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A new species of *Maraenobiotus* Mrázek, 1893 (Copepoda: Harpacticoida: Canthocamptidae) from Colombian Andean mosses, with an identification key for the American species

SANTIAGO GAVIRIA[1*] & DANIELLE DEFAYE[2]
[1]*University of Vienna, Dept. of Limnology and Bio-Oceanography & Technisches Büro für Biologie, Fred-Raymond-Gasse 19/2/4, A-1220 Vienna, Austria.* *santiago.gaviria@gmx.at;* *https://orcid.org/0000-0002-5959-7919*
[2]*27 rue Gaston Charlet, F-87000 Limoges, France.* *danielle.defaye@mnhn.fr;* *https://orcid.org/0000-0002-1524-6973.*
[*]*Corresponding author.*

Abstract

Maraenobiotus wellsi **sp. nov.** (Canthocamptidae) is described based on material collected in mosses in the "páramo" region of the Andean Cordillera of Colombia. The new species is closely related to *M. australis* Apostolov, 2001 from Tierra de Fuego in Argentina, but can be distiguished by the shape of the caudal rami, the insertion point of its terminal seta IV, and the chaetotaxy of distal segments of legs 3 and 4. We discuss morphological differences with other congeners inhabiting South America (Peru), *i.e. M. naticochensis* Delachaux, 1917*, M. fontinalis* Harding, 1955 and *M. fontinaloides* Löffler, 1960. Major distinguishing features were observed in the chaetotaxy of legs 2 and 3, the morphology and size of the caudal rami, and the ornamentation of the anal operculum. We also discuss morphological characters that distinguish the new species from those living exclusively in mosses, such as *M. cuspidatus* Štěrba, 1968 and *M. canadensis* Flössner, 1992, and those reported from mosses and other habitats *i.e.. M. vejdovskyi* Mrázek, 1893, *M. brucei brucei* (Richard, 1898), *M. zschokkei* Kreis, 1920, *M. brucei himalayensis* Chappuis, 1928b, *M. truncatus* (Gurney, 1932)*, M. insignipes elgonensis* Chappuis, 1936, *M. insignipes nepalensis* Löffler, 1968 and *M. kinabaluensis* Löffler, 1973. A distribution map of American species and an identification key for females are provided.

Key words: Crustacea, geographical distribution, morphology, taxonomy, tropical high mountains

Introduction

The harpacticoid copepod genus *Maraenobiotus* Mrázek, 1893 was proposed for a new species, *Maraenobiotus vejdovskyi* Mrázek, 1893, collected from groundwaters of the Czech Republic. Today, *Maraenobiotus* comprises 28 species (Walter & Boxshall 2019) with two of them containing several subspecies: *Maraenobiotus insignipes* (Lilljeborg, 1902) with six subspecies besides the nominal species (*M. i. alpinus* Keilhack, 1909; *M. i. indicus* Chappuis, 1928b, *M. i. elgonensis* Chappuis, 1936; *M. i. altissimus* Löffler, 1968; *M. i. nepalensis* Löffler, 1968 and *M. i. kysylcumicus* Borutzky, 1972) and *Maraenobiotus brucei* (Richard, 1898) with six subspecies besides the nominal species (*M. b. carpathicus*, Chappuis, 1928a; *M. b. himalayensis* Chappuis, 1928b; *M. b. malayicus* Chappuis, 1931; *M. b. caucasicus* Borutzky, 1934; *M. b. africanus* Chappuis, 1936 and *M. b. estonicus* Fefilova, 2010).

Additions to the species list were published by Brancelj & Karanovic (2015), who described *Maraenobiotus slovenicus* **n. sp.**, from groundwaters in Slovenia. In the same publication, they also proposed two new species, *M. galassiae* Brancelj & Karanovic, 2015 and *M. pescei* Brancelj & Karanovic, 2015 for previously reported "populations" of *M. vejdovskyi* from Italy, and *M. ishidai* Brancelj & Karanovic, 2015 for a "population" of *M. vejdovskyi* from Japan. Based on their analysis of morphological differences between subspecies, Brancelj & Karanovic (2015) elevated four subspecies of *M. vejdovskyi* to species rank, namely *M. anglicus* Gurney, 1932, *M. arctica* Keilhack, 1909, *M. tenuispina* Roy, 1924 and *M. truncatus* Gurney, 1932. As they argued for abandoning subspecific divisions of *M. vejdovskyi*, the subspecies *M. vejdovskyi zschokkei* Kreis, 1920 can be re-established with its original species rank as *M. zschokkei* Kreis, 1920.

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Species of the genus *Maraenobiotus* are mainly inhabitants of cold-water environments such as those located at middle to high latitudes in the Northern (Gurney 1932; Borutzky 1964; Flössner 1988, 1992; Fefilova 2010; Novikov & Sharafutdinova 2020) and Southern (Apostolov 2001) Hemispheres, on high mountains of temperate (Thiébaud 1927; Chappuis 1928a, Gaviria 1998, Jersabek *et al*. 2001) and tropical (Delachaux 1917; Chappuis 1928b, 1936; Harding 1955; Löffler 1960, 1965, 1968, 1973; present study) regions, and in groundwater environments of Europe (Mrázek 1893; Flössner 1988; Bassamakov & Apostolov 1989; Pesce *et al*. 1994; Janetzky *et al*. 1996; Gaviria 1998; Brancelj & Karanovic 2015). Groundwaters are well known to be cold habitats (Griebler & Mösslacher 2003).

Löffler (1968) already called attention to the distribution of *Maraenobiotus* in tropical mountain region, the genus being apparently absent in habitats with permanently warm temperatures. At tropical latitudes, the lowermost limit of species of the genus is 2,000 m altitude in running waters and 3,000 m in lentic water-bodies (Löffler 1968). From an evolutionary perspective, Löffler already analyzed the trend of speciation of the genus in cold regions of tropical high mountain regions such as the Ruwenzori, Mount Kenya and Mount Elgon in eastern Africa (Löffler 1965), where populations of very closely related subspecies were established in habitats located close to one another.

Some species, such as *M. australis* Apostolov, 2001, *M. canadensis* Flössner, 1992 and *M. cuspidatus* Štěrba, 1968, are semi-terrestrial and have been found exclusively in wet mosses, whereas other (sub)species such as *M. brucei brucei*, *M. brucei himalayensis*, *M. insignipes elgonensis*, *M. insignipes nepalensis*, *M. zschokkei*, *M. kinabaluensis* Löffler, 1973, and *M. vejdovskyi* live in aquatic environments but have also been reported from wet mosses. *Maraenobiotus truncatus* is semi-terrestrial, inhabiting wet leaves and mosses (Janetzky *et al.* 1996).

During a faunistic survey of microcrustaceans in the "páramo" region of the Andean Cordillera, corresponding to the humid zone above the Andean forest, we found three species of harpacticoid copepods inhabiting wet mosses in the Boyacá State, Colombia. Those species were identified as the parastenocaridid *Colombocaris isabellae* Gaviria, Defaye & Corgosigno, 2017 and two canthocamptid copepods. One of the canthocamptids corresponds to *Epactophanes richardi* Mrázek, 1893, the second one to the genus *Maraenobiotus*. The tabular key provided by Wells (2007) did not lead to any known species of the genus. As its morphological characters could not be assigned to any known species, it here described as a new species based on the study of a single female and one copepodid V stage. No males were found in the sample.

Material and methods

The sample containing harpacticoid copepods was collected by S. Gaviria, N. Aranguren and C. Motta in wet mosses growing on stones in the Páramo de Cómbita, Boyacá, Colombia (5°45‘00‘‘N, 73°20‘29‘‘W) at 3,039 m.a.s.l. (Fig. 1). The sample was processed in the laboratory, and live animals were sorted and fixed in 70% ethanol. Specimens were transfered to glycerine and then to lactic acid to clear the tissues. Copepods for taxonomic study were dissected using sharpened tungsten needles or studied undissected. Two specimens of the genus *Maraenobiotus* were found, one of them a stage V copepodid. The temporarily mounted adult specimen was used for drawings of body parts, mouth appendages and legs.

Animals were examined under a Leica DMLB compound microscope equipped with a drawing tube. Illustrations were further completed by examining the adult female with a Nikon Ellypse 200 microscope. Final plates were produced with digital inking using a Wacom Intus Protablet and the Adobe Photoshop CS3 program after scanning the drawings.

Finally, both specimens were transferred into lactophenol, each on a separate slide, and sealed with varnish. Specimens were deposited in the limnological collection of the Universidad Pedagógica y Tecnológica de Colombia UPTC, Tunja, Boyacá, Colombia (UPTC-L). Descriptive terminology follows Huys & Boxshall (1991).

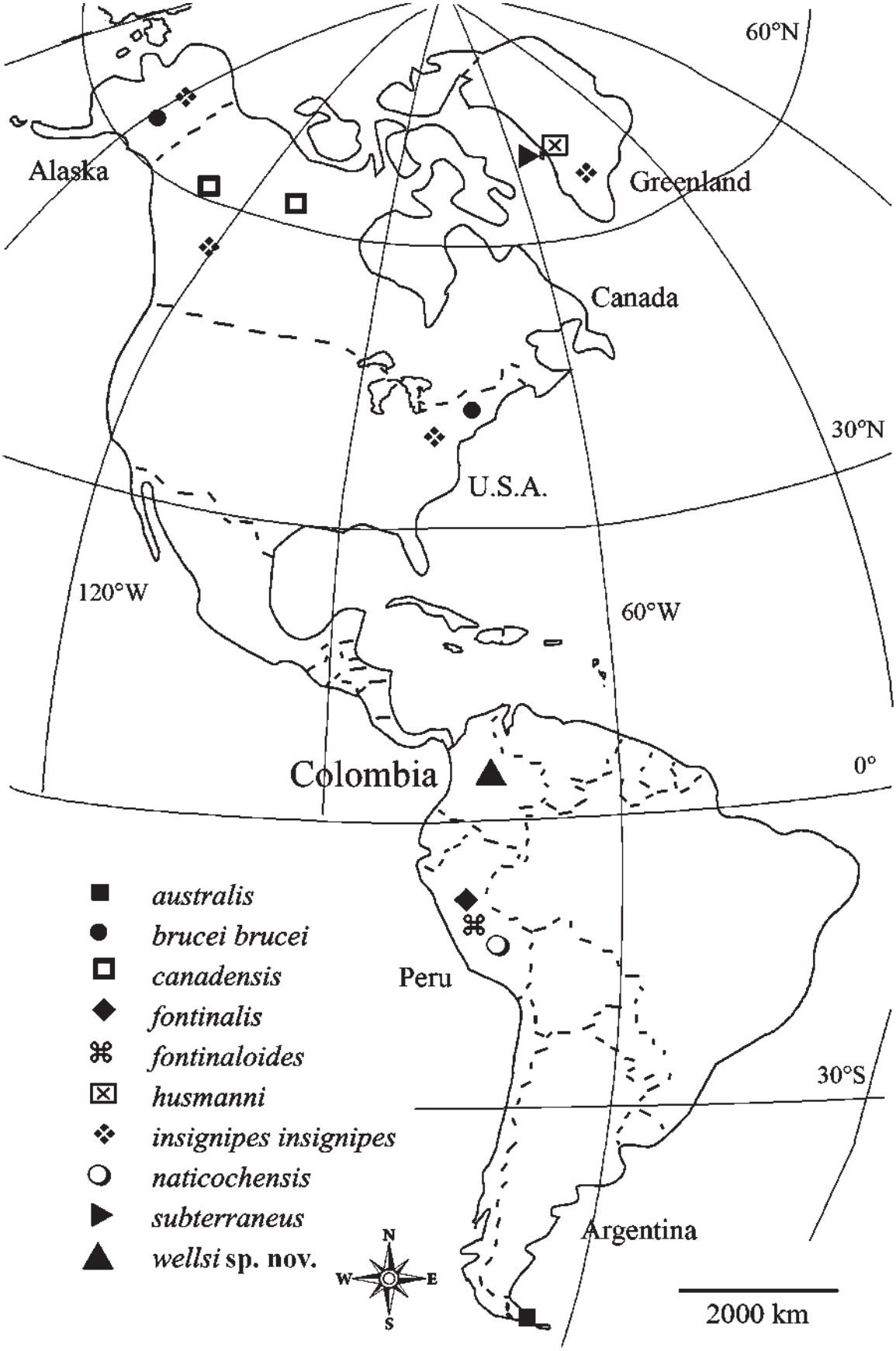

FIGURE 1. Geographical distribution of the species of *Maraenobiotus* known on South and North America.

Taxonomic description

Order Harpacticoida Sars, 1903

Family Canthocamptidae Sars, 1906

Genus *Maraenobiotus* Mrázek, 1893

Maraenobiotus wellsi sp. nov.
(Figs. 2–5)

Type locality. Wet mosses of the genus *Sphagnum* growing on stones in the Páramo de Cómbita (the humid region of the Andean Cordillera above the Andean forest), Boyacá, Colombia (5°45‘00‘‘N, 73°20‘29‘‘W) at 3,039 m.a.s.l. (Fig. 1).

Material examined. Holotype female, dissected and mounted on one slide in lactophenol, registered as UPTC-L 0001. Paratype copepodid UPTC-L 0002. Both specimens from the type locality.

Etymology. The new species is named after the late Professor John B. J. Wells, School of Biological Sciences, Victoria University of Wellington, New Zealand, for his valuable contribution to the systematics of harpacticoid copepods.

Differential diagnosis. Female. *Maraenobiotus* of small size, with urosomites 2–5 with rows of spinules ventrally and laterally near the posterior margin, dorsal row of spines located only near free lateral margin. Urosomites 2 (genital-double somite) and 3 with a ventral row of spinules showing a gap in the middle of the row. Anal operculum with nine spinules, reaching beyond the posteriormost margin of the anal somite. Caudal rami conical, longer than wide, caudal setae IV and V not inflated at their base proximal to breaking point. Seta IV slightly inflated distal of breaking point. Antennary exopod one-segmented with four setae. Mandibular palp one-segmented with four setae. Maxilliped comprising syncoxa, basis and 1-segmented endopod bearing one seta and one claw. Leg 1 with 2-segmented exopod and endopod. Legs 2–4 with 3-segmented exopod and 2-segmented endopod. Last segment of exopod of legs l–4 with five major elements, last segment of endopod of legs 1–4 with three, four, five and five major elements, respectively. Leg 5 exopodal lobe longer than baseoendopod, exopod with three elements, baseoendopod distal lobe with five elements.

Description of holotype (female). Habitus (Fig. 2A–B) cylindrical, nauplius eye colourless. Body length 575 µm, measured from tip of rostrum to posterior margin of caudal rami (without caudal setae). Cephalosome constituting 24% of body length. Body comprising prosome (consisting of cephalosome and three free pedigerous somites, first pedigerous somite fused to cephalosome) and urosome (consisting of fifth pedigerous somite, genital double-somite, three abdominal somites and caudal rami). Prosome and urosome with sensillae distributed dorsally and laterally as shown in Fig. 2A–B. Cephalosome with median small oval integumentary window located dorsally. Body somites with smooth posterior margin. Genital double-somite completely fused. Median copulatory pore located at about halfway the length of genital double-somite. Urosomites 2–5 with row of spinules inserted near posterior margin of somite, dorsally only near lateral margin. Urosomites 2 and 3 bearing ventral row of spinules showing gap in the middle.

Anal somite (Fig. 4A) with lateroventral spinules near posterior margin, extending beyond posterior margin of somite. Anal operculum (Fig. 4A) large, trapezoidal, free margin with nine spinules, extending beyond posteriormost margin of anal somite.

Caudal rami conical, about 1.3 times as long as wide (Fig. 4A). Numbering system for setation elements, see Fig. 4A. Rami with two lateral setae (II and III, seta I absent), seta II inserted approximately in middle of ramus, seta III inserted beyond middle of ramus (seta II inserted anteriorly to dorsal seta VII, seta III inserted approximately at same level as seta VII), three terminal setae (IV–VI) and one dorsal seta (VII). Setae IV, V and VII with breaking plane. Setae IV and V not inflated proximal to breaking plane. Seta IV slightly inflated at its base, distal to breaking plane, spinulose, 1.7 times longer than caudal ramus. Seta V long and spinulose (observed in paratype copepodid, Fig. 2C), distal part of seta V of holotype lost during dissection. Seta V partially inserted ventral to seta IV. Seta VI thin and naked, shorter than caudal ramus. Dorsal seta (seta VII) inserted at posterior third of ramus. Row of eight spinules inserted ventrally near posterior margin of ramus (Fig. 3A), row of four spinules inserted distally near inner margin of ramus (Figs. 3A, 4A), two small spinules on dorsal surface near base of dorsal margin and one spinule on lateral surface inserted near each base of setae II and III (Fig. 4A–B).

Antennule 8-segmented (Fig. 3B), with armature formula from distal to apical segment: 0, 4, 3, 1 + aesthetasc (seta and aesthetasc with conjointed bases), 2, 0, 1, 4 + 2 and aesthetasc (2 setae and aesthetasc with conjointed bases). Aesthetasc of segment 4 reaching middle of segment 8, slightly longer than the three distal segments combined. Aesthetasc on segment 8 almost as long as the three distal segments combined.

Antenna (Fig. 3C), with praecoxa and allobasis lacking ornamentation. Endopod one-segmented, inner margin with four spinules followed by two naked spines from proximal to distal, apical margin with one naked spine, two naked setae and three geniculate setae, most outer geniculate seta shorter than the other two. Exopod one-segmented, inner margin with one bipinnate seta, distal margin with two naked setae and one outer bipinnate seta.

Mandible (Fig. 4C), palp one-segmented with four distal setae. Coxa with outer lobe, gnathobase with five teeth and one lateral seta.

Maxillule (Fig. 4D) 3-segmented, praecoxal arthrite with five apical spines (three robust, one bifid, one thin). Coxa with one strong spine and one long seta. Basis with distal spine and three accessory lateral setae.

Maxilla (Fig. 4E), syncoxa with two endites, outer endite inflated at its basis, with two lateral accessory setae, inner endite with one naked seta. Basis with claw accompanied at base by two accessory lateral setae. Endopod absent.

Maxilliped (Fig. 4F), syncoxa short, ornamented with one bipinnate seta on distal inner corner and a row of minute spinules on outer margin. Basis with a row of spinules near inner margin. Endopod one-segmented, bearing one claw and one seta on distal margin.

Legs 1–4: for major armature, see Table 1, intercoxal sclerite with concave distal margin and naked surface. Distribution of spinules on segments of leg rami (exopod and endopod) as shown in Fig. 5A–D.

TABLE 1. Female leg armature of *Maraenobiotus wellsi* **sp. nov.** Spines indicated by Roman numerals, setae by Arabic numerals.

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

Leg 1 (Fig. 5A): coxa with one outer short spinule and two smaller spinules inserted on distal corner; basis with one spine on outer margin, a row of spinules on anterior surface near base of endopod and one strong spine on inner margin, inserted on distal corner near base of endopod. Exopod and endopod 2-segmented. Exopod shorter than endopod; first segment with one unipinnate spine on outer margin; second segment longer than first with five major elements: two unipinnate spines on outer margin, one unipinnate spine and one geniculate seta on apical margin, and one geniculate seta on inner margin. Geniculate setae longest. Endopod with first segment as long as exopod, 2.5 times longer than wide, inner margin with one naked spine inserted subapically; second segment, apical margin with two naked setae, inner seta 2.7 times longer than outer seta and 1.2 times longer than endopod, inner margin with one naked spine inserted subapically.

Leg 2 (Fig. 5B): coxa with one very large spinule on distal outer corner; basis with one unipinnate spine on distal outer margin. Exopod 3-segmented; first and second segments with one robust spine on outer margin subapically; third segment with one unipinnate robust spine inserted subapically, apical margin with one outer unipinnate spine and one inner bipinnate seta, spine shorter than seta, inner margin with two naked slender spines. Endopod 2-segmented, as long as the two first exopodal segments combined; first segment, inner margin with one naked spine inserted subapically; second segment, distal margin with one bipinnate seta and one unipinnate seta, inner margin with two naked setae.

Leg 3 (Fig. 5C): coxa, without armature on outer margin, anterior surface with row of small spinules near distal inner corner; basis with long naked seta on outer margin. Exopod 3-segmented; first and second segments as in leg 2; third segment with one unipinnate robust spine on outer margin, apical margin with one outer unipinnate spine and one bipinnate seta, inner margin with two unipinnate slender spines inserted at 1/2 and 2/3 of segment. Endopod 2-segmented; first segment with one naked slender spine on inner margin; second segment with one bipinnate seta on outer margin, apical margin with two bipinnate setae, outer seta 2.5 times longer than inner seta, inner margin with two naked slender spines.

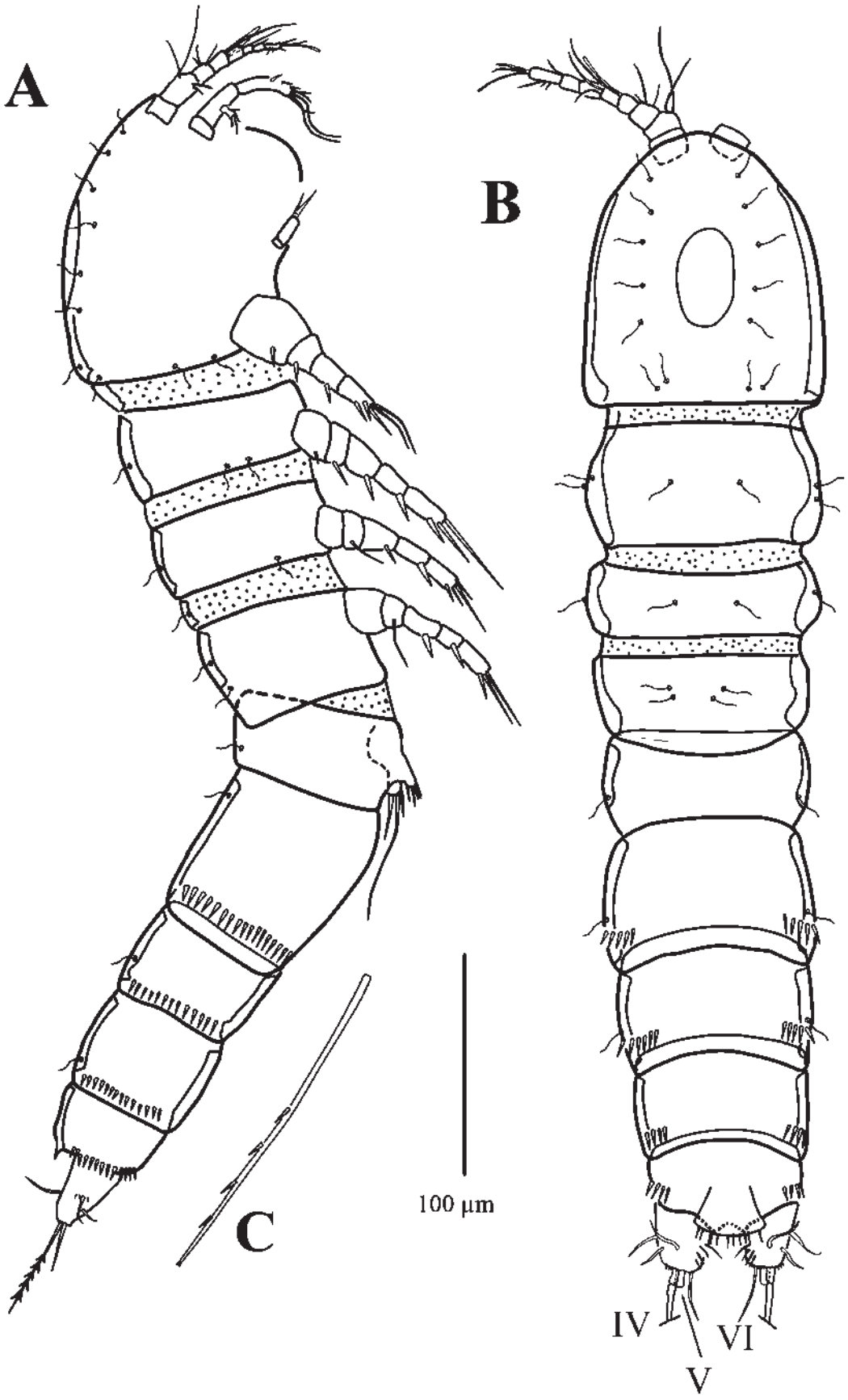

FIGURE 2. *Maraenobiotus wellsi* **sp. nov.**, female: A, habitus of holotype, lateral; B, habitus of holotype, dorsal; C, caudal seta V of paratype. Seta V (distal to breaking plane) missing in holotype.

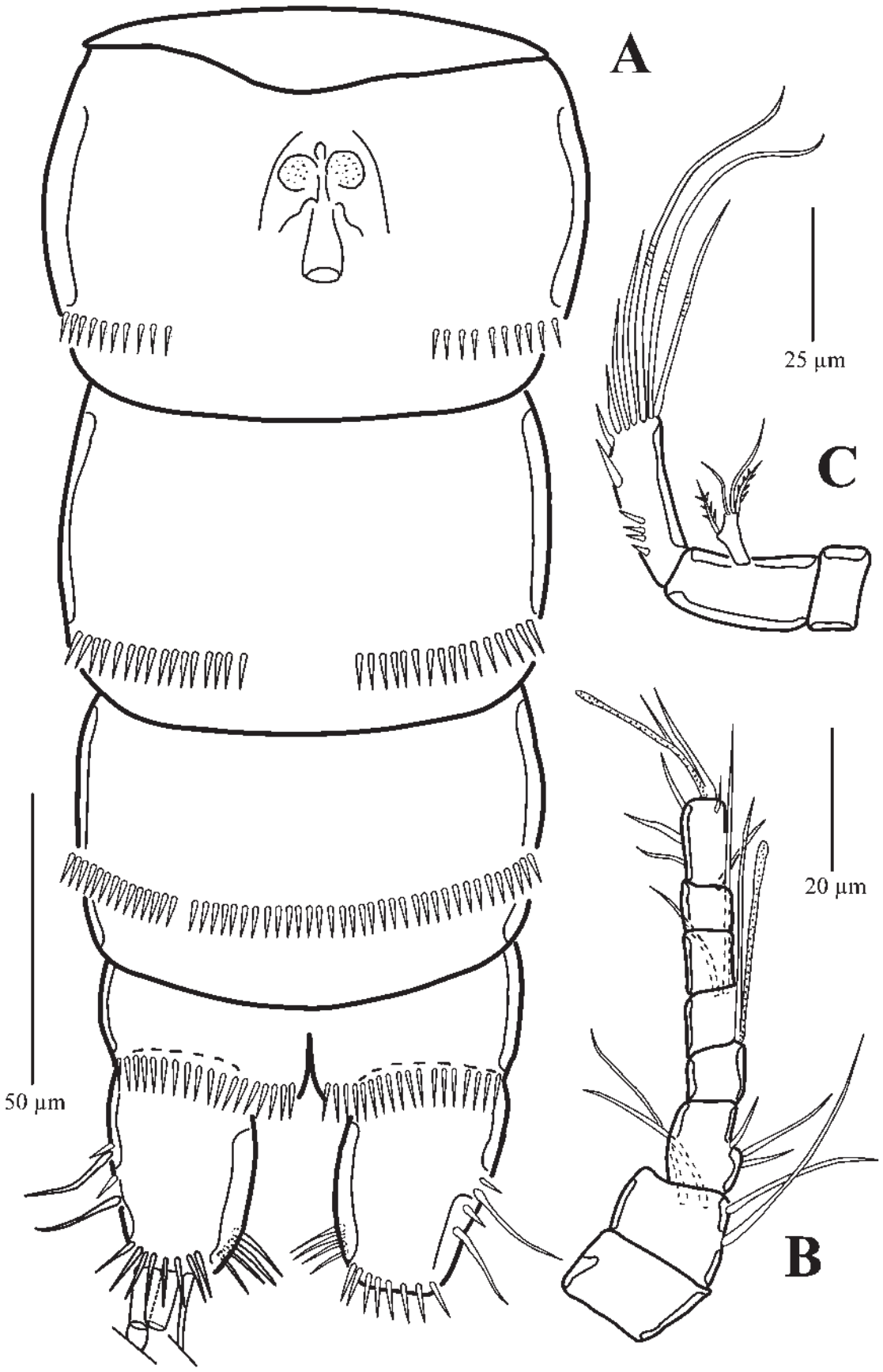

FIGURE 3. *Maraenobiotus wellsi* **sp. nov.**, female (holotype): A, genital double-somite and abdominal somites, ventral view; B, antennule; C, antenna.

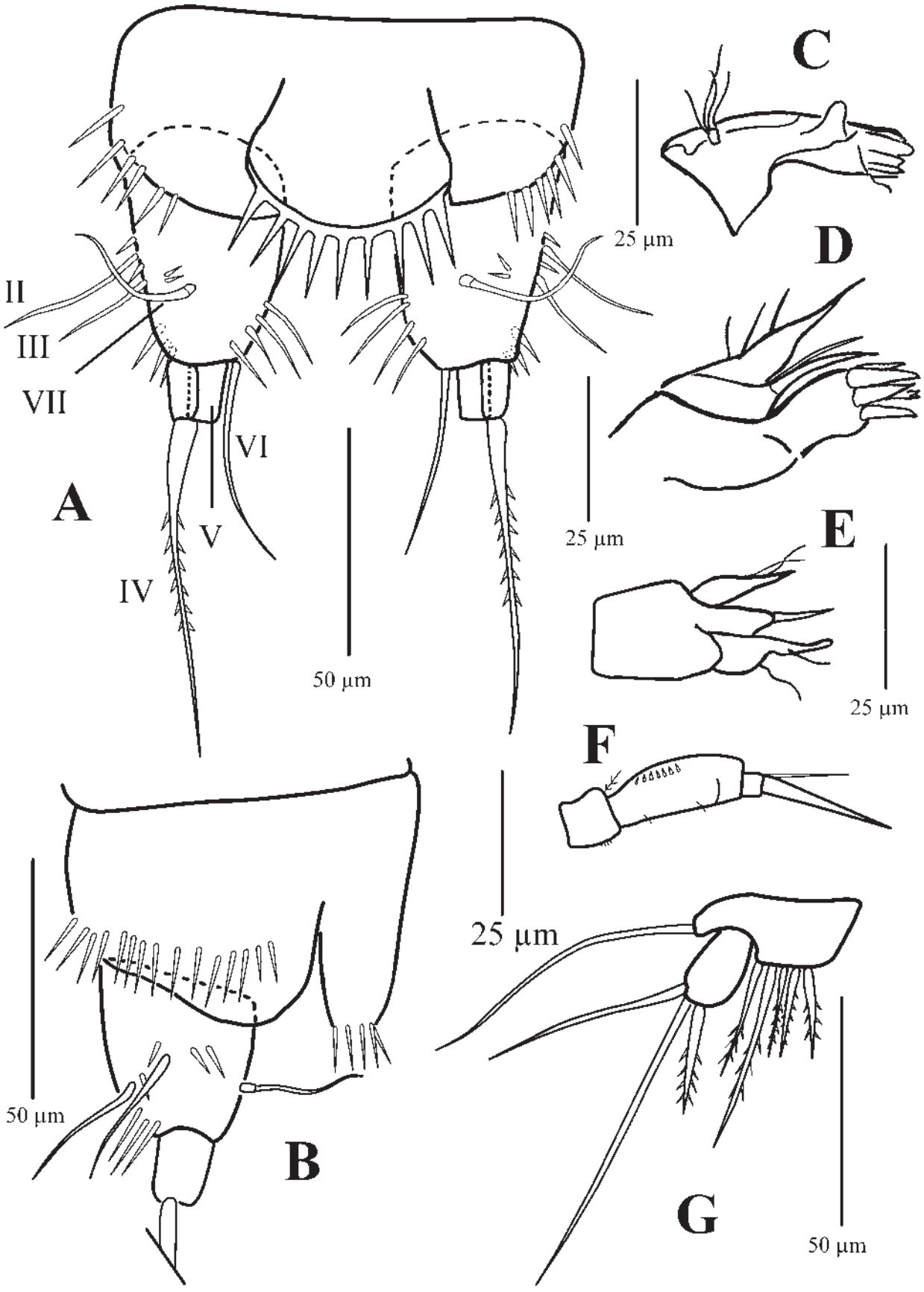

FIGURE 4. *Maraenobiotus wellsi* **sp. nov.**, female (holotype): A, anal somite and caudal rami, dorsal view; B, anal somite and caudal rami, lateral view; C, mandible; D, maxillule; E, maxilla; F, maxilliped; G, leg 5.

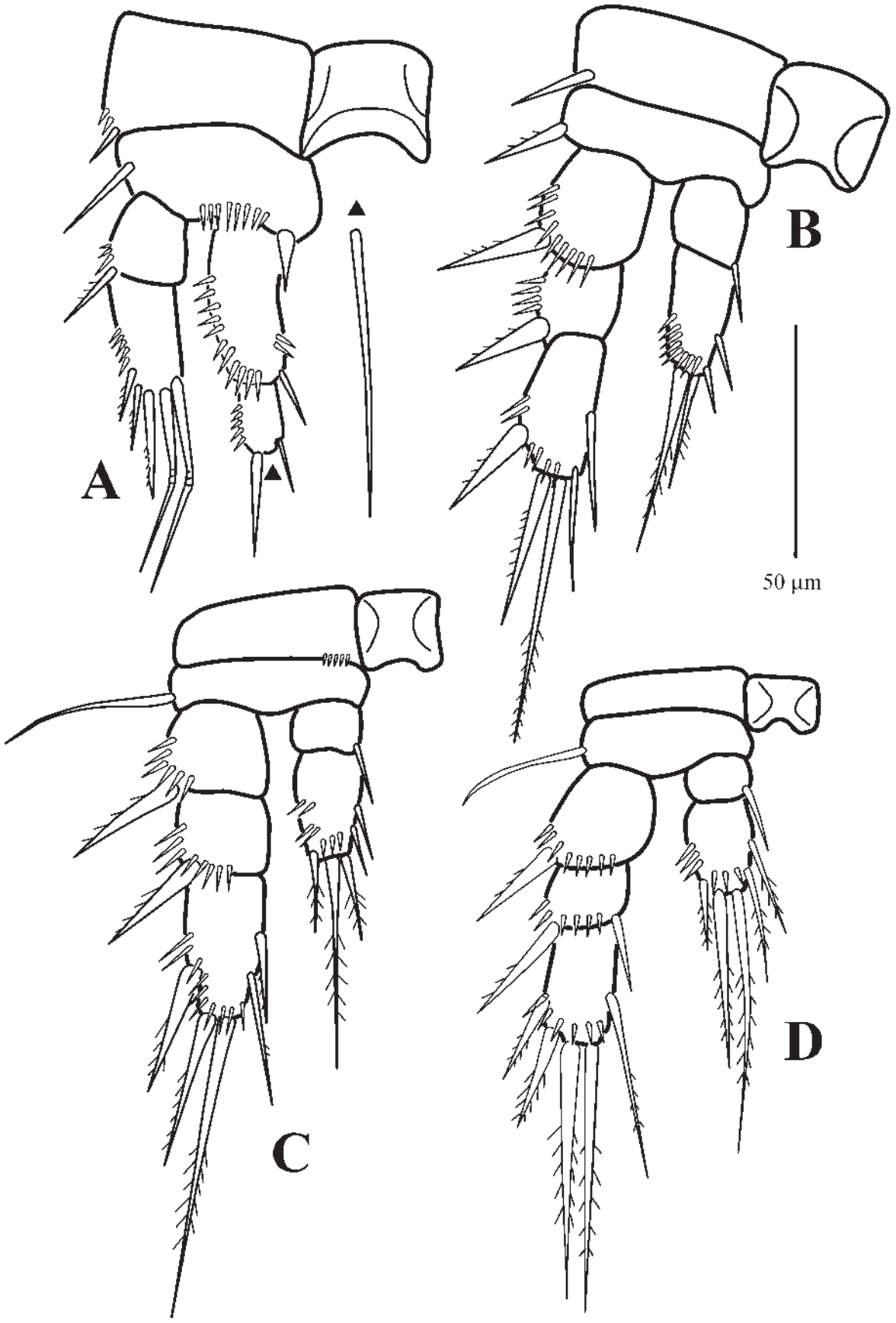

FIGURE 5. *Maraenobiotus wellsi* **sp. nov.**, female (holotype): A, leg 1 (arrow indicates position of the inner seta in the apical margin of second segment of endopod); B, leg 2; C, leg 3; D, leg 4; all frontal view.

Leg 4 (Fig. 5D): smaller than leg 3, coxa without armature and ornamentation. Basis with naked seta on outer margin. Exopod 3-segmented; first segment with unipinnate robust spine on outer margin; second segment with unipinnate robust spine on outer margin and naked slender spine on inner margin; third segment, outer margin with two bipinnate robust spines inserted distally, apical margin with two bipinnate, almost identical, setae, inner margin with one long bipinnate seta. Endopod 2-segmented; first segment as in leg 3; second segment with five bipinnate setae: outer margin with one seta inserted subapically, apical margin with two setae, inner seta 1.5 times longer than outer seta, inner margin with two setae inserted at 1/2 and 3/4 of segment.

Leg 5 (Fig. 4G): intercoxal sclerite fused to baseoendopods. Baseoendopods separated at base, lateral margin with one long naked seta; endopodal lobe short, not reaching beyond 1/3 of length of exopod, bearing five bipinnate spines with following length ratios: 1.25 (outermost):1.5:1.0:1:0:1.0 (innermost). Exopod oval, 1.7 times longer than wide, with three elements: outer margin with one naked seta inserted subapically, apical margin with one naked outer seta and one bipinnate inner spine, seta 2.9 times longer than spine.

Leg 6: not observed.

Remark. The sample also contained one copepodid specimen (length 388 μm) (UPTC–L 0002) (antennule 7-segmented, anal somite longer than preceding somite), with caudal rami bearing all 6 caudal setae). As the holotype was missing the distal portion of seta V (beyond the breaking plane, possibly broken during sorting), its existence could be confirmed by its presence in the copepodid.

Discussion

The female specimens described here show characters which allow us to attribute them to the genus *Maraenobiotus*, particularly their small size, somites with posterior margin not denticulated, antennules 8-segmented, maxilla without endopod, anal operculum rounded and armed with spinules, leg 1 with 2-segmented exopod and endopod, legs 2 to 4 with 3-segmented exopod, bearing an outer spine on first and second segments and with 2-segmented endopod, leg 5 with baseoendopod not prominent, bearing 3–6 setae and exopod distinct, bearing 3–4 setae. The armature of leg 5 can be interpreted as composed by major elements. In *Maraenobiotus wellsi* **sp. nov.**the baseoendopod of leg 5 bears five spines, and its exopod bears two setae and one spine.

Species of the genus *Maraenobiotus* are found all around the world, with the exception of Australia. The genus comprises 27 species and 14 subspecies currently recognized (Walter & Boxshall 2019).

On the American continent the genus is now represented by ten species (Fig. 1), two of which, *M. brucei brucei* and *M. insignipes insignipes*, are Holarctic in distribution (Defaye & Dussart 2011) and three are known only from the northern Nearctic region in Greenland (*M. husmanni* Flössner, 1988, *M. subterraneus* Flössner, 1988) and Canada (*M. canadensis* Flössner, 1992). The southernmost record of the genus in North America corresponds to a report of *M. insignipes insignipes* in a gravel stream in Virginia (Palmer *et al*. 1995). In their chapter on Copepoda of the North American Freshwater Invertebrates, Williamson & Reid (2001) included only *M. brucei brucei*, *M. insignipes insignipes* and *M. canadensis* as species of the genus known at that time in North America. Löffler (1972, 1973) mentioned the presence of the genus *Maraenobiotus* in high mountain regions of Central America, unfortunately without species determination.

In South America five species are now known: *M. australis* in Argentina (Tierra del Fuego), *M. naticochensis* Delachaux, 1917, *M. fontinalis* Harding, 1955 and *M. fontinaloides* Löffler, 1960 from high mountain localities of the Andean Cordillera of Peru, and *M. wellsi* **sp. nov.** in Colombia (Fig. 1).

Species of the genus inhabit small lentic and lotic water-bodies, springs and subterranean environments. Some of them also live in semi-terrestrial habitats such as mosses (Löffler 1968; Flössner 1992; Apostolov 2001) or wet forest soils (Janetzky *et al*. 1996). In the Vienna forest in Austria, *M. truncatus* has been observed in debris (E. Christian, Univ. of Agriculture, Vienna; 2014, pers. commn).

The discussion below is restricted to morphological differences between the new species and both its congeners in South America, and species recorded worldwide from wet mosses. As the male of *M. wellsi* **sp. nov.** is unkown, the morphological comparison refers only to the morphology of the female. Setae and spines of legs are referred as "major elements".

1) Table 2 compares the morphological traits of the South American species. The new species can be distinguished mainly by the size, shape and ornamentation of the caudal rami, the ornamentation of the anal operculum, the armature of legs 1–4 and the segmentation of the antennary exopod.

Except for *M. australis*, for which the size is unknown, the Colombian species (575 µm), together with the Peruvian *M. fontinalis* (560 µm), seem to be the smallest in length compared with the other South American species (*M. fontinaloides* 690–940 µm, *M. naticochensis* 800 µm). *M. wellsi* **sp. nov.** is similar to *M. australis* in the reduced dorsal ornamentation of the abdominal somites, the number of spinules on the anal operculum, and the segmentation and armature of the mandibular exopod. It can be distinguished by the shape of the caudal rami (conical in *M. wellsi* **sp. nov.**, rectangular in *M. australis*) and the armature of legs 3 and 4. *M. wellsi* **sp. nov.** shows five major elements on the last segment of the endopod of leg 3 (four in *M. australis*) and five on the exopod of leg 4 (six in *M. australis*). The anal operculum of *M. australis* is shorter than the anal somite, whereas in *M. wellsi* **sp. nov.** it reaches the posteriormost margin of the same somite (Fig. 4A–B). The ornamentation of the caudal rami also differs in these species: there are no spinules on the ventral surface along the distal margin of the rami in *M. australis*, whereas *M. wellsi* **sp. nov.** has a row of eight spinules in that position (Fig. 3A).

Maraenobiotus wellsi can easily be distinguished from *M. naticochensis* by the ornamentation of the anal operculum (naked in the latter, spinulose in the former), the morphology of the caudal rami (width:length ratio, 1:1.5 in *M. naticochensis*, 1:1.3 in *M. wellsi* **sp. nov.**), its shape (barrel-like in *M. naticochensis*, conical in *M. wellsi* **sp. nov.**) and the origin of the caudal seta IV in relation to seta V (ventral in *M. naticochensis*, dorsal in the new species). They show also differences in the armature of legs 1 and 2. *M. naticochensis* shows two major elements on the last endopod segment of leg 1 (three in *M. wellsi* **sp. nov.**) and three on the last endopod segment of leg 2 (four in *M. wellsi* **sp. nov.**).

In relation to *M. fontinaloides*, the new species shows a higher number of spinules on the anal operculum (20) than *M. wellsi* **sp. nov.** (9), and differs in the armature of legs 2 and 3. *Maraenobiotus wellsi* **sp. nov.** bears a higher number of major elements on the last segment of exopod of leg 2 (five elements), whereas *M. fontinaloides* only bears four major elements. The latter species has more major elements (six) on the last segments of leg 3 exopod (five in *M. wellsi* **sp. nov.**). In addition, the caudal rami on *M. fontinaloides* is longer (1:1.5–2.0 times as long as wide) than in the new species (1:1.3) and barrel-shaped (conical in *M. wellsi* **sp. nov.**). Setae IV and V of *M. fontinaloides* are strongly inflated at their base immediately distal to their insertion points on the caudal rami; in *M. wellsi* **sp. nov.**, seta IV is slightly inflated at its base distal to its breaking plane; no information can be provided about the distal part of seta V because it was lost during sorting (in the copepodid, seta V is incompletely developed).

Maraenobiotus wellsi **sp. nov.** can be differentiated from *M. fontinalis* by the morphology of the caudal rami (as long as wide in *M. fontinalis*, 1:1.3 in *M. wellsi* **sp. nov.**), the armature of leg 3 (last segment of exopod with six major elements in *M. fontinalis*, five in *M. wellsi* **sp. nov.**), and the number of segments of the antennary exopod (two in *M. fontinalis*, one in *M. wellsi* **sp. nov.**). Moreover, the number of spinules on the anal operculum of *M. fontinalis* is much higher (20 in *M. fontinalis*, 9 in *M. wellsi* **sp. nov.**).

2) The following 11 species and subspecies of *Maraenobiotus* have – like the new species –been recorded from wet mosses: *M. australis, M. brucei brucei*, *M. brucei himalayensis*, *M. canadensis, M. cuspidatus*, *M. insignipes elgonensis, M. insignipes nepalensis, M. kinabaluensis*, *M. truncatus, M. vejdovskyi* and *M. zschokkei.* We therefore considered it important to analyse the morphological differences between *M. wellsi* **sp. nov.** with the other species adapted to live in this environment. The species mentioned above are distinguished from the new species mainly by the morphology of leg 1, armature of legs 2–4, ornamentation of the abdominal somites, segmentation and armature of the mandibular palp (Table 3), and the form of the apical caudal setae.

The morphological differences between *M. australis* and *M. wellsi* **sp. nov.** were already indicated above. The new species can be distinguished from *M. vejdovskyi* and *M. zschokkei* by the different number of major elements on the distal exopodal segment of leg 3 (six in *M. vejdovskyi* and *M. zschokkei*, five in *M. wellsi* **sp. nov.**) and the distal endopodal segment of leg 4 (four in *M. vejdovskyi* and *M. zschokkei*, five in *M. wellsi* **sp. nov.**). In addition, both *M. vejdovskyi* and *M. zschokkei* carry four elements on the baseoendopod of leg 5 compared to five in *M. wellsi* **sp. nov.**

In relation to *M. brucei brucei*, there is a clear difference in the distribution of the dorsal spinule row on the abdominal somites compared with *M. wellsi* **sp. nov.** In the former species, these rows are present with middorsal gaps, whereas in the new species they are almost absent. Moreover, the size of the caudal rami is twice longer that wide in *M. brucei brucei* (1.3 times longer than wide in *M. wellsi* **sp. nov.**). The chaetotaxy of leg 2 also differs: in *M. brucei brucei* the third exopodal segment bears four setae and spines, whereas five in *M. wellsi* **sp. nov.**

TABLE 2. Morphological characters distinguishing the species of *Maraenobiotus* (females) of South America (elements = setae or spines, exp = exopod, enp = endopod); body length excluding caudal ramus setae; * according to Apostolov (2001: Figs. 12–15).

Species	*australis*	*fontinalis*	*fontinaloides*	*naticochensis*	*wellsi* **sp. nov.**
Distribution	Argentina	Peru	Peru	Peru	Colombia
Body length (in µm)	?	560	690 –940	800	575
Caudal ramus shape	rectangular	conical	barrel-shaped	barrel-shaped	conical
Caudal ramus seta IV, origin in relation to seta V	ventral, partially displaced	dorsal, partially displaced	dorsal, totally displaced	ventral, totally displaced	dorsal, partially displaced
Caudal ramus width:length ratio	1.3	1.0	1.5–2.0	1.5	1.3
Anal operculum number of spinules	9	20 or more	20	0	9
Antennary exopod: number of segments /number of elements on apical segment	1/4	2/4	?	?	1/4
Legs 1–4, distal segment of rami, number of elements:					
Leg 1, exp : enp	5 : 3	5 : 3	5 : 3	5 : 2	5 : 3
Leg 2, exp : enp	5 : 3 (4)*	5 : 4	4 : 4	5 : 3	5 : 4
Leg 3, exp : enp	5 : 4*	6 : 5	6 : 5	?	5 : 5
Leg 4, exp : enp	6 : 5 *	5 : 5	5 : 5	?	5 : 5

TABLE 3. Morphological characters distinguishing the species of *Maraenobiotus* (females) found in mosses (elements = setae or spines, exp = exopod, end = endopod; first abdominal somite = genital double-somite); * somite 1 with 1, 2 or 3 rows of spinules, complete or with gap(s); somite 2 with complete row of spinules or with gap(s); somite 3, row of spinules almost absent; ** according to Apostolov 2001: Figs. 12–15).

	australis	*brucei brucei*	*brucei himalayensis*	*canadensis*	*cuspidatus*	*insignipes elgonensis*
Distribution	Argentina	Holarctic	India, Nepal, Turkey	Canada	Mongolia	Kenya
Mandibular palp: number of segments/ number of setae	1/4	1/5	2/5	1/3	2/5	2/5
Abdomen, dorsal rows of spinules	almost absent	with central gap	complete on somites 1 & 2	absent	with central gap	complete, with gap(s) or absent
Leg 1, length first endopodal segment	reaches end of exp-2	reaches ½ of exp-2	reaches ½ of exp-2	reaches ½ of exp-2	reaches end of exp-2	?
Leg 2–4, distal segment, number of elements:						
Leg 2, exp : enp	5 : 3**	4 : 4	4 : 4	5 : 4	5 : 4	5 : 4
Leg 3, exp : enp	5 : 4**	5 : 5	5 : 5	6 : 4	6 : 5	6 : 5
Leg 4, exp : enp	6 : 5**	5 : 5	5 : 5	5 : 4	5 : 4	5 : 5

TABLE 3. (Continued)

	insignipes nepalensis	*kinabaluensis*	*truncatus*	*vejdovskyi*	*zschokkei*	*wellsi* **sp. nov.**
Distribution	Nepal	Malaysia (Borneo)	Europe	Palearctic	Central Europe (Alps)	Colombia
Mandibular palp: number of segments/ number of setae	2/5	2/5	1/2–3	1/5	1/3	1/4
Abdomen, dorsal rows of spinules	very variable*	complete	?	absent	absent on somite 1, complete on somites 2 & 3	almost absent
Leg 1, length first endopodal segment	?	reaches ¾ of exp-2	?	reaches ¾ of exp-2	reaches ½ of exp-2	reaches end of exp-2
Leg 2–4, distal segment, number of elements:						
Leg 2, exp : enp	5 : 4	5–6 : 4	5 : 4	5 : 4	5 : 4	5 : 4
Leg 3, exp : enp	6 : 5	6 : 5	6 : 5	6 : 5	6 : 5	5 : 5
Leg 4, exp : enp	5 : 5	5 : 3–4	5 : 4	5 : 4	5 : 4	5 : 5

Compared with *M. brucei himalayensis,* there is a difference in the armature of leg 5: *M. brucei himalayensis* bears four setae and spines on the basoendopod, whereas five in *M. wellsi* **sp. nov.** Moreover, the mandibular palp of *M. brucei himalayensis* is 2-segmented bearing five setae, whereas in *M. wellsi* **sp. nov.** it is represented by one segment and four setae.

Maraenbiotus wellsi **sp. nov.** can easily be differentiated from *M. truncatus* by the morphology of the caudal setae IV, V and VI, which are truncate in the latter species. In relation to *M. cuspidatus*, the morphology of the caudal seta VI is different in both species: it is S-shaped at its base in *M. cuspidatus* while it is straight in *M. wellsi* **sp. nov.** Moreover, the mandibular palp is 2-segmented and bears five setae in the former species, whereas it is one-segmented and bears four setae in the new species. Compared with *M. kinabaluensis*, the new species can be distinguished by the ornamentation of the abdominal somites (row of spinules dorsally continuous in *M. kinabaluenisis*, almost absent in *M. wellsi* **sp. nov.**) and by the armature of the mandibular palp (five setae in *M. kinabaluensis*, four in *M. wellsi* **sp. nov.**).

The new species can be distinguished from *M. insignipes elgonensis* and *M. insignipes nepalensis* by the segmentation and armature of the mandibular palp (one-segmented with four setae in the new species, 2-segmented with five setae in both latter taxa) and the armature of leg 3 (last segment of exopod with six major elements in both subspecies of *M. insignipes*, five in *M. wellsi* **sp. nov.**).

Finally, in *M. canadensis* the first endopodal segment of leg 1 is shorter (reaching middle of the second exopodal segment) than in *M. wellsi* **sp. nov.** (reaching apical margin of exopod). Moreover, the armature of both rami of leg 3 is different in *M. canadensis* (exopod with six elements and endopod with four), whereas in *M. wellsi* **sp. nov.** exopod and endopod each bear five elements.

The discovery of this new species in the wet tropical high mountain zone or "páramo" represents the first record of the genus *Maraenobiotus* in Colombia. In South America, it was reported until now only from southern Argentina and central Peru. The "páramo" region of the Americas is a cold habitat rich in submerged and semi-terrestrial mosses, particularly of the genus *Sphagnum*. This makes it highly likely to find other species of the genus *Maraenobiotus* there. As the "páramo" ecosystem extends from Ecuador to Venezuela and Costa Rica (Gaviria 1993), species of the genus *Maraenobiotus* can no doubt be found in these countries too. An effort should be made to find the male of *M. wellsi* **sp. nov.** as well.

Moreover, the present record of the canthocamptid *Epactophanes richardi* Mrázek, 1893 in the same habitat as *M. wellsi* **sp. nov.** constitutes the second record of that species in Colombia. *Epactophanes richardi* was collected previously from "páramo" soils of Monserrate (4°38'N, 71°02'W) at 3,230 m.a.s.l (Sturm 1978; Gaviria & Aranguren 2007) near the city of Bogotá and it is probably widely distributed in that environment.

Identification key for American species of *Maraenobiotus*

Females

1	Leg 2, exopod 3 with 4 setae and spines	2
-	Leg 2, exopod 3 with 5 setae and spines	3
2	Caudal rami dorsally without sigmoid chitinous thickening; caudal setae IV and V bulbous at their base	*M. fontinaloides*
-	Caudal rami dorsally with sigmoid chitinous thickening; caudal setae IVand V straight, not bulbous at their base	*M. brucei brucei*
3	Anal operculum without spinules	*M. naticochensis*
-	Anal operculum with spinules	4
4	Leg 3, distal exopodal segment with six setae and spines	5
-	Leg 3, distal exopodal segment with five setae and spines	6
5	Leg 3, second endopodal segment with five setae and spines; leg 5, baseoendopod with five elements	9
-	Leg 3, second endopodal segment with four setae and spines; leg 5, baseoendopod with four elements	*M. canadensis*
6	Leg 4, distal exopodal segment with six setae and spines	*M. australis*
-	Leg 4, distal exopodal segment with five setae and spines	7
7	Leg 4, second endopodal segment with four setae and spines; leg 1, proximal endopodal segment reaching to 2/3 length of second exopodal segment	*M. subterraneus*
-	Leg 4, second endopodal segment with five setae and spines; leg 1, proximal endopodal segment extending to apical margin of second exopodal segment	8
8	Caudal ramus 2.0–2.5 times longer than broad, dorsally with sigmoid chitinous thickening, innen margin unarmed, seta VI thick, basally leaf-like enlarged; mandibular palp 2-segmented	*M. husmanni*
-	Caudal ramus 1.3 times longer than broad, dorsally without chitinous thickening, inner margin armed with four spinules inserted subapically, seta VI thin, bassally not enlarged; mandibular palp 1-segmented	*M. wellsi* **sp. nov.**
9	Caudal ramus conical, as long as broad; leg 1, proximal endopodal segment reaching to at least apical margin of second exopodal segment	*M. fontinalis*

- Caudal ramus barrel shaped, 1.7 times longer than broad; leg 1, proximal endopodal segment reaching to middle of second exopodal segment . . . . . *M. insignipes insignipes*

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