head, triangular, with rounded tip. Dorsal sensillae and ventral pore orifice subdistal.

Antennule (Figure 9A) 9-segmented with segment II twice as long as segment I, both without special processes. Setal armament: I(1)-II(9)-III(8)-IV(4+Aesth)-V(2)-VI(4)-VII(2)-VIII (2)-IX(7+Aesth). All setae smooth, except plumose seta on segment I.

Antenna (Figure 9B, C) with smooth coxa. Basis ornamented with spinules along outer margin. Exopodite one-segmented bearing 2 lateral and 1 apical serrate element. Subdistal spinule row present. First endopodal segment with seta. Second segment with 11 appendages, and ornamented with rows of spinules along outer and inner margin.

Mandible (Figure 9D) with long one-segmented endopodite and a somewhat shorter 3-segmented exopodite. Coxa-basis prominent, bearing three setae on medial margin. Surface ornamented with 2 rows of spinules in proximal half. Endopodal segment bearing 2 medial setae, and 7 distal ones. Exopodite with 2, 1 and 3 setae on proximal to distal segment, respectively.

Maxillule and maxilla as in *Aigondiceps bocki* (Lang, 1948). Maxilliped (Figure 11D) robust. Syncoxa with 3 setae, and several rows of spinules. Basis with two setae, and a spinule row on inner margin of palm. Endopodite with dentate claw and two setae.

P1 (Figure 10A) with large semi-triangular and smooth praecoxa. Coxa tapering distally, sparsely ornamented with spinules. Basis with strong outer and medial elements, and furnished with some spinules along medial and distal margin. Exopodite and endopodite 3-segmented. Terminal exopodal segment with 4 elements: proximal one spinulose, subdistal one and outer apical one comb-shaped, inner distal one geniculate. First endopodal segment slightly longer than exopodite, with inner pectinate seta arising halfway in distal half. Second segment as long as wide, without appendages. Third endopodal segment, 3 times as long as wide, bearing two geniculated terminal elements.

P2 (Figure 10B) and P3 (Figure 10C) with a sparse pattern of spinules on frontal surface of coxa. Preacoxa not observed. Basis with strong spinulose outer element in P2, and a slender smooth seta in P3. Medial distal corner of basis with a sharp triangular process. Exopodites 3-segmented, endopodites 2-segmented. The latter reaching beyond middle of terminal exopodal segment in P2, and towards the middle in P3. Chaetotaxy in Table 2. Inner element of proximal endopodal segment of P2 slender and spinulose.

P4 (Figure 11A) with ornamented coxa. Basis with rounded medial margin, and with a slightly acute median process on distal margin. Exopodite, rather long, three-segmented with deeply incised hyaline fringes. Third segment with very slender outer spines. Inner elements on third segment robust: proximal one spinulose along one margin, median one pectinate, and distal one spinulose on both sides (Figure 11B). Endopodite two-segmented, not reaching the distal margin of first exopodal segment. Proximal endopodal segment with pectinated inner element. Distal segment shorter than proximal one with inner element pectinate, and distal an outer elements spinulose.

P5 (Figure 11E) with distinct endopodal lobe, and articulating exopodite. The former with 5 elements: 3 inner and 2 apical. Exopodite tapering distally, with undulate outer margin, and bearing 6 elements: 1 inner subdistal, 1 apical, and 4 outer ones. Surface of rami smooth, except for minute spinules along inner and outer margin of the endopodal lobe.

P6 vestiges (Figure 8A) separate, each bearing 3 setae: inner and outer one plumose, median one smooth. Genital area situated in proximal half of somite. Copulatory pore Ω-shaped, leading to a short gonoduct.

Description of Male: Habitus closely resembling that of female, slightly shorter (810 μm), and with separated genital somites. Urosomites, except P6 bearing one, with a complete transversal row of minute spinules close to the posteroventral margin (Figure 8B).

Caudal rami (Figure 7D, E) somewhat more slender that those of female, and with two triangular extensions on apical outer margin (Figure 8B).

Antennule (Figure 9E) 12-segmented, haplocerous, with segment II, 1.75 times longer than segment I. Setal armament: I(1)-II(11)-III(5)-IV(2)-V(8+Aesth)-VI(2)-VII(1)-VII I(2 short flame-shaped)-IX(1)-X(2)-XI(2)-XII(7+Aesth). Setae on segments V–VII simple and smooth. Antenna, mouthparts and P1 as in the female.

P2 (Figure 12C) and P3 (Figure 12D) exopodites as in the female. Endopodite P2 having a more slender aspect than in female. Inner distal seta slightly shorter than segment. Outer distal seta wide in proximal half, very slim in distal half. Outer element slightly shorter than outer terminal one, with the same appearance. Endopodite P3 resembling that of female closely, but outer sub-distal spine serrate along outer margin of stem, and slightly bend.

P4 (Figure 12E) with protopodal components and endopodite as in female. Distal outer corner of second exopodal segment closely resembling that of the female. Distal exopodal segment with two inner elements: proximal one serrate, distal one pectinate. Outer distalmost element larger than in female P4, and spinulose.

P5 (Figure 12A) with baseoendopodites fused medially. Endopodal lobe prominent, bearing one subdistal and two distal spines. Left exopodite two-segmented, right ramus one-segmented. Both with 6 appendages: 1 on proximal segment, 5 on distal segment in the case of two-segmented ramus. Distal and inner subdistal element spiniform.

Right P6 vestiges articulating, left one fused with somite (Figure 8B). Each bearing 3 long elements: inner one serrate, median and outer one smooth.

Variability: The exopodite of the left antenna of a female specimen displayed a rather bizare morphology. Instead of a typical one-segmented ramus, this exopodite is distinctly two-segmented, bearing the two normal lateral spines on the proximal segment. The second segment, clearly articulating with the proximal one, is slightly longer than wide, and bears a subdistal and a distal spiniform element (Figure 9B).

Secondly, a male specimen possess two-segmented exopodites of the P5 on both sides (Figure12B).

Copepodid development

COPEPODID I

Body (Figure 13A, B) with five somites, 350 μm long. Head nearly as long as half entire body length. Integument of somites smooth, except for transversal row of spinules on ventral surface of anal somite, and near articulation between anal somite and caudal rami. Rostrum bell-shaped with one pair of sensillae and ventral pore orifice. Anal operculum slightly arcuate, smooth.

Caudal rami (Figure 13C, D) three times as long as wide, nearly rectangular, with undulating lateral margins. Seven elements: biarticulate dorsal seta located in distal fifth of inner margin, 3 lateral setae, 2 principal terminal setae fused near implantation, and one seta located close to distal dorsal edge. Three pore orifices present.

Antennule (Figure 15A) 6-segmented with principal aesthetasc on second one. Setal armament: I(1)-II(3+Aesth)-III(2)-IV(2)-V(2)-VI(7+Aesth). Segment I and II equal in dimensions. All setae smooth, no pore orifices found.

Antenna (Figure 15G) with distinct basis and one-segmented exopodite. The latter rather large, bearing 3 lateral setae (subdistal one very slender) and one apical seta. Outer and dista margin with a crown of minute spinules. Abexopodal seta on first endopodal segment present. Second segment with 4 lateral setae/spines and 6 distal ones. Outer distal corner of second segment with a long hyaline tube pore.

Mandible with formed gnathobasis. Coxa-basis with 3 setae. Rami with adult chaetotaxy, exopodite two-segmented. Maxillule with epipodal seta and with 4 and 3 setae on exopodite and endopodite, respectively. Maxilla and maxilliped as in adult.

P1 (Figure 16A) with distinct protopodal components and one-segmented rami. Medial spine on basis absent. Subdistal outer and distal outer spines on exopodite comb-shaped. Inner distal one geniculated. Endopodite with a distinct inner median seta, and 3 apical ones. Inner one very slim, median one long and smooth, and outer one spiniform.

P2 (Figure 16B, protopodal components broken during dissection) with one-segmented rami, bearing 5 and 3 setae/spines on exopodite and endopodite, respectively.

P3 (Figure 15B) represented as a small lamellar extention of the posterior margin of second pedigerous somite, ornamented with two slender setae.

P4 (Figure 15B) present as a minute blunt triangular extension of posterolateral margin of third pedigerous somite. Appendages absent.

COPEPODID II

Habitus (Figure 14A, B) with 6 somites, length 430 μm, with length of head attending 1/4 of entire body length. Integumental ornamentation of somites as in stage I. Rostrum still bell-shaped as in preceeding stage, but slightly constricted in middle.

Caudal rami (Figure 14C, D) conical in dorsal and lateral view, about 3 times as long as wide. Seven elements: 3 lateral setae, 1 biarticulated dorsal seta located in distal third near inner margin, and 3 terminal setae. Inner principal seta long, not modified at base. Outer principal seta, not fused with inner one, and slightly shorter than ramus. Inner terminal seta as long as ramus. Three pore orifices present.

Antennule (Figure 15B) 7-segmented with principal aesthetasc on segment II. The latter slightly longer than segment I. Setal armament: I(1)-II(5+Aesth)-III(1)-IV(3)-V(2)-VI(2)-VII(7+Aesth). All setae smooth, no pore orifices found.

Antenna (Figure 15H) with basis and endopodal segments as in preceeding stage. Exopodite proportionally distinctly shorter, with a large smooth seta in middle of inner margin, a second one implanted subdistally and a short slender apical one. Apical margin of segment furnished with a crown of minute spinules. Mouthparts as in the adults.

P1 (Figure 16C) with well developed protopodal components, and a medial spine on the basis. Rami 2-segmented. Endopodite with distinctly larger proximal segment (about as long as entire exopodite) than distal one. The latter with 2 geniculated setae. Chaetotaxy in Table 3. P2 (Figure 16D) with well developed protopodal components and 2-segmented rami. Endopodite smaller than exopodite, with subequal segments. Chaetotaxy in Table 3. P3 (Figure 16E) with well de-

Table 3. Setal complement of the copepodids of *Mwania phytocola* n. sp.[a]

Stage	P1		P2		P3		P4	
	EXO	END	EXO	END	EXO	END	EXO	END
CI	0,2,3	1,1,1	0,2,3	0,2,1	2			
CII	0,1-0,2,2	1,0-0,1,1	0,1-0,2,2	0,0-0,2,1	1,2,3	0,2,1	2	
CIII	0,1-0,2,3	1,0-0,1,1	1,1-0,2,3	0,0-0,2,1	0,1-1,2,2	0,0-0,2,1	1,2,3	0,2,1
CIV	0,1-0,2,3	1,0-0,1,1	1,1-1,2,3	1,0-0,2,1	1,1-2,2,3	1,0-1,2,1	0,1-4,2,3	1,0-0,2,1
CV ♀	0,1-0,1-0,2,2	1,0-0,0-0,1,1	1,1-1,1-0,2,3	1,0-1,2,1	1,1-1,1-1,2,3	1,0-1,2,1	1,1-1,1-3,2,3	1,0-1,2,1

[a] Notation x,y,z means: x inner elements, y apical elements, z outer elements.

veloped protopodal components, and one-segmented rami. Exopodite long ovate, with subdistal outer element remarkablely long, slender and curved inwards. Inner seta of exopodite minute. Endopodite ovate, smaller than exopodite. Chaetotaxy of rami in Table 3.

P4 (Figures 14B and 19A) represented as a small lobe on third pedigerous somite, bearing an outer pinnate and an inner smooth element.

P5 (Figure 14B) appearing as a small blunt triangular extension on posterolateral margin of fourth pedigerous somite. No appendages.

COPEPODID III

Habitus as in preceeding stage, except for the additional 7th somite. Body length: 500 μm. Rostrum, caudal rami, and integumental ornamentation as in stage II.

Antennule (Figure 15C) 7-segmented, with segment II more than twice as long as segment I, and bearing principal aesthetasc. Setal armament: I(1)-II(9+Aesth)-III(2)-IV(4)-V(2)-VI(2)-VII(7+Aesth). All setae smooth, except the one on segment I. No pore orifices found. Basis and endopodite of antenna as in copepodid II. Antennal exopodite (Figure 15I) with long smooth lateral seta, and spinulose subdistal and terminal one. Mouthparts as in adult.

P1 (Figure 16F) differs from preceeding stage by the addition of outer proximal spine on second exopodal segment, and by slightly longer first endopodal segment. P2 (Figure 16G) resembling previous stage closely, except for additional outer proximal spine on second exopodal segment, and appearance of inner element on first exopodal segment. P3 (Figure 16H) with well developed protopodal segments and 2-segmented rami. Endopodite not reaching towards middle of second exopodal segment. Outer subdistal element on second exopodal segment with normal spinulose appearance. P4 (Figure 19B) with protopodal components developed, and rami one-segmented. Endopodite reaching towards distal third of exopodite. The latter with a slender, smooth, and inwards bended subdistal outer element. Chaetotaxy of legs in Table 3.

P5 with same appearance as P4 in preceeding stage. Idem for P6 which displays same morphology as P5 in preceeding stage (Figure 19E).

COPEPODID IV (Female)

Habitus (Figure 17A) fusiform, with 8 somites, distinctly divided in prosome and urosome. Body length: 628 μm. Integument of somites smooth, except for transversal spinule row on ventral surface of anal somite, and near articulation with caudal rami. Anal operculum arcuate, having a transversal row of minute spinules on dorsal surface. Rostrum wide at base, narrowing rapidly towards apex. One pair of sensillae and a ventral pore orifice.

Caudal rami (Figure 17B) conical, strongly tapering towards distal edge. Lateral, dorsal and terminal setae as in preceeding stage. Inner terminal seta very short. Inner margin furnished with small spinules in proximal third.

Antennule (Figure 15D) 8-segmented with second segment 1.5 times as long as segment I. Pore orifice on segments I and II. Setal armament: I(1)-II(7)-III(10+Aesth)-IV(2)-V(4)-VI(2)-VII(2)-VIII(7+Aesth). All setae smooth, except the one on segment I.

Antenna with additional terminal spine on terminal endopodal segment (adult chaetotaxy). Exopodite as in preceeding stage. Mouthparts as in adult, and P1 as in preceeding stage.

P2 (Figure 18A) differs from stage III in the addition of an inner seta on second exopodal segment, and in the addition of a (short) inner seta on first endopodal segment. P3 (Figure 18B) with slightly more elongated appearance than in the preceeding stage.

Exopodite with inner seta on first segment and an additional outer spine and inner seta on second segment. Endopodite with inner seta on first and second segment.

P4 (Figure 19C) with protopodal components more resembling adult shape than in preceeding stage. Exopodite and endopodite 2-segmented. Second exopodal segment elongated with subdistal outer element spiniform. Second endopodal segment shorter than first one. Chaetotaxy of rami in Table 3.

P5 (Figure 20A) with both opposite legs fused medially. Endopodal end exopodal lobe distinct, equally high and wide. Exopodal lobe with 5 setae: 3 outer ones, one apical and one inner seta. Pore orifice on outer margin below subdistal seta. Endopodal lobe with two apical setae and a subapical seta. Below the latter, a minute hyaline cone, probably representing a second pore. Inner subdistal pore orifice between implantation of inner distal and subdistal element. Outer baseoendopodal extension short, bearing one seta. Surface below exopodal lobe with pore orifice.

P6 (Figure 19E) as the P5 in preceeding stage, with two setae. Penultimate somite without the blunt triangular extension on the posterolateral margin.

Variability: The right antennule of the specimen here described shows an incomplete separation of the future segments II and IV (Figure 16F). Distally from the suture there are 4 setae and the aesthetasc. Thus, it appears that the setal complement of the adult antennular segment IV is already present in the copepodid IV stage while the setal complement of the adult segment III will be completed in the last copepodid stage.

COPEPODID V (Female)

Habitus (Figure 17C) as in stage IV but with 9 somites. Division between prosome and urosome distinct. Body length: 700 μm. Rostrum, caudal rami and integumental ornamentation as in copepodid IV.

Antennule (Figure 15E) 9-segmented, with second segment twice as long as first one. Setal complement as in adult. Pore on segments I and II with short hyaline tube.Other buccal parts as in the adult.

P1 (Figure 18C) with 3-segmented endopodite. Comb-shaped outer spines on ultimate exopodal segment present. Terminal setae on endopodite geniculated. Integumental ornamentation almost as in adult.

P2 (Figure 18D) and P3 (Figure 18E) with general appearance as in adult. Setal complement as in adult , but inner elements on endopodal and exopodal segments short, robust, with a large lumen.

P4 (Figure 19D) with 3-segmented exopodite and 2-segmented endopodite. Setal complement as in adult but inner elements on endopodal and exopodal segment short and robust.

P5 (Figure 20B) with distinct endopodal and exopodal lobe. Both opposite legs fused medially. Outer baseoendopodite seta arising from short conical pedistal. Exopodal lobe twice as high as endopodal lobe, bearing 6 setae: 4 outer, a apical and a inner one. Endopodal lobe with 5 elements: 3 inner and 2 apical ones.

P6 (Figure 19G) represented as a slightly elevated sockle along posterior margin of somite which bears 3 setae: a very short outer one, and 2 slender and long inner ones.

Discussion

Thus far, no copepodid development of a tetragonicipitid has been described (Ferrari, 1988; Dahms, 1993). The subsequent addition of segments of the natatorial legs throughout the development follows the basic pattern from primairy buds towards legs with 2-segmented rami in the fourth copepodid, and an adult segmentation of the rami in the fifth stage. Setal addition in the subsequent stages follows the common pattern which results in the presence of an adult setal complement in the fifth copepodid.

In contrast with most other harpacticoid developmental constraints, the primairy bud of the legs 4–6 is preceeded by a small, but distinct blunt triangular processus on de ventrolateral corner of the posterior margin of the somite. Leg 4 seems to be present, as such in copepodid I, leg 5 in copepodid II and leg 6 in copepodid III.

Presence of cuticular structures as indicators of the onset of the legs 4–6, has been described for harpacticoids only in the family Ectinosomatidae (Dahms, 1993). Herein, the onset of those legs in the first three copepodid stages is indicated by the presence of sharp triangular flaps, which appear to display a very species specific morphology. The small blunt triangular processus in Tetragonicipitidae differs significantly from their homologes in the Ectinisomatidae.

Comparable structures have been described in the early copepodids of *Eudiaptomus gracilis* (G.O. Sars, 1863), Calanoida and *Cyclops vicinus* Uljanin, 1875, Cyclopoida, by Kiefer (1978). In these two species, the primary bud of the legs 4–6, is preceeded by a

small rounded processus on the posterior margin of the somite. Personal observations on other representatives of the calanoids and cyclopoids revealed that this particular element seems to be a general phenomenon in these ordines. Such structures appear also in *Tetragoniceps unguis* Wells & Rao, 1989 (Fiers, pers. obs.).

The P3 and P4 setal development is characterized by a curious phenomenon. Both legs possess in their one-segmented stage (copepodid II for P3, copepodid III for P4) a particular outer subdistal element on the exopodite. Instead of being spiniform as the other outer spines, this element has a relatively broad proximal part and a long slender and smooth distal part which seems to be typically inwards curved. This element is re-shaped as a normal spiniform appendage during the following molt. Observations on the copepodid development of *Tetragoniceps unguis* revealed a comparable modification of the subdistal outer spine in the second and third copepodid stage.

As far as we know, such juvenile characteristic has never been described for a harpacticoid copepod. The only indication so far that such contraints may be present in other harpacticoids has been provided by Vincx & Heip (1979) whom described the development of *Canuella perplexa* T. & A. Scott, 1893. In this species the P3 and P4 seems to bear a setiferous subdistal outer element in the copepodids 2 and 3. This seta becomes re-shapen into a spiniform element during the transition between the third and the fourth stage for the P3 and P4. However, whether this observation is similar with that observed here for *Mwania phytocola* is not clear at this moment.

More evidence for a comparative juvenile transformation was described in two representatives from two different poecilostomatoid families (Kim, 1994; Constanzo et al., 1997): *Conchyliurus quintus* Tanaka, 1961 of the Clausiidae and *Lichomolgus forficula* Thorell, 1859 belonging to the Lichomolgidae. We suppose that a similar condition can be found in other poecilostomoids, but the consulted illustrations are not sufficiently detailed to reach a conclusion.

The serial addition of segments during the development of the antennule resembles in all aspects the developmental additions in Thalestridae, Tegastidae and Peltiidae as shown by Dahms (1989). The addition of segments occurs first in that part situated distal from the principal aesthetasc-bearing segment (segment II) during transition between copepodid I and II. Addition of segments proximal from the principal aesthetasc-bearing segment starts during the molt between copepodid III and IV, and terminate during the transition between copepodid IV and V, resulting in the adult number of segments.

In the 6-segmented antennule of the first copepodid, the setal complement of segments I, IV, V and VI is complete (=adult). Addition of setae happens only in the aesthetasc-bearing segment (and its subsequent additions) and in the two segments distal from the latter. The complete adult complement is archieved in the last copepodid stage (in the female). Here too, we see two distinct growth patterns as the number of setae is complete in the segments distal of the aesthetasc-bearing segment in copepodid III whereas setal addition proceeds on the aesthetasc-bearing segment and those situated proximal from the latter from copepodid II until copepodid V.

During development, two appendages, the antennal exopodite and the endopodite of the first leg, show reductions of setal elements.

The antenna appears in the first copepodid with the abexopodal seta on the first endopodal segment and 10 setae/spines on the second one. The 11-th element appears first in the fourth stage. The exopodite is proportionally much larger in the first stage than in the next stages and bears 2 long and 1 slim lateral seta, and a slim apical one. The exopodite becomes drastically re-shapen during the molt between copepodid I and II. The segment in this stage is much smaller, resembling the adult morphology, and retains only the median lateral, the subdistal and the apical element. The latter still remains short and slim in this stage, but archieves its spiniform appearance during the transition between the second and third stage.

The P1 endopodite originates in the first copepodid with 3 terminal setae on the (sole) endopodal segment: 2 apical setae and a subdistal outer spine. The innermost seta is remarkable short and slim in comparison with the other two elements. During the molt from stage I to II, the endopodite becomes re-shaped in a 2-segmented ramus with only two appendages on the distal segment. The inner minute seta present in the first copepodid disappeared. In addition, the subdistal spine of the first copepodid becomes a geniculated element, and is relocated on a more apical position on the terminal segment in the second copepodid. Based on this observation, we deduce that the outer terminal element of the adult P1 endopodite is homologous with the subdistal outer spine found in the other legs. Consequently, the setal notation of the second endopodal segment for the adults is noted as 0.1.1 instead of 0.2.0 (see Table 2).

In conclusion, development of the several appendages in this representative of the Tetragonicipitidae follows a normal pattern of additions of segments and setae. The development is, however characterized in this family by some features (curved seta in P3 and P4, and the triangular lobes preceeding the primairy bud of the legs) which seems to belong to the ground pattern of copepod development.

Genus Neogoniceps gen. nov.

Diagnosis: Tetragonicipitidae with a nonfoliaceous fifth leg in the female, and a short first antennular segment, with a strong sclerotised rim on first segment. Rostrum small, not dimorphic. Body fusiform, with dimorphic caudal rami. Principal caudal setae not fused at base, bulbous in female. Antennule 8-segmented, with segment II longer than segment I. Segment I with a arcuate dorsal ridge. Segment II with 8, segment III with 7 and segment IV with 4 setae and the principal aesthetasc. First endopodal antennal segment without abexopodal setae. Exopodite with 3 elements. Male antennule 8-segmented, with aesthetasc and a large bulbous element on segment IV. Mandible with equally sized rami: endopodite one-segmented, exopodite 2-segmented. Maxilliped with one seta on basis, and two additional setae on endopodal claw. P1 exopodite 3-segmented, endopodite 2-segmented, the former with comb-shaped elements on third segment, the latter with two terminal setae. Exopodites of P2–P4 3-segmented, endopodites 2-segmented. Setal complement in Table 4. Endopodites P2–P3 large. Endopodite P4 with distal segment twice as long as proximal one. P5 exopodite articulating with baseoendopodite, ovate shaped, bearing 6 elements. Endopodal lobe with 5 elements. P6 vestiges bearing 3 setae. Sexual dimorphism in urosome and antennule. P2 typically modified. P3 with slender and curved subdistal outer spine on distal endopodal segment. Distal outer corner of second exopodal segment of P4 modified. P5 with one-segmented exopodite on both sides, bearing 5 elements: ditsal one and inner subdistal one spiniform. Endopodal lobe with 3 spiniform appendages. P6 with a long inner spiniform element and a median and outer slender smooth seta.

Type species: *Neogoniceps martinezi* spec. nov., by monotypy.

Etymology: The generic name is a conjuction of *Neo* (Greek: new, young), *Gonia* (Greek: angle) and *Ceps* (Latin: caput, head). The gender is masculine.

Table 4. Setal complement of the legs in *Neogoniceps martinezi* n. gen., n. sp.

	EXO	END
P1	0-0-0.2.2	1-0.1.1
P2	1-1-1.2.2	1-1.2.1
P3	1-1-2.2.2	1-1.2.1
P4♀	1-1-3.2.2	1-1.2.1
P4♂	1-1-2.2.2	1-1.2.1

Justification

We cannot ignore the fact that *Neogoniceps* and *Aigondiceps* Fiers, 1995 are closely related taxa, and even can be considered as sister taxa. Both taxa share quite some features, not found in other tetragonicipitid taxa: the presence of only a single seta on the inner margin of the maxilliped palm, the outspoken differences of the caudal rami between both sexes, the compact exopodite of the female P5, and the short P5 exopodite of the male, bearing a reduced number of setae. However, *Neogoniceps* differs in several aspects significantly from its sister taxon.

The most remarkable difference between both genera is the body shape. Whereas *Aigondiceps* has a clear distinction between prosome and urosome, *Neogoniceps* retained the original (plesiomorphic) fusiform body plan in which the body gently tapers towards the ultimate somite. The fusiform body shape occurs in the related *Mwania* and in the more primitive Tetragonicipitidae as *Diagoniceps* Willey, 1935, *Odaginiceps* Fiers, 1995, and *Paraschizopera trifida* Yeatman, 1980.

Neogoniceps displays a series of apomorphic character states (inclusive convergent ones), justifying the definition of this taxon.The absence of an abexopodal seta on the first endopodal segment of the antenne is seldom seen within the group of Tetragonicipitidae without a folliaceous female P5. Thus far, only *Paraschizopera menaiensis* is known to lack this element (see below for discussion).

Secondly, the short 8-segmented antennule in male and female is clearly apomorphous as 8-segmented antennules are only known in a few species of the genera *Tetragoniceps* and *Phyllopodopsyllus*, genera which are definitely not directly related with the clade under discussion. Moreover, the highly specialized elements on the inner surface of the palm of the male

clasping antennule differs significantly from the unmodified elements on the antennules of the males of *Aigondiceps* and *Mwania*. Here too, such modifications are known only in *Paraschizopera menaiensis*, but this species cannot be considered as directly related with the *Aigondiceps-Mwania-Neogoniceps* clade.

Finally, and more noticeable, is the reduced number of spines on the third exopodal segments of the P2–P4 with only 2 spines instead of 3 as in the sister taxa. From the above described copepodid constraint, we know that the addition of the proximalmost outer spine on the third segment happens during the molt between stage 4 and 5. In *Neogoniceps* the development of these spines is altered as is demonstrated in the description of its latest copepodids, below.

Neogoniceps martinezi spec. nov.
Figures 21–30.

Type material: Holotype female, dissected, mounted on 6 slides, labeled 4260 A-F;allotype male, dissected on 3 slides, COP 4261 A-C; preserved paratypes: 3 ♀♀, 3♂♂, 1 ♀ and 1♂ Cop V (COP 4259); dissected paratypes: 1 ♀, mounted on 2 slides, COP 4254A-B; 1 ♀ Cop V (COP 4262 A-B), 1♂ Cop IV (COP 4263), 1♂ Cop V (COP 4264 A-B)

Type-locality: Peru, Pucusana (20 km south of Lima). Sublittoral sandsample at 50cm water depth. Leg. P. Martinez Abrizu, 11 October 1992.

Etymology: The specific name honours our friend and colleague Pedro Martinez Abrizu (Oldenburg) who offered us this material to study.

The adults

Description of Female. Habitus (Figure 21A, B) fusiform, with nearly parallel prosomal somites, and urosomites tapering towards anal somite. Length, including rostrum and caudal rami, 790 μm. Genital double-somite with a marked dorsal and lateral fringe. Head about 1/4 of total body length. Hyaline fringes of all somites smooth. Anal operculum arcuate and furnished with two parallel rows of spinules.

Caudal rami (Figure 21C, D) convergently implanted on anal somite. Robust appearance, with nearly straight outer margin and arcuate inner one. Outer distal edge protruded forming a rounded flap, furnished with gross spinules on its margin, and bearing ditsal outer seta. Proximal outer dorsal area strongly sclerotized forming a semi-triangular plateau, parallel with outer margin. Inner proximal corner furnished with a horse shoe shaped pattern of slim spinules. Profile of rami in cross section triangular, with tip forming inner margin. Biarticulated dorsal seta arising in middle, close to outer margin, and both proximal lateral setae in proximal third of margin. Principal setae globulous at base, not fused. Inner terminal seta (Figure 24A) very short.

Rostrum with broad base, rapidly narrowing distally, not reaching behind middle of first antennular segment. One pair of sensillae, and a pore orifice on ventral surface

Antennule (Figure 22B, C, D) 8-segmented, with segment II longer (1.5 times) than segment I. The latter with a heavely sclerotised arcuate dorsal rim, close to posterior directed margin. Hyaline pore tube on segment I and II.Pore Setae smooth, except for the one on segment I. Setal complement: I(1)-II(8)-III(7)-IV(4+Aesth)-V(2)-VI(4)-VII(4)-VIII (7+Aesth).

Antenna (Figure 22A) with strongly developed coxa. Basis rather short, furnished with some spinules in distal half of abexopodal margin. Exopodite one-segmented with a distal spinule row, bearing 3 elements: 2 serrate distal ones, and 1 short and smooth lateral one. Endopodite without seta on first segment, and 11 elements on second segment.

Mandible (Figure 22E) with a long seta and several teeth along biting edge. Pars molaris small. Coxa-basis with 3 setae, and ornamented with two rows of long spinules on surface, and short spinules near implantation of setae. Exopodite and endopodite equally sized, the former two-segmented, the latter one-segmented. Proximal segment of exopodite with 2 setae, distal one with 4 setae: 2 lateral and 2 distal. Endopodite bearing 2 setae located in middle of medial margin, and distal 7 setae.

Maxillule and maxilla as in the preceeding species. Maxilliped (Figure 22F) with slender syncoxa, ornamented with a distal and proximal row of spinules, and bearing 3 setae on subdistal inner corner. Basis with a single inner seta on palm, and furnished with a longitudinal row of spinules parallel with inner margin (posterior surface). Endopodite with smooth claw and 2 accessorial setae.

P1 (Figure 23A) with large triangular praecoxa and ovate coupler. Coxa nearly quadrate, densely furnished with transversal rows of spinules on anterior surface. Basis rather high, with spiniform outer and medial element, both with antennuated tip. Exopodite three-segmented with comb-like subdistal and outer apical spines (Figure 23B). Inner apical element geni-

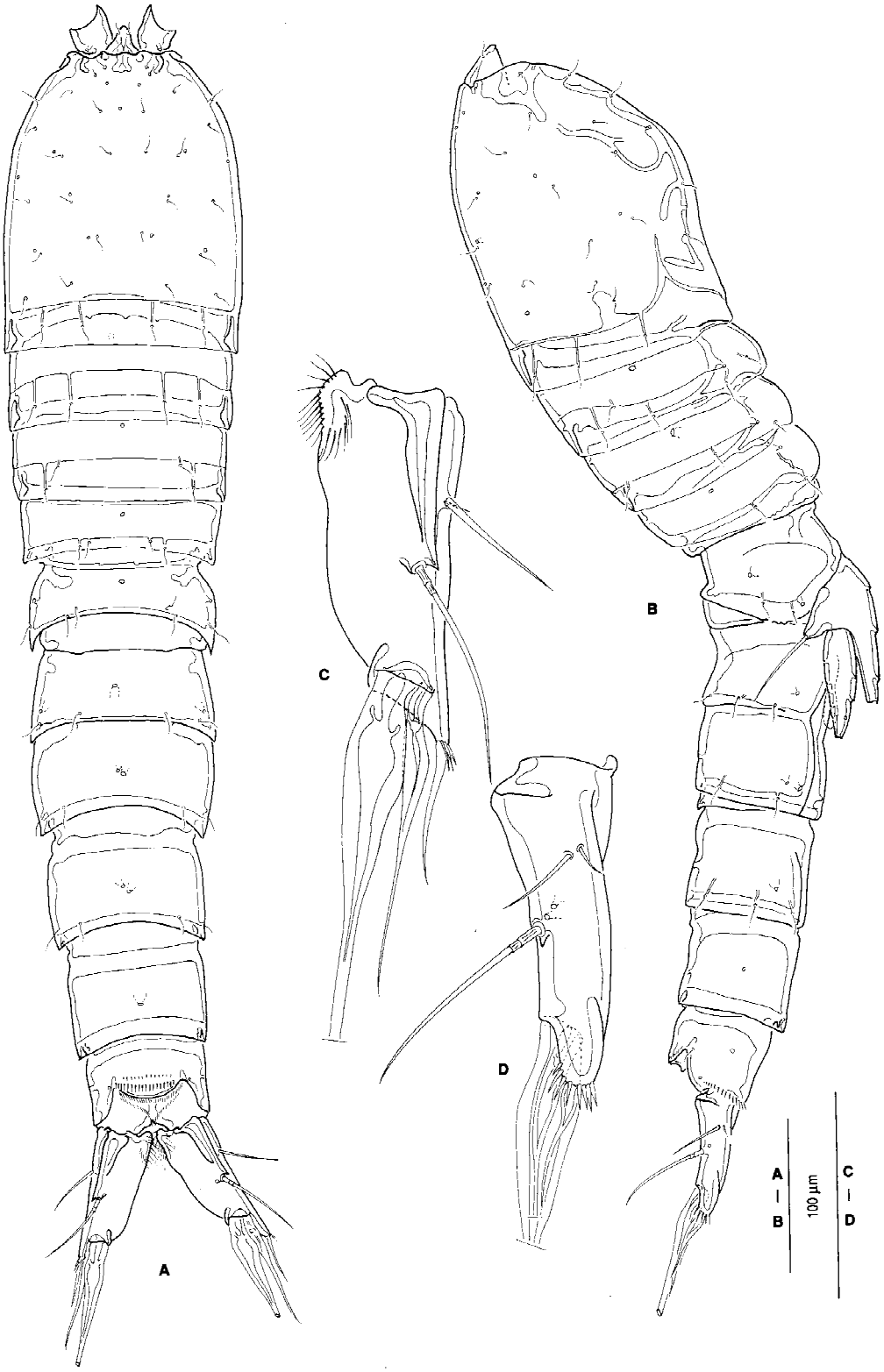

Figure 21. Neogoniceps martinezi n. gen., n. spec.: (A) female habitus, dorsal view; (B) idem, lateral view; (C) right caudal ramus of female, dorsal view; (D) idem, lateral view.

Figure 22. Neogoniceps martinezi n. gen., n. spec.: (A) antenna; (B) female antennule, ventral view; (C) antennular segments I and II, dorsal view; (D) segment VII, opposite side, dorsal view; (E) mandible; (F) maxillipeds; (G) segments IV-VIII of male antennule, dorsal view; (H) inner view of segments IV-VII of male antennule.

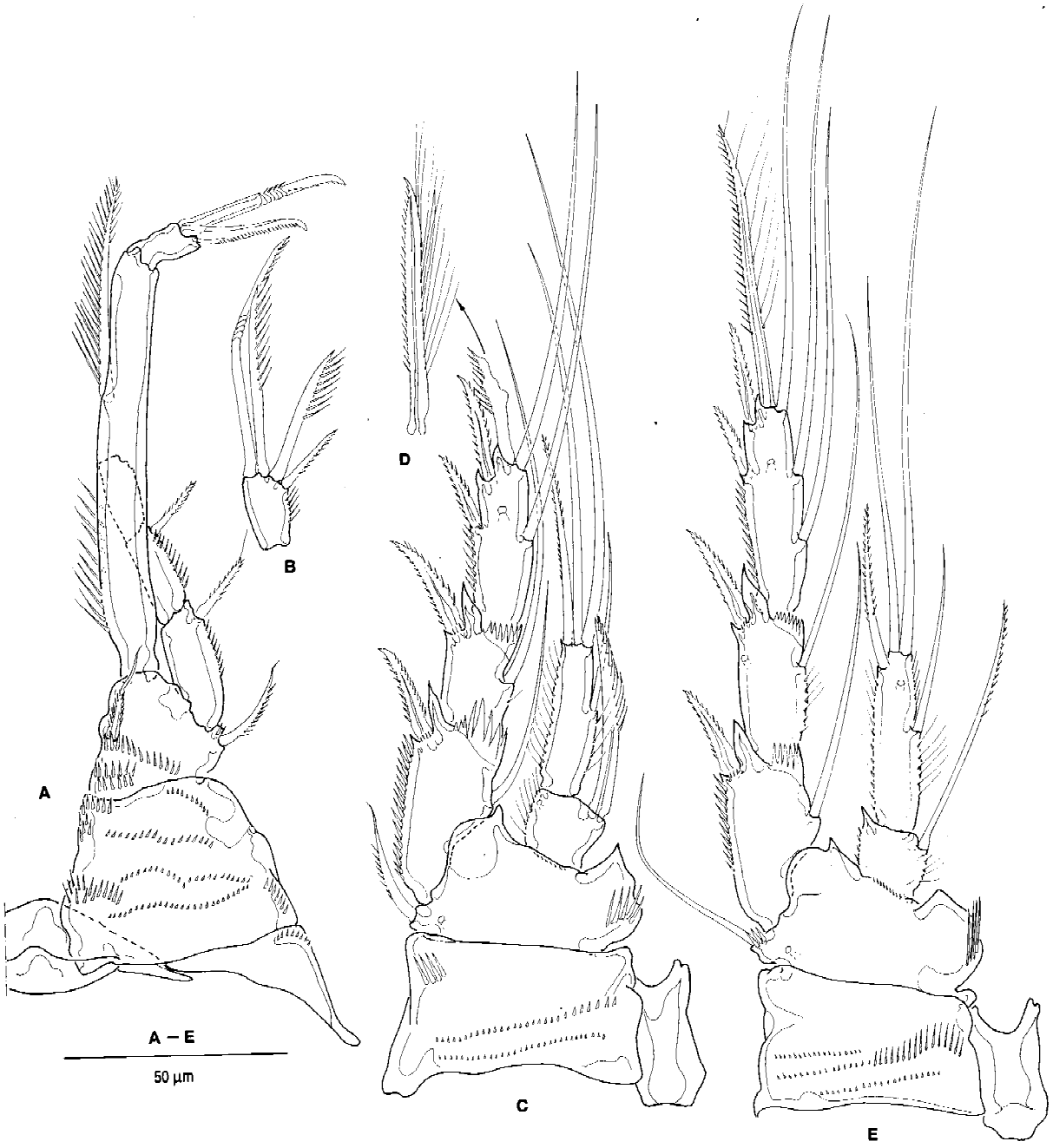

Figure 23. Neogoniceps martinezi n. gen., n. spec.: (A) female P1, anterior view; (B) distal exopodal segment of same leg; (C) female P2, anterior view (outer distal spine aberrant); (D), normal outer distal spine of P2 (opposite ramus); (E) female P3, anterior view.

culated. Endopodite rather long and two-segmented. Proximal segment 7.5 times as long as wide, with inner pectinate seta arising in second half. Second endopodal segment short, at the most 1.5 times as long as wide, bearing two terminal geniculated setae.

P2 (Figure 23C, D) and P3 (Figure 23E) with quadrate coxa, furnished with transversal rows of spinules on anterior surface. Coupler with concave distal border, smooth surface. Basis with antennate spiniform outer seta in P2, and long and slander outer seta in P3. Median distal border arcuate with distinct distalmost

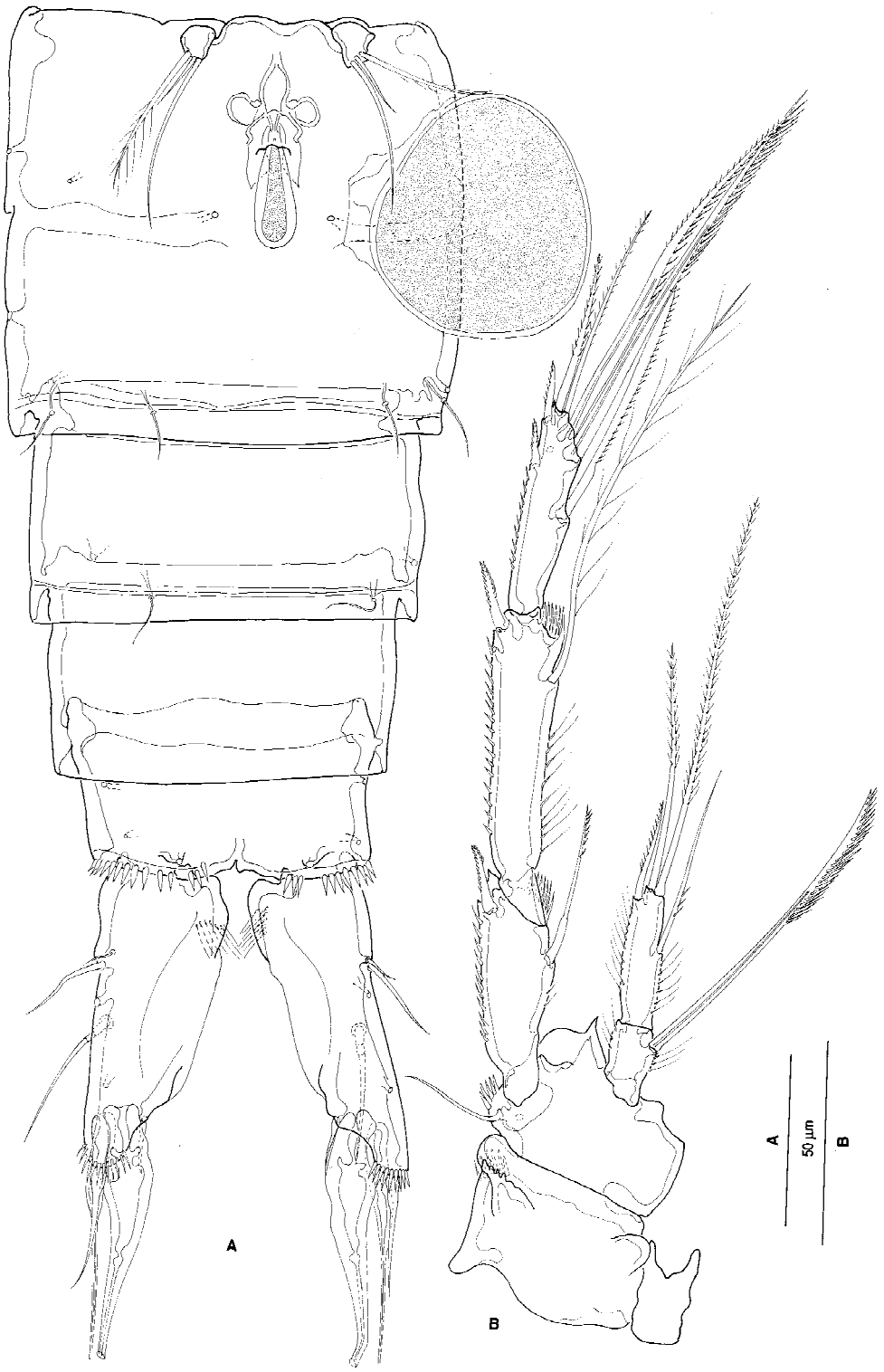

Figure 24. Neogoniceps martinezi n. gen., n. spec.: (A) female urosome, ventral view; (B) female P4, anterior view.

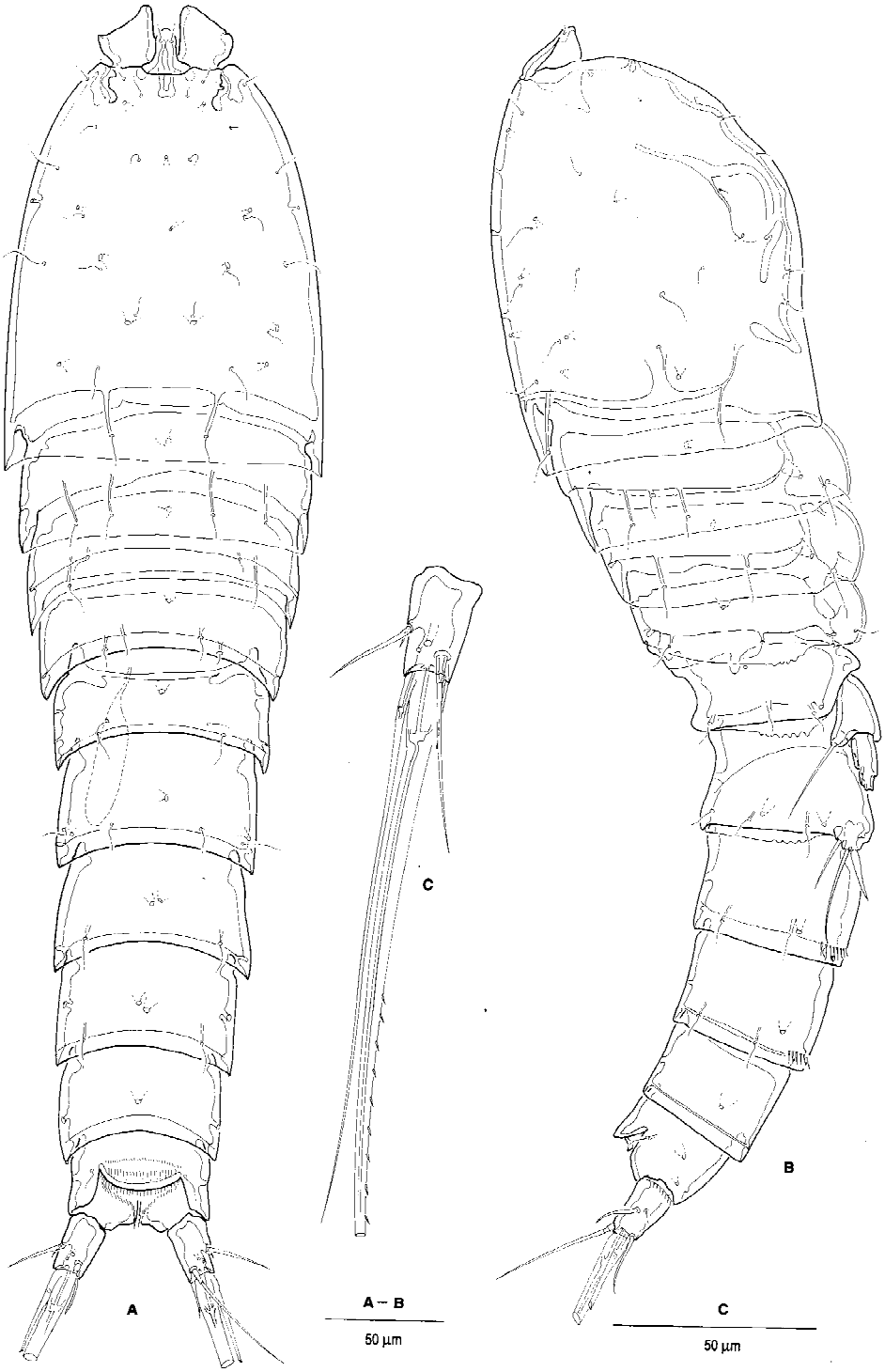

Figure 25. Neogoniceps martinezi n. gen., n. spec.: (A) male habitus, dorsal view; (B) idem, lateral view; (C) left caudal ramus, dorsal view.

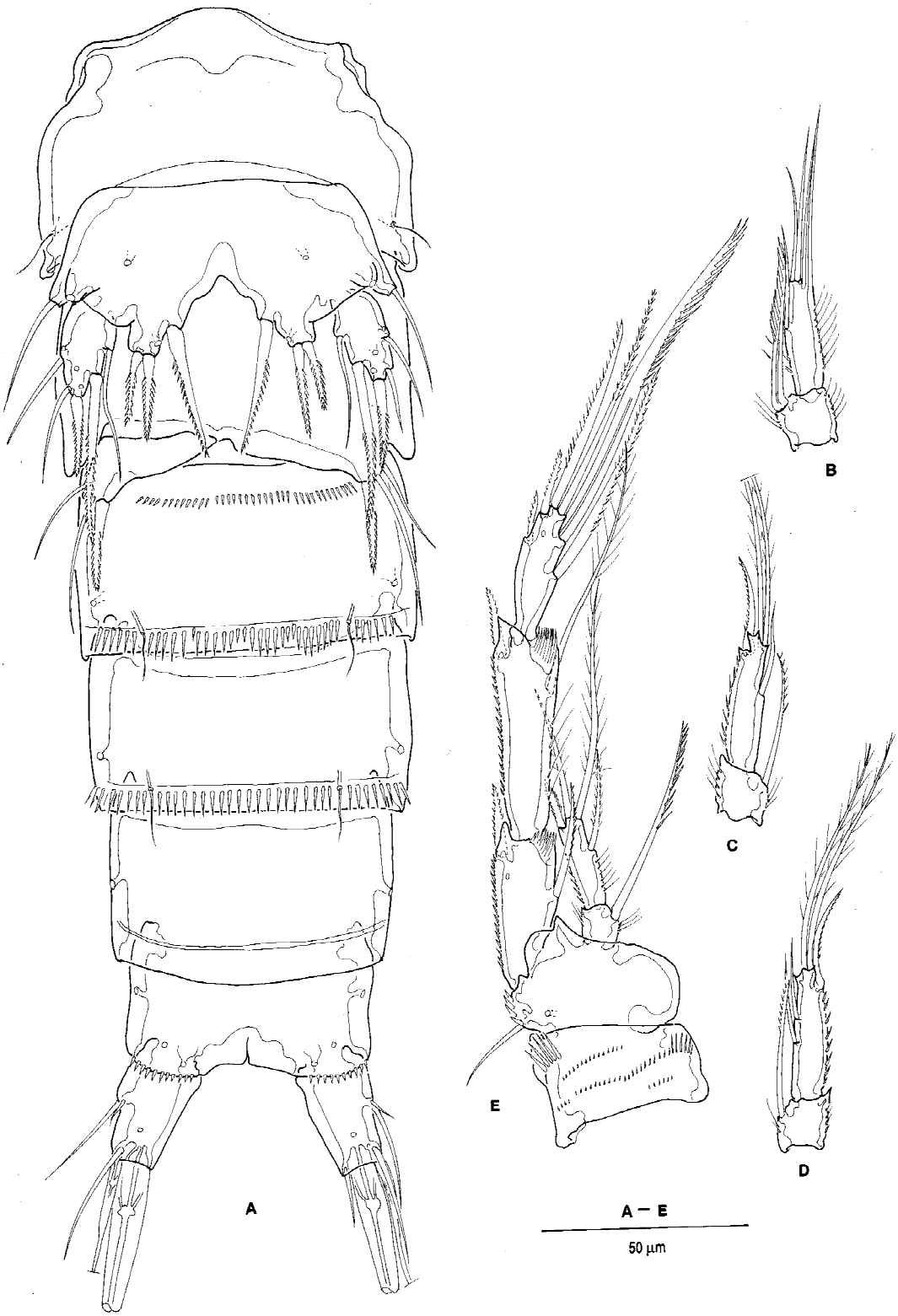

Figure 26. Neogoniceps martinezi n. gen., n. spec.: (A) male urosome, ventral view; (B) endopodite of male P2, anterior view; (C) left endopodite of male P3, anterior view (normal chaetotaxy); (D) right endopodite of male P3, anterior view (aberrant chaetotaxy); (E) male P4, anterior view.

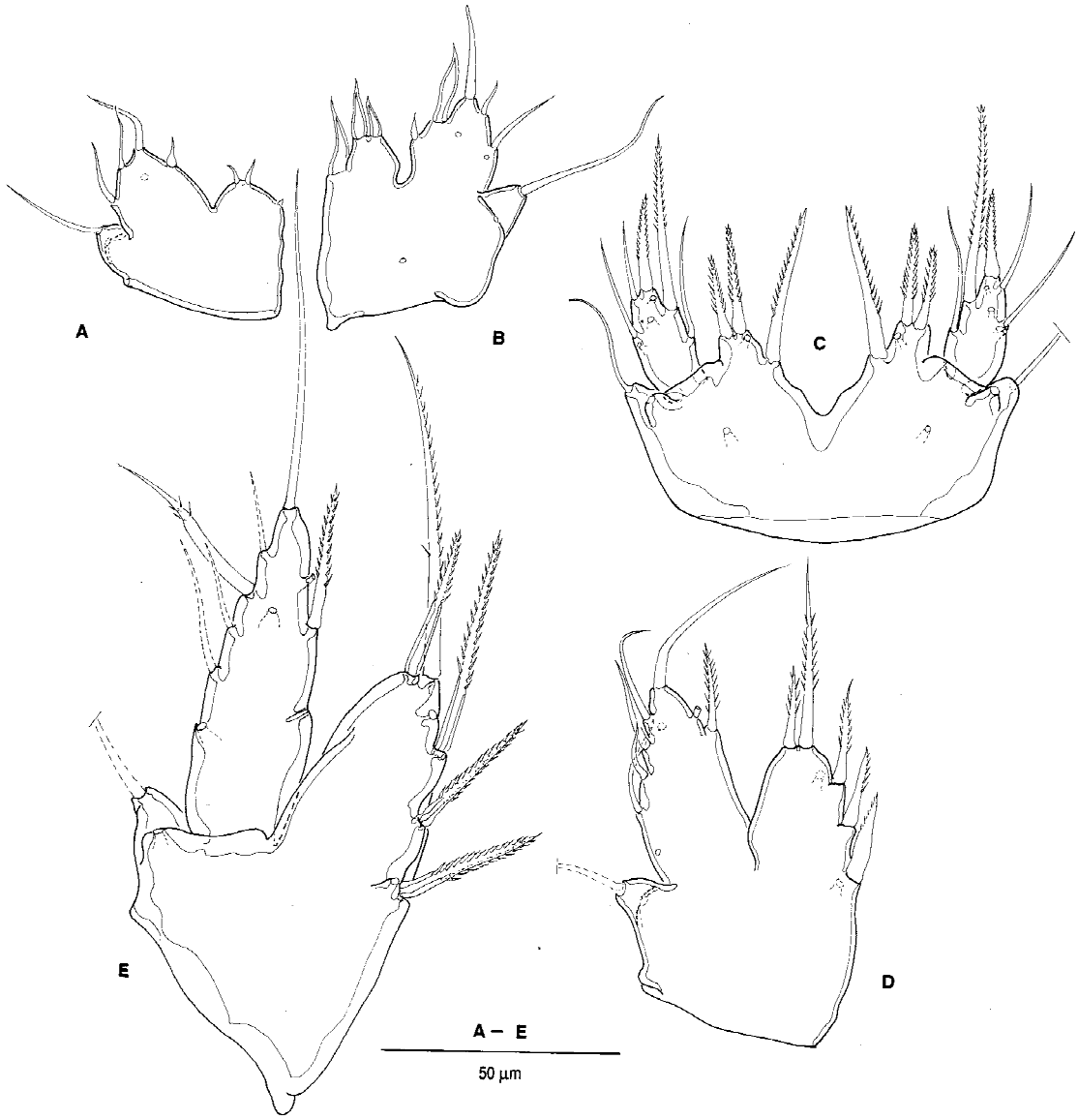

Figure 27. Neogoniceps martinezi n. gen., n. spec.: (A) P5 of male copepodid IV; (B) P5 of male copepodid V; (C) P5 of adult male; (D) P5 of female copepodid V; (E) P5 of adult female.

tip. Medial distal edge triangular, accute in P2, rounded in P3. Exopodite three-segmented with deeply incised hyaline fringes on inner distal edges of first and second segment. Endopodite two-segmented reaching to articulation between second and third exopodal segment. Inner element of proximal endopodal segment of P2, robust and pectinate in distal half of outer margin. Inner element on P3 endopodite slender, and only slightly pectinate in distal half. Chaetotaxy of the legs in Table 4.

P4 (Figure 24B) with quadrate coxa, furnished with a short row of spinules on anterior surface, and two strongly slerotized rims on posterior surface. Basis with short outer seta, and arcuate mediodistal margin. Medial margin with small rounded process. Exopodite three-segmented with deeply incised hyaline fringes. Inner elements on third segment robust and pectinate. Endopodite two-segmented, reaching towards articulation between first and second exopodal segments. Inner element on proximal segment long, robust, and pectinate along distal third of stem.

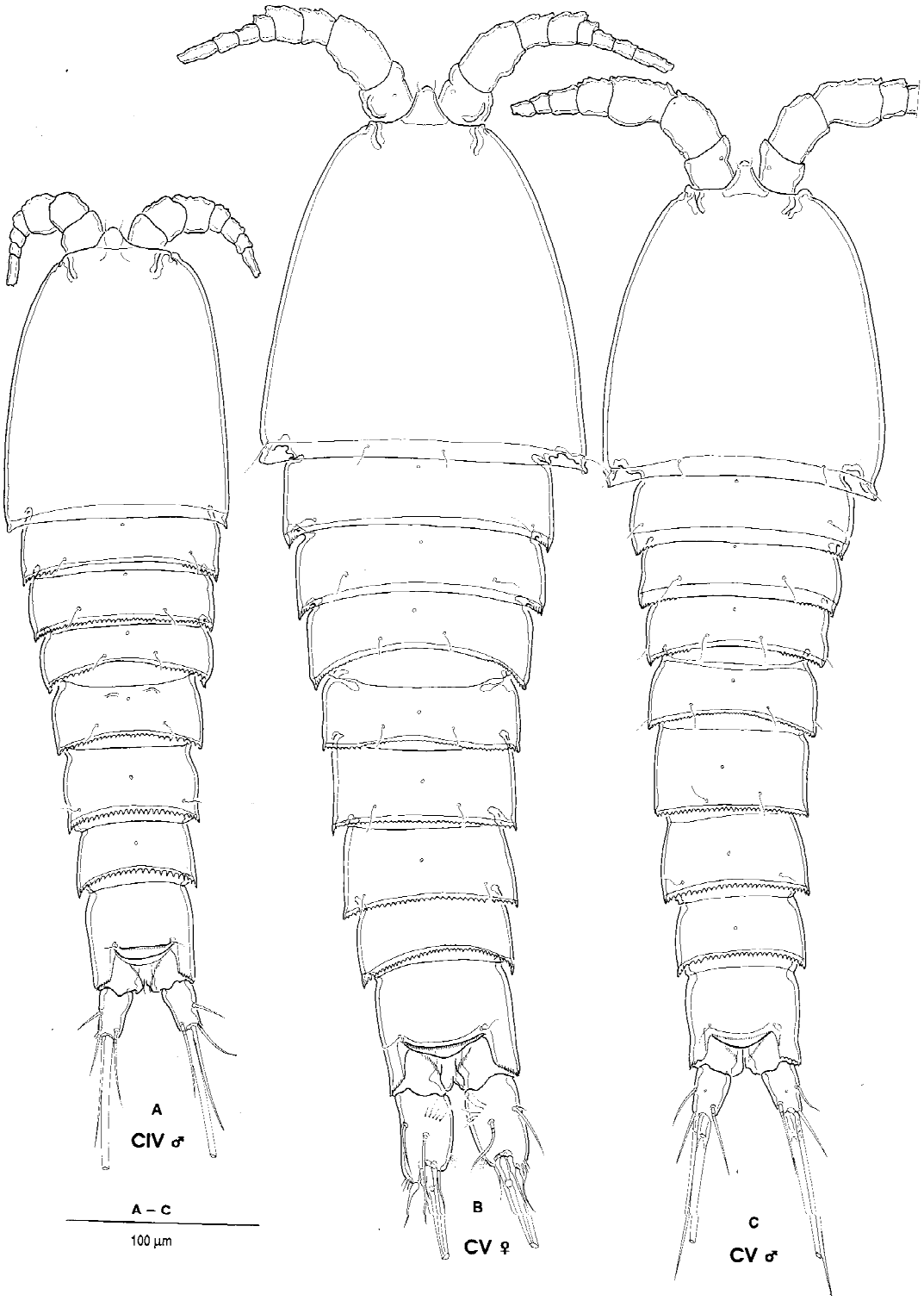

Figure 28. Neogoniceps martinezi n. gen., n. spec.: (A) habitus of male copepodid IV, dorsal view; (B) idem of female copepodid V; (C) idem of male copepodid V.

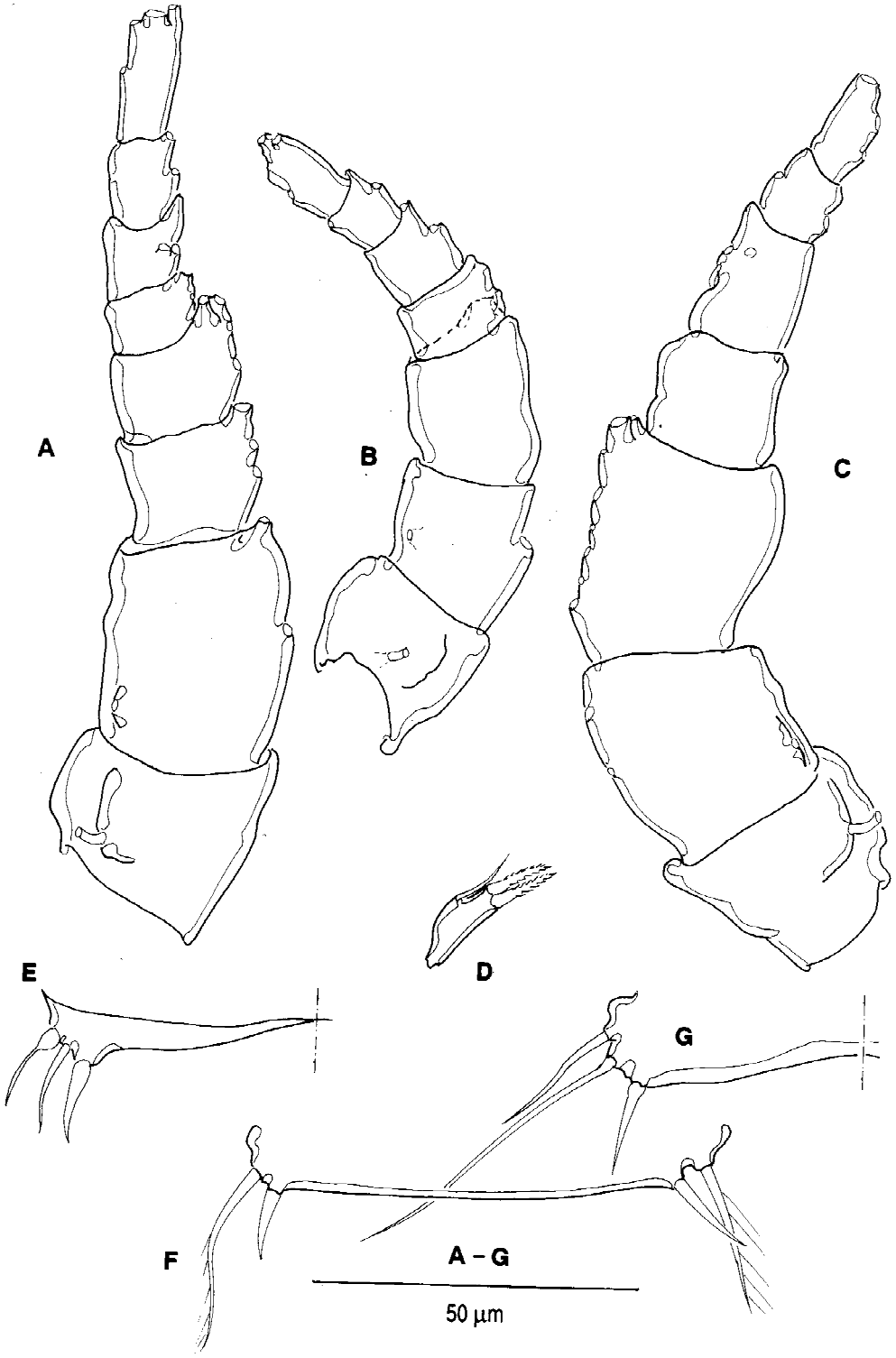

Figure 29. Neogoniceps martinezi n. gen., n. spec.: (A) antennule contour of female copepodid V; (B) antennule contour of male copepodid IV; (C) idem, of male copepodid V; (D) exopodite of antenna, male copepodid IV; (E) P6 of female copepodid V; (F) P6 of male copepodid IV; (G) idem of male copepodid V.

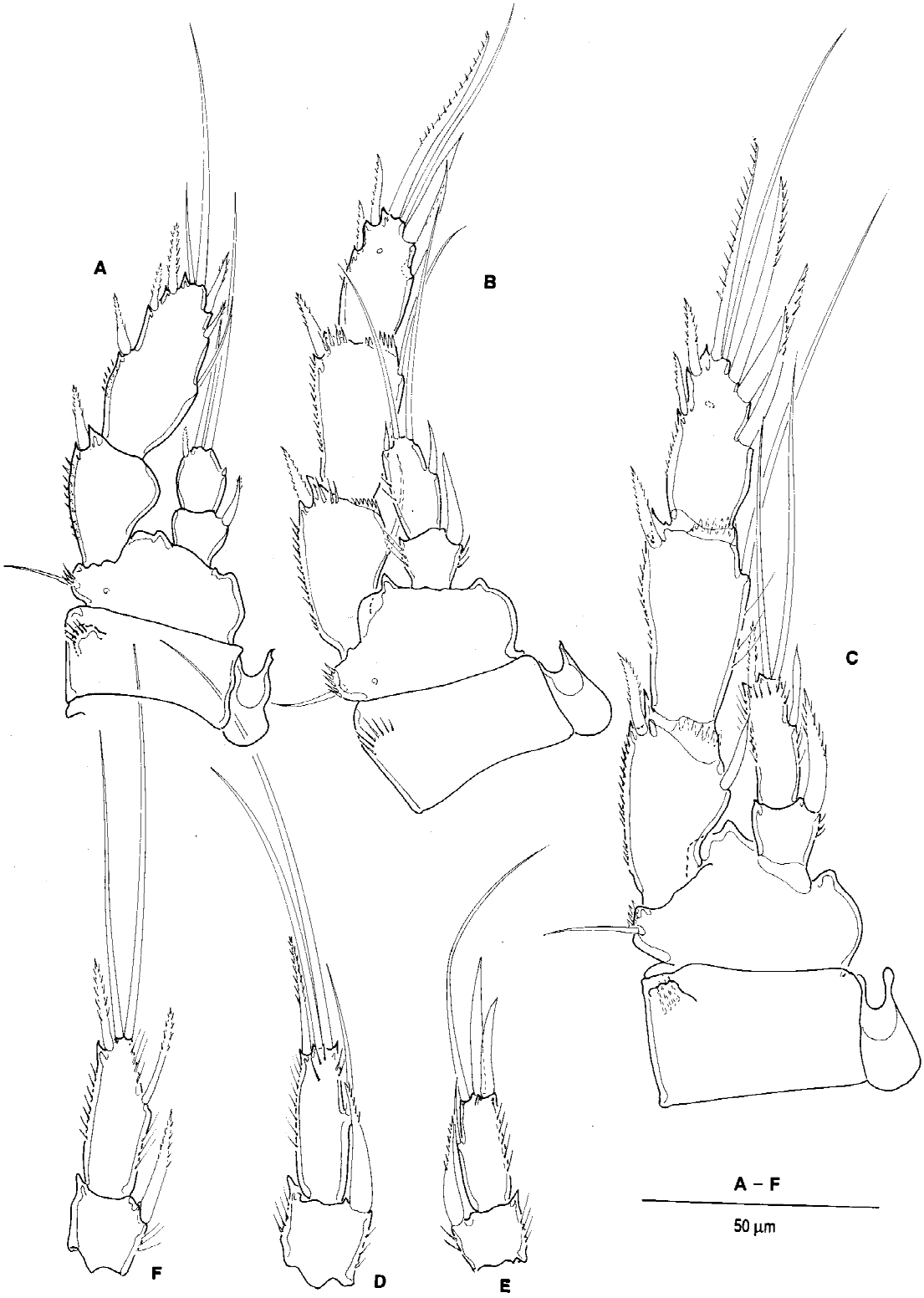

Figure 30. Neogoniceps martinezi n. gen., n. spec.: (A) P4 of male copepodid IV, anterior view; (B) idem of male copepodid V, anterior view; (C) idem of female copepodid V, posterior view; (D) endopodite P2 of female copepodid V; (E) idem of male copepodid V; (F) endopodite P3 of female copepodid V.

P5 (Figure 27E) with ovate endopodal lobe and long ovate exopodite, the latter reaching beyond distal corner of endopodal lobe. Exopodite with six elements: 4 along outer margin, 1 apical one and 1 along inner margin. Endopodal lobe with 5 elements: 3 inner ones, and 2 apical ones. Surface and margins of the rami devoid of integumental structures.

P6 vestiges (Figure 24A) separated, each bearing three setae: outer one plumose, median and inner one smooth. Genital area situated in proximal half of somite. Gonopore without notable differentiated area in front of orifice.

Description of Male: Habitus (Figure 25 A, C) fusiform with tapering pedigerous somites, and parallel sided urosome. Body length: 530 μm. Ventral surface of third urosomite with a transversal row of spinules in posterior third, and a a transversal row parallel to the posterior margin. Fourth urosomite only with posterior row on ventral surface.

Caudal rami (Figure 25C) totally different of those of the female. Short (1.5 times as long as wide), cylindrical and convergently implanted on anal somite. Both proximal lateral setae implanted in middle of margin, distal one located near distal margin, and slightly more ventrally. Biarticulate dorsal seta situated subdistally, close to medial margin. Principal terminal setae not bulbous at base. Inner one rigid, outer one slender, more than 5 times as long as ramus. Inner terminal one shorter than ramus.

Antennule (Figure 22G, H) 8-segmented, with segment II 1.5 times as long as segment I. Carena and pore orifices present. Setal complement: I(1)-II(11)-III(7)-IV(11+Aesth)-V(4)-VI(2)-VII(1)-VI II(10+Aesth). Segment IV with a large modified (blunt, ovate) element on inner distal edge. Segment V with 3 normal slender setae and a short conical rigid element in proximal half of inner margin. Elements on segment VI flame-shaped: ventral one short, dorsal one long.

P2 (Figure 26B) and P3 (Figure 26C) with exopodites as in the female. Endopodite P2 with long pectinate element on proximal segment. Distal segment with inner seta and inner distal seta equal in size, almost as long as segment. Outer distal element with hyaline appearance and sharp. Outer subdistal element longer than outer distal one, with hyaline appearance, and not articulating with segment. Inner seta on proximal segment of P3 endopodite (Figure 26C) just reaching distal margin of second segment. Distal margin of distal segment with accute corners. Apical setae plumose, subdistal outer spine spinulose along outer margin, rather rigid, and curved outwardly.

P4 (Figure 26E) with a rounded medial inner margin of the basis, lacking blunt process near articulation with endopodite. Third exopodal segment proportionally shorter than in female, and bearing one inner element less. Outer distal corner of median exopodal segment extended in a broad triangular process. Endopodite as in female.

P5 (Figure 27C) with baseoendopodites of opposite legs fused together. Endopodal lobe rather short but distinct, bearing 2 apical spines and one inner subapical element, smooth along one side of the stem, spinulose at the opposite side. Both exopodites one-segmented, bearing 5 elements: 2 short and smooth outer ones, an apical spinulose one, and 2 inner ones. Subdistal inner one long and spinulose, proximal inner one slender and smooth.

Right P6 vestige (Figure 26A) articulating on somite, left one fused. Each with three appendages: outer and median slender and smooth, inner one rigid and spinulose.

Variability: The allotype male bears on the second endopodal segment of the left male third leg two inner smooth setae instead of the normal one (Figure 26D). The holotype female lacks the setal element on the inner side of the palm of the richt maxilliped.

Description of latest copepodids

COPEPODID IV (male)

Habitus (Figure 28A) fusiform, rapidly tapering towards anal somite. Body with 8 somites, with distinct division between prosome and urosome. Head about 1/3 of entire body length (420 μm). Posterior hyaline fringe of head smooth, of the succeeding somites undulate. Anal operculum arcuate, with a transversal row of minute spinules on dorsal surface.

Caudal rami short, about 1.5 times as long as wide, slightly tapering posteriorly, and bearing 7 elements. Rostrum separated from head, small, bell-shaped.

Antennule (Figure 29B) 7-segmented, with segment II only slightly longer than segment I. Arcuate rim on dorsal surface of segment I present. Setal complement: I(1)-II(8)-III(10+Aesth)-IV(2)-V(4)-VI(4)-VII(7+Aest h).

Antenna with basis, endopodite and exopodite (Figure 29D) with complement as in adult but with shorter segments and setae on exopodite. Mouthparts as in adult.

P1–P4 with two-segmented rami. Chaetotaxy of the legs in Table 5. P1 exopodite with typical outer sub-distal and outer distal comb-like spines on second segment. Endopodite of P1 with geniculated setae on terminal segment. P4 (Figure 30A) with sub-equal endopodal segments. Inner seta on distal segment very small.

P5 (Figure 27A) separated from supporting somite, and not fused medially with opposite leg. Distinct exopodal and endopodal lobe, with 4 and 2 setae, respectively. P6 (Figure 29F) represented as a transversal long plate on ventral posterior margin of somite, each side bearing 2 elements: inner one short, robust and smooth, outer one long an plumose.

COPEPODID V (female)

Habitus (Figure 28B) fusiform, rapidly tapering towards anal somite. Body with 9 somites, of with head nears 1/3 of entire body. Division between prosome and urosome distinct. Length, including caudal rami and rostrum, 570 μm. Rostrum and posterior hyaline fringes of somites as in preceeding stage.

Caudal rami long ovate, about twice as long as wide, with outer distal edge protruded. The latter bearing distalmost lateral seta and spinules along the distalmost rim. Biarticulate dorsal seta with a median position. Proximal lateral setae arising in proximal half of margin. Outer terminal seta and inner terminal one shorter than ramus, the former somewhat thickened near the base. Inner principal one not bulbous at the base. Dorsal integument of ramus furnished with a short row of slim spinules in proximal third, and a short row in distal third, near inner margin.

Antennule (Figure 29A) 8-segmented, with segment II nearly twice as long as segment I, and with distinct carena on dorsal surface of the latter. Setal complement: I(1)-II(8)-III(7)-IV(4+Aesth)-V(2)-VI(4)-VII(4)-VIII (7+Aesth). Only seta on segment I pinnate. Pore orifices present, the one on segment I with a hyaline tube.

Antenna as in stage IV, but distal setae on exopodite as long as segment. Mouthparts as in adult. P1 with propodal components and rami as in adult, including shape of spines and setae, except for the short non-pectinate inner element on first endopodal segment.

P2–P4 with 3-segmented exopodites and 2-segmented endopodites. Chaetotaxy (see Table 5) as in adult. Shape of outer and apical setae and spines as in adult, inner ones short with large lumen (see Figure 30C, D, F).

P5 (Figure 27D) with distinct endopodal and exopodal lobe, the latter somewhat higher than the former. Outer baseoendopodal extension short, conical, with associated pore orifice present. Endopodal lobe with 5 elements: 3 inner and 2 apical ones. Two pores present. Exopodal lobe with 6 elements: 4 outer, an apical and an inner one. Three pore orifices present.

P6 (Figure 29G) represented as a long triangular plate, diferentiated from somite by descreet suture, with three smooth elements on a slightly protruded flap: inner one short, robust, median slender, and outer one bulbous at base.

COPEPODID V (male)

Habitus (Figure 28C) resembling that of female copepodid V, differs however in the following aspects: smaller body length (495 μm), shorter head (less than 1/3 of body), less wide body somites, and shape of caudal rami. The latter as in the preceeding stage.

Antennule (Figure 29C) 7-segmented with second segment 1.5 times longer than first one. Carena on first segment, and pore orifices on first and second segment present. Setal complement: I(1)-II(11)-III(12+Aesth)-IV(2)-V(3)-VI(3)-VIII(7+Ae sth). All setae slender and smooth, except pinnate seta on segment I. Antenna, mouthparts and P1 as in female.

P2–P4 with 3-segmented exopodites and 2-segmented endopodites. Outer and apical setae and spines as in the adult, inner ones short, robust, and with a large lumen. Chaetotaxy of the rami in Table 5. Endopodite P2 (Figure 30E) with inner apical seta on

Table 5. Setal complement of the last copepodids of *Neogoniceps martinezi* n. sp.

	CIV		CV	
	EXO	**END**	**EXO**	**END**
P1	0-023	1-011	0-0-022	1-011
P2	1-223	1-121	1-1-122	1-121
P3	1-323	1-121	1-1-222	1-121
P4 ♀	?	?	1-1-322	1-121
P4 ♂	0-323	1-121	1-1-222	1-121
P5 ♀	?	?	6	5
P5 ♂	4	2	5	3
P6 ♀	?	-	3	3
P6 ♂	2	-	3	3

'-': Means not applicable.

second segment twice as long as segment length. Outer distal and outer subdistal one short and robust with large lumen and a hyaline appearance. P3 endopodite as in female copepodid V.

P5 (Figure 27B) with 3 short robust elements on endopodal lobe and 5 elements (2 outer, an apical, and 2 inner ones) on exopodal lobe. Outer extension of baseoendopodite well developed, conical, with pore orifice.

P6 (Figure 29G) represented as a transversal plate along posteroventral margin of somite, bearing 3 elements: inner short and robust, median long and slender, outer short and slender.

Discussion

The type-series of *Mwania phytocola*, described above, comprised only the female copepodid stages. The material of *Neogoniceps martinezi* studied herein didnot contain a complete copepodid series neither, but yielded some male specimens in the fourth and fifth copepodid stage. We assume that the copepodid development of *Neogoniceps martinezi* is quite similar with that of *Mwania phytocola* as described above, especially in the serial addition of segments in the rami of the natatorial legs. The only exception, is that the P1 endopodite remains 2-segmented in the copepodid V and adult of *Neogoniceps*, whereas this ramus becomes 3-segmented in the latest copepodid stage of *Mwania phytocola.*

Setal appearance on the exopodites evidently will be different from that of *Mwania phytocola* which displays a reduced inner chaetotaxy of the terminal segments in P2 and P3. We assume that in *Neogoniceps* the inner seta on the third exopodal segment of the P2, is present from the first copepodid on, and that the proximal inner seta on the terminal exopodal segment appears in copepodid III where the exopodite leg is transformed in a 2-segmented ramus.

The development of the inner elements on the P4 exopodite seems to be accelerated, as in the two-segmented situation (copepodid IV) the 3 inner elements of the future terminal segment and the one of the future median segment are present in the female. The male fourth copepodid is characterized by the presence of only 3 inner elements, which represent 2 inner of the future terminal segment and the inner one of the future median segment.

Dimorphic characteristics in the endopodites appear only in the second leg in the fifth copepodid stage of the male. The outer distal and outer subdistal element are voluminous short smooth appendages. Remarkably is that the inner distal seta in this stage is very long (as in the female copepodid). Its length becomes vastly reduced during the terminal molt, resulting in a slender seta, distinctly shorter than the other appendages.

The collection didnot contain a female copepodid IV, but based on the observations presented above for the female P5 of *Mwania phytocola* in this stage, we assume that sexual differences between the male and female P5 are already present. The female P5 exopodal and exopodal lobe are more protruded and bear both one seta more than in the male. In the fifth copepodid, the difference are more pronounced as both sexes display an adult number of appendages on the rami.

Secondary sexual modifications in Tetragonicipitidae

Besides the typical harpacticoid dimorphism (habitus, urosome including caudal rami, antennule and fifth leg) tetragonicipitids display secondary dimorphism in either the endopodites and/or the exopodites of the swimming legs. However, in several cases, these modifications have been overlooked or erroneously interpreted. In the following paragraphs, occurence and homology of the sexual dimorphic modifications of the exopodites and of the P2 endopodite are analysed. In the light of these observations, the generic diagnosis of the genus *Paraschizopera* is discussed.

Exopodal dimorphism

The statement (Huys, 1995: p.26) that the thoracopodal exopodites in *Diagoniceps laevis* Willey, 1930 and *Aigondiceps bocki* (lang, 1948) lack sexual dimorphism is misleading. Fiers (1995) demonstrated the presence of a markedly prolongation of the outer distal corner of the male first exopodal segment of the P3 and the second exopodal segment of the P4 in *D. laevis*. In contrast, dimorphic modifications occur only on the second segment of the male P4 exopodite in *A. bocki*.

Of more importance however, is the sexual difference of the setal formula of the P4 exopodite. Although the differences between males and females seem often overlooked, Fiers (1995) speculated that almost all tetragonicipitid males bear one seta (inner pectinated one) less on the third exopodal segment

of the P4 than in the females. The only exceptions known thus far are those species having a 222 complement in the female (*Odaginiceps clarkae* Fiers, 1995 and *O. elegantissima* Fiers, 1995) and *Paraschizopera menaiensis* (Geddes, 1968) which displays a 323 complement in both sexes. Thus, it is quite reasonable to assume that the female of *Diagoniceps* spec. Bodin, 1979 (= *Diagoniceps brevicauda* Huys, 1995) has a normal setal formula of the P4 exopodite being 1-1-323 and does not displays a unique complement as stated by Huys (1995: p. 25). Taking this amendment in consideration, the key to the species of the genus *Diagoniceps sensu* Huys, 1995, should be avoided as it inevitablely will lead to misidentification if females of *Diagoniceps* spec. Bodin, 1979 will be found.

Huys (1995) correctly interpreted the chaetotaxy (3 endopodal, 6 exopodal elements) of the fifth leg of *Paraschizopera beckeri* Wells, 1981 as an indication that the juvenile specimen used in the available descriptions (Becker, 1972; Becker & Schriever, 1979) is a male copepodid V. The proportional lengths of the antennular segments corroborate this statement. Following the same reasoning as in the previous paragraph, it is highly possible that the (adult) female displays a setal formula in the P4 with three inner elements on the distal segment. The assumption that an additional seta will be added during the final moult is unlikely. The general development of chaetotaxy in copepods and observations on tetragonicipitid copepodids presented above for *Mwania phytocola*, *Neogoniceps martinezi*, and species of the genus *Tetragoniceps* (pers. obs.) revealed that the differences between male and female chaetotaxy of the P4 are present in the last copepod stage (CV). Apart from elongation and pectination of the inner elements, no changements of the setal number during the final moult could be deduced from the available material. Thus here too, the key to the species of the genus *Paraschizopera* compiled by Huys (1995) should be used most carefully as the discrimination between *P. trifida* and *P. beckeri* is based only on the number of appendages on the distal segment of the P4 exopodite.

Homology of the P2 endopodite setal complement

The distal segment of the endopodite of the female P2 has maximally 4 appendages, arranged as follows: 1 inner median seta, two apical setae, and one outer subdistal spiniform element. Such setal formula is known for the three species assembled in the genus *Aigondiceps*, and the closely related genera *Mwania* n. gen. and *Neogoniceps* n. gen. All other taxa lack the median inner element, but retain the two apical setae and the outer subdistal spiniform element.

The second endopodal segment of the male P2 bears an equal number of elements as the females. The inner median seta seems unmodified in the male, but the morphology of the apical setae and the outer subdistal appendage is quite different. The inner apical seta is distinctly shorter than in the female, while the outer apical is a large smooth lanceolate element, with a defined articulation at the insertion place with the segment. The outer element, equally lanceolate and smooth as the inner apical one, does not articulate with the segment, and its lumen seems to be continuous with the inner tissue of the segment. In addition, this outer element often has a pure apical position, instead of the sub-distal location of the spine in the female.

Based on the number and the location of the appendages on the second segment in the male P2 endopodite, it is evident that they are homologous with the elements of the female P2 endopodite. Evidently, Huys' (1995) interpretation of the setal homology in the generic definition of *Paraschizopera* (i.e. outer spine missing, distal setae modified) is erroneous as the male bears the same number of elements on the P2 as in the female.

The genus Paraschizopera *Wells, 1981*

Today, the genus assembles three species: *P. beckeri* Wells, 1981 of which only a single male fifth copepodid is known, *P. trifida* (Yeatman, 1980) of which only the female morphology is known, and *P. menaiensis* (Geddes, 1968), the only species of which both sexes are described. *P. beckeri* and *P. trifida* are known from the East Pacific, the former from a deep station off Peru, the latter from a more shallow station near Seatle (U.S.A.).

Thus far, *P. menaiensis* (Geddes, 1968) is known from the type locality (Menaibridge, U.K.) and La Rochelle on the French Atlantic coast (Bodin, 1979). In both cases, only a single male and female were encountered. The specimens from Wales were examined by Huys (1995), those from La Rochelle by Fiers (1995).

The only stricking difference between the specimens from both localities was found in the male P4 endopodite. Whereas the male from Wales displays the same number of setae as in the female, the French specimen bears an additional inner seta on the second endopodal segment. Huys (1995: p. 25) claimed that

Table 6. Chaetotaxy of the three species assigned to *Paraschizopera* Wells, 1981

	P2		P3		P4 ♀		P4 ♂	
	EXO	**END**	**EXO**	**END**	**EXO**	**END**	**EXO**	**END**
P. beckeri	1-0-022	1-021	1-1-022	1-121	1-1-322[a]	1-121[a]	1-1-222	1-121
P. trifida	1-0-022	1-021	1-1-022	1-121	1-1-322	1-121	1-1-222[a]	1-121[a]
P. menaiensis	1-0-023	1-021	1-0-023	1-021	1-1-323	1-021	1-1-323	1-[0,1]21

[a]: Setal complement deduced.

the additional seta in the French specimen is a tubular extension of a pore which he observed in the male paratype specimen. However, re-examination of the French specimen clearly revealed that the additional seta (and the pore orifice) is present and that the illustration given by Bodin (1979) is correct (Bodin, in litt.).

Whether the French specimens represent a distinct species is impossible to conclude at this moment. With only 2 male specimens known thus far, there is no sufficient evidence if the presence or absence of an additional seta on the male P4 endopodite has to be regarded as a specific characteristic or falls within the range of specific variability.

The setal complement of the legs (see Table 6) clearly divide the genus *Parascizopera* in two. The two species from the East Pacific bear only two outer spines on the terminal exopodal segments (apomorphous), but retained in the third and fourth leg an inner seta on the median segments and a full complement on the distal endopodal segments (plesiomorphies). In contrast, *P. menaiensis* possess three outer spines on the terminal exopodal segments (plesiomorphy), but has in the third and fourth the inner seta on the median exopodal segment and the distal endopodal segments reduced (apomorphies). Moreover, both East Pacific species bear a well developed abexopodal seta on the first endopodal segment of the antenna. In *P. menaiensis*, however, this seta is not present. In addition, the two East Pacific species are described as having no epipodal seta on the maxillule, a condition rarely found among the Tetragonicipitidae (cfr. *Pteropsyllus*). This has to be confirmed as the epipodal seta is easily overlooked. This seta is definitly present in *P. menaiensis* as illustrated in Fiers, 1995.

The two East Pacific species differ also significantly from *P. menaiensis* in the proportional lengths of the endopodites. Where the former have very long endopodites, reaching to the third exopodal segment in P2 and P3, and beyond the articulation of the first and second segments in P4, the latter possess very short endopodites reaching only to the middle of the second exopodal segment at the most. In the primitive *Mwani phytocola* n. gen., n. sp. described above, the same phenomenom is observed. In this taxon, the endopodites are considerably much longer than in the more advanced taxa.

The systematic position of the genus *Paraschizopera* within the Diosaccidae has been subject of several contributions (Becker, 1972; Becker & Schriever, 1979; Wells, 1981; Mielke, 1992), until recently when Huys (1995) correctly removed this taxon from its original family to the Tetragonicipitidae. It is evident that *Paraschizopera* is to be considered as a very primitive taxon within the family (viz. 3-segmented P1 endopodite, terminal endopodal segment of P1 with 3 elements; antennule with subequal first and second segment; unmodified fifth leg in female, bearing 6 elements on its exopodite).

In the present conditions, it is premature to splitt up the genus with the assignation of the East Pacific species to *Paraschizopera* and to reinstate the genus *Nidiagoceps* Fiers, 1995 for *P. manaiensis*. The generic diagnosis of *Paraschizopera*, however, as amended recently by Huys (1995) should be consulted with caution as it is largely based upon the characteristics of the Atlantic species.

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References

Becker, K.-H., 1972. Eidonomie und Taxonomie abyssaler Harpacticoidea. Ph.D.dissertation, Christian Albrechts Universität, Kiel: 162 pp.

Becker, K.-H. & G. Schriever, 1979. Eidonomie und Taxonomie abyssaler Harpacticoida (Crustacea, Copepoda). Teil III. 13 neue Tiefsee-Copepoda Harpacticoida der Familien Canuellidae, Cerviniidae, Tisbidae, Thalestridae, Diosaccidae und Ameiridae. Meteorforsch. Erg. (D)31: 38–62.

Bodin, Ph., 1979. Copépodes harpacticoides marins des environs de La Rochelle. 5 -Espèces nouvelles ou incertaines. Vie et Milieu 27(3), sér. A: 311–357.

Bodin, Ph., 1997. Catalogue des nouveaux Copépodes harpacticoïdes marins (édition 1997). Doc. Trav. Inst. r. Sc. Nat. Belg. 89: 1–304.

Brazier, M. D., 1975. An outline history of seagrass communities. Palaeontology 18: 681–702.

Constanzo, G., N. Cresencenti & N. Calafiore, 1997. Copepodid stages of *Lichmolgus forficula* Thorell 1859 (Copepoda, Poecilostomatoida, Lichomolgidae), a copepod associated with *Phallusia mammillata* (Cuvier, 1815). J. Nat. Hist. 31: 1019–1028.

Dahms, H.-U., 1989. Antennule development during copepodite phase of some representatives of Harpacticoida (Copepoda, Crustacea). Contr. Zool. 59(3): 159–189.

Dahms, H.-U., 1993. Copepodid development in Harpacticoida. Microfauna Mar. 8: 195–245.

Ferrari, F. D., 1988. Developmental patterns in numbers of ramal segments of copepodpostmaxillipedal legs. Crustaceana 54(3): 256–293.

Fiers, F., 1995. New Tetragonicipitidae (Copepoda, Harpacticoida) from the Yucatecancontinental shelf (Mexico), including a revision of the genus *Diagoniceps* Willey. Bull. Inst. r. Sc. Nat. Belg., Biol. 65: 151–236.

Geddes, D. C., 1968. A new species of *Diagoniceps* (Copepoda Harpacticoidea), and two previously undescribed male harpacticoids from the Isle of Anglesey. J. Nat. Hist. 2: 439–448.

Huys, R., 1995. Some remarks on the taxonomic status of *Paraschizopera* Wells, 1981 (Copepoda: Harpacticoida). Hydrobiologia 308: 23–28.

Kiefer, F., 1978. Das Zooplankton der Binnengewässer. 2. Teil. Freilebende Copepoda. Die Binnengewässer 26: 1–343.

Kim, I.-H., 1994. Copepodid stages of *Conchyliurus quintus* Tanaka, 1961 (Poecilostomatoida, Clausidiidae) associated with bivalve molluscs. Hydrobiologia 292/293: 161–169.

Lang, K., 1948. Monographie der Harpacticiden. Hakan Ohlosson, Lund, Vol. 2: 1682 pp.

Mielke, W., 1992. Description of some benthic Copepoda from chile and a discussion on the relationships of *Paraschizopera* and *Schizopera* (Diosaccidae). Microfauna Mar. 7: 79–100.

Vincx, M. & C. Heip, 1979. Larval development and biology of *Canuella perplexa* T. and A. Scott, 1983 (Copepoda, Harpacticoida). Cah. Biol. Mar., 20: 281–299.

Wells, J. B. J., 1981. Keys to the aid in the identification of marine harpacticoid copepods. Amendment Bulletin No. 3. Zool. Publ. Victoria Univ. Wellington 75: 1–13.

Willey, A., 1930. Harpacticoid copepoda from Bermuda - Part I. Ann. Mag. Nat. Hist. ser.10, 6: 81–114, Pl. V.

Yeatman, H. C., 1980. A new species of *Diagoniceps* (Copepoda, Harpacticoida) and a partial redescription of *Diagoniceps laevis* Willey. Crustaceana 38(2): 121–126.