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On some deep-sea Stenheliinae from the Gulf of California and the west coast of the Baja California Peninsula (Mexico): *Wellstenhelia euterpoides* sp. nov., and *Wellstenvalia wellsi* gen. et sp. nov. (Copepoda: Harpacticoida: Miraciidae)

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Abstract

At present, only 11 species of harpacticoid copepods have been described from the deep sea of the Gulf of California and the west coast of the Baja California Peninsula. These efforts had until recently been focused exclusively on the families Ameiridae Boeck, Argestidae Por, and Rhizothrichidae Por. Preliminary analyses revealed also an important contribution of the subfamily Stenheliinae Brady (Miraciidae Dana) to the overall species richness and diversity of deep-sea benthic copepods from the west coast of the Baja California Peninsula, and the central and southern Gulf of California. One new species of the genus *Wellstenhelia* Karanovic & Kim, 2014, *We. euterpoides* **sp. nov.**, and one new genus and species, *Wellstenvalia wellsi* **gen. et sp. nov.**, are herein described from sediment samples taken at eight sampling stations in the west coast of the Baja California Peninsula and in the central and southern Gulf of California. *Wellstenhelia euterpoides* **sp. nov.** seems to be closely related to *We. euterpe* Karanovic & Kim, 2014 with which it shares the reduced armature complement of the baseoendopod of the female fifth leg. The so far monotypic genus *Wellstenvalia* **gen. nov.** was found to be closely related to *Muohuysia* Özdikmen, 2009 and *Wellstenhelia.* Some comments on the relationships between the new genus proposed here and other stenheliin genera and species are provided as a contribution towards the monophyly of the subfamily.

Key words: Mexico, new taxa, taxonomy

Introduction

At present, only 11 species of harpacticoid copepods have been described from the deep sea of the Gulf of California and the west coast of the Baja California Peninsula (Gómez & Conroy-Dalton 2002; Gómez & Díaz 2017; Gómez 2018a, b, c, d). These efforts had until recently been focused exclusively on the families Ameiridae Boeck, Ancorabolidae Sars, Argestidae Por, and Rhizothrichidae Por. Preliminary analyses revealed also an important contribution of the subfamily Stenheliinae Brady (Miraciidae Dana) to the overall species richness and diversity of deep-sea benthic copepods collected during four oceanographic cruises on board research vessel "El Puma" (Universidad Nacional Autónoma de México) in the west coast of the Baja California Peninsula, and the central and southern Gulf of California (Fig. 1). The subfamily Stenheliinae is currently composed of thirteen genera, *Anisostenhelia* Mu & Huys, 2002 (monotypic), *Beatricella* Scott, 1905 (monotypic), *Cladorostrata* Tai & Song, 1979 (two species), *Delavalia* Brady, 1869 (50 species), *Itostenhelia* Karanovic & Kim, 2014 (two species), *Lonchoeidestenhelia* Gómez, 2000 (monotypic), *Melima* Por, 1964 (five species), *Muohuysia* Özdikmen, 2009 (monotypic), *Onychostenhelia* Itô, 1979 (two species), *Pseudostenhelia* Wells, 1967 (three species), *Stenhelia* Boeck, 1865 (eight species), *Wellstenhelia* Karanovic & Kim, 2014 (eight species), and *Willenstenhelia* Karanovic & Kim, 2014 (six species). It is a predominantly shallow-water taxon and only few representatives, all of the genus *Delavalia*, are known from the deep sea (>200 m depth), *D. diegensis* (Thistle & Coull, 1979) (San Diego Trough, 1200 m depth) (Thistle & Coull 1979), *D. noodti* (Schriever, 1982) and *D. islandica* (Schriever, 1982) (Island-Faroer-

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Ridge, 500 m depth) (Schriever 1982), *D. lima* (Becker & Schriever, 1979) (Peru Trench, 920 m depth) (Becker & Schriever 1979), and *D. gundulae* (Willen, 2003) (Edison Seamount, 1440 m–1446 m depth) (Willen 2003). An additional species, *Stenhelia* "spec 6" (most probably an undescribed species of *Delavalia*) was also recorded by Willen (2003) from the Angola Basin at 5,389 m depth. Similarly, in their appendix A, George *et al*. (2014) reported four as yet unidentified species of *Delavalia* found in sediment samples taken from the Angola Basin at 5,389 m depth, of which one could be conspecific to Willen's (2003) *Stenhelia* "spec 6". Several attempts have been made to understand the origin of deep-sea stenheliins. Mu & Huys (2002) argued that the presence of a characteristic two-segmented P1 ENP (ENP2 reduced and with three elements of which the apical one is multiplumose and flagellate) and the long caudal rami in some deep-sea species of *Delavalia* (*e.g. D. diegensis*, *D. noodti*, *D. islandica*) and in some shallow water species (*e.g. D. longipilosa* (Lang, 1965), *D. coineauae* (Soyer, 1971), *D. intermedia* (Marinov & Apostolov, 1981)) could indicate that the deep-sea lineage originated from shallow water ancestral stocks. Willen (2003) confirmed the origin of deep-sea stenheliins and noted that deep-sea species of her *S. longicaudata*-group (*D. noodti*, *D. islandica*, *D. lima*, and *D. diegensis*) are related to some shallow-water species of the same species-group (*e.g. D. longipilosa*, *D. longicaudata* (Boeck, 1873), *D. coineauae*, *D. intermedia*, and *D. mastigochaeta* (Wells, 1965)), and that *D. gundulae*, which belongs to her predominantly shallow-water *normani*-group, could represent a different colonization event of deep-sea habitats. The report of other deep-sea stenheliin genera from the Gulf of California and adjacent waters, previously known only from shallow locations seems to further confirm the origin of deep-sea stenheliins, and are the subjects of other contributions in this volume.

The genus *Wellstenhelia* is currently known from Korea and China only. Here we describe a new species, *We. euterpoides* **sp. nov.**, from the deep-sea of the west coast of the Baja California Peninsula and Gulf of California. Additionally, we propose a new genus, *Wellstenvalia* **gen. nov.**, closely related to *Muohuysia* and *Wellstenhelia*, to accommodate a new species found in sediment samples from the same region. Some comments towards the monophyly of the subfamily are given.

This is the seventh contribution on deep-sea harpacticoids and the first of a series of papers on deep-sea stenheliins from the Gulf of California and adjacent waters dedicated to Prof J. B. J Wells.

Materials and methods

Sediment samples for meiofaunal analyses were taken in August 2000 at the Southern Gulf of California from Carmen basin to off Nayarit State, in February 2007 at the Southern Trough of Guaymas Basin, in July-August 2012 off the west coast of Baja California Sur, and in May 2014 off the west coast of Baja California, during Talud IV, X, XV and XVIB cruises, respectively (Fig. 1), on board the research vessel "El Puma" of the Universidad Nacional Autónoma de México (UNAM). Sediment samples were collected at depths ranging from 520 m to 2,120 m during Talud IV cruise using a multiple sediment corer equipped with six cores of 30 cm in length and sampling surface of 3.9 cm^2, and from 379 m to 1902 m during Talud X cruise, from 325 m to 2,000 m during Talud XV cruise, and from 750 m to 2,037 m during Talud XVIB cruise, using a box corer from which triplicate sub-samples were taken with 69 cm^2 cores of 20 cm in length. The upper 3 cm layer of sediment was preserved in 70% alcohol (Talud IV cruise) and in 96% alcohol (Talud X, XV and XVIB cruises), and sieved through 500 and 38 µm sieves to separate macro- and meiofauna. Meiofauna was sorted at a magnification of 40X using an Olympus SZX12 stereomicroscope equipped with DF PLAPO 1X objective and WHS10X eyepieces, and harpacticoid copepods were stored separately in 1 ml vials with 96% ethanol. Illustrations and figures were made from whole individuals and its dissected parts using a Leica DMLB microscope equipped with L PLAN 10X eyepieces, N PLAN 100X oil immersion objective, and drawing tube. The dissected parts were mounted on separate slides using lactophenol as mounting medium. Huys & Boxshall (1991) was followed for general terminology.

Abbreviations used in the text: acro, acrothek; ae, aesthetasc; BENP, baseoendopod; ENP, endopod; EXP, exopod; EXP (ENP)1 (2,3), first (second, third) exopodal (endopodal) segment; *MW*, *Muohuysia*-*Wellstenhelia* lineage; *MWW*, *Muohuysia*-*Wellstenhelia*-*Wellstenvalia* lineage; P1-P6, first to sixth legs; *WW*, *Wellstenhelia*-*Wellstenvalia* lineage.

The type material was deposited in the Copepoda collection of the Instituto de Ciencias del Mar y Limnología, Unidad Académica Mazatlán (ICML-EMUCOP).

The map showing the sampling locations (Fig. 1) where the new taxa were found was prepared with SimpleMappr (Shorthouse 2010).

Following Recommendation 25A (ICZN, 1999), the genera *Wellstenhelia* and *Willenstenhelia* were abbreviated *We.* and *Wi.*, and *Muohuysia* and *Melima* were abbreviated *Mu.* and *Me.*, respectively, when used in a binomen.

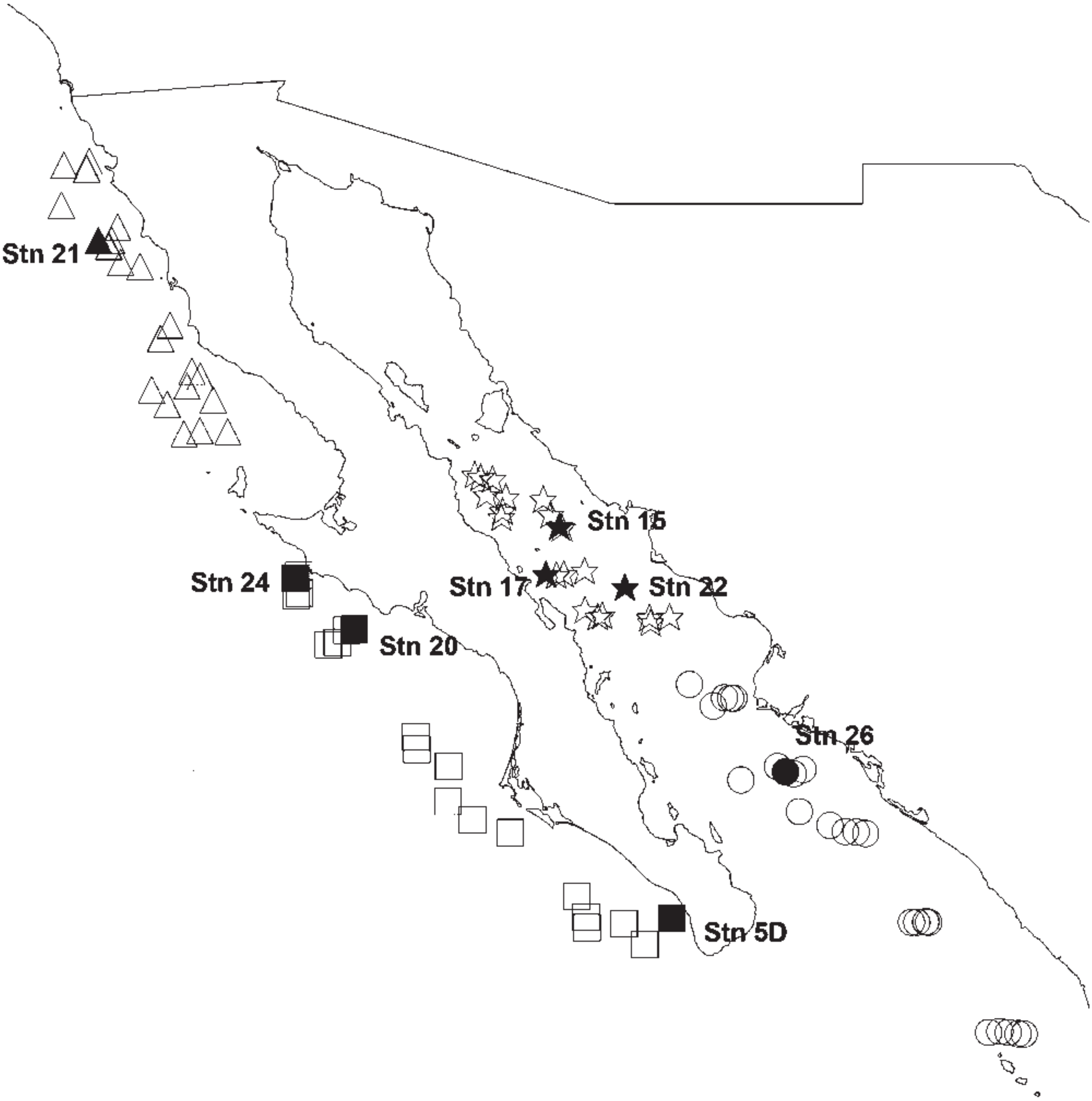

FIGURE 1. Sampling locations visited during oceanographic cruises Talud IV (circles), Talud X (stars), Talud XV (squares) and Talud XVIB (triangles). Full figures represent positive collection of *Wellstenhelia euterpoides* **sp. nov.** (Stn 22—Talud X—, and Stn 20 and 24—Talud cruise XV) and *Wellstenvalia wellsi* **sp. nov.** (Stn 15 and 17—Talud X—, and Stn 5D and 24—Talud XV—, and Stn 21—Talud XVIB).

Systematics

Order Harpacticoida Sars, 1903

Family Miraciidae Dana, 1846

Subfamily Stenheliinae Brady, 1880

Genus *Wellstenhelia* Karanovic & Kim, 2014

Type species. *Wellstenhelia calliope* Karanovic & Kim, 2014 (by original designation).

Other species. *Wellstenhelia clio* Karanovic & Kim, 2014; *W. erato* Karanovic & Kim, 2014; *W. euterpe* Karanovic & Kim, 2014; *W. euterpoides* **sp. nov.**; *W. melpomene* Karanovic & Kim, 2014; *W. qingdaoensis* (Ma & Li, 2011); *W. hanstroemi* (Lang, 1948); *W. bocqueti* (Soyer, 1971).

Wellstenhelia euterpoides sp. nov.

(Figs. 2–7)
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Type locality. Off La Bocana, Baja California Sur (Eastern Tropical Pacific), Mexico; Talud XV cruise, sampling station 20 (26.54278°N, 113.93889°W); depth, 479 m; organic carbon content, 3.18%; organic matter content, 5.47%; sand 47.08%; clay, 7.75%; silt, 45.16%.

Other localities. Off San Pablo Bay, Baja California Sur (Eastern Tropical Pacific), Mexico; Talud XV cruise, sampling station 24 (27.11806°N, 114.6008°W); depth, 1039 m; organic carbon content, 3.26%; organic matter content, 5.60%; sand 35.53%; clay, 7.95%; silt, 56.52%.

Central Guaymas Basin, Gulf of California, Mexico; Talud X cruise, sampling station 22 (27.0167°N, 110.8944°W); depth, 1642 m; organic carbon content, 4.27%; organic matter content, 7.35%; sand, 9.56%; clay, 11.34%; silt, 79.10%.

Specimens examined. From the type locality. Adult female holotype preserved in alcohol (EMUCOP-020812-03) from which the left antenna was dissected and mounted onto one slide; August 2, 2012; coll. S. Gómez.

From other localities. Adult female paratype dissected and mounted onto eight slides (EMUCOP-010812-09) from sampling station 24 (Talud XV cruise; August 1, 2012; coll. S. Gómez), and dissected female paratype mounted onto six slides (EMUCOP-130207-03) from sampling station 22 (Talud X cruise; February 13, 2007; coll. S. Gómez).

Etymology. The Ancient Greek sufix *εἶδος*, eîdos, meaning likeness makes reference to the resemblance of the new species with *W. euterpe.*

Description of female. Total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 490 µm to 580 µm (*n* = 2); habitus pyriform, widest at posterior end of cephalothorax, tapering posteriad (Fig. 2A).

Prosome consisting of cephalothorax with fused first pedigerous somite, and second to fourth free pedigerous somites. Cephalothorax slightly longer than wide, with hyaline fringe broad and smooth. Free pedigerous somites without expansions laterally nor dorsally; without spinular ornamentation; integument smooth and weakly sclerotized; hyaline fringe of second and third pedigerous somites broad and smooth, of fourth pedigerous somite narrower; width of second to fourth pedigerous somites decreasing progressively.

Urosome (Fig. 2B–D) consisting of fifth pedigerous somite (first urosomite), genital double-somite (genital—second urosomite—and third urosomites fused), two free urosomites, and anal somite; urosomites without expansions laterally nor dorsally; integument weakly sclerotized.

Fifth pedigerous somite visibly narrow; with surface sensilla as shown (Fig. 2B–C); without spinular ornamentation; hyaline fringe narrow.

Second and third urosomites completely fused ventrally (Fig. 2D) forming genital double-somite, with dorsolateral trace of division (Fig. 2B–C) between original segments; 1.2 times as long as wide, widest part measured proximally close to P6; anterior half of genital double-somite with few sensilla and two sets of spinules dorsally as shown (Fig. 2B), ventrally without surface ornamentation; posterior half of genital double-somite with dorsolateral sensilla and spinules as shown (Fig. 2B–C), ventrally with two sensilla and medial row of spinules (Fig. 2D), posterior hyaline fringe broad and smooth. Genital complex hardly distinguishable; copulatory pores not exposed; paired genital apertures located ventrolaterally and covered by P6.

Fourth urosomite with few sensilla dorsally (Fig. 2B), with few sensilla and some spinules laterally (Fig. 2C), and with two sensilla and medial row of spinules ventrally (Fig. 2D); posterior hyaline fringe broad and smooth.

Fifth urosomite without sensilla or spinules (Fig. 2B–D).

Anal somite three times as wide as long (Fig. 2A–B); with spinules around joint of caudal rami (Fig. 2A–D);

ventrally (Fig. 2D) with spinules along each side of medial cleft and with two pores. Anal operculum semicircular, flanked by one sensillum on each side, posterior margin with transverse row of small spinules (Fig. 2A–B).

Caudal rami elongate, about 6.4 times as long as wide (Fig. 2A–E) and as long as fourth, fifth and anal somite combined; with small spinules at base of setae I and II, and III (Fig. 2E); with seven elements (Fig. 2A–G); seta I a spine, ventral to seta II, both subdistal on lateral margin; seta III subdistal, arising ventrally; seta IV and V distal, with fracture plane, the former seemingly normal and with outer spinules, the latter rat-like and bipinnate; seta VI issuing at inner distal corner; dorsal seta VII triarticulate at base, situated subdistally close to inner margin.

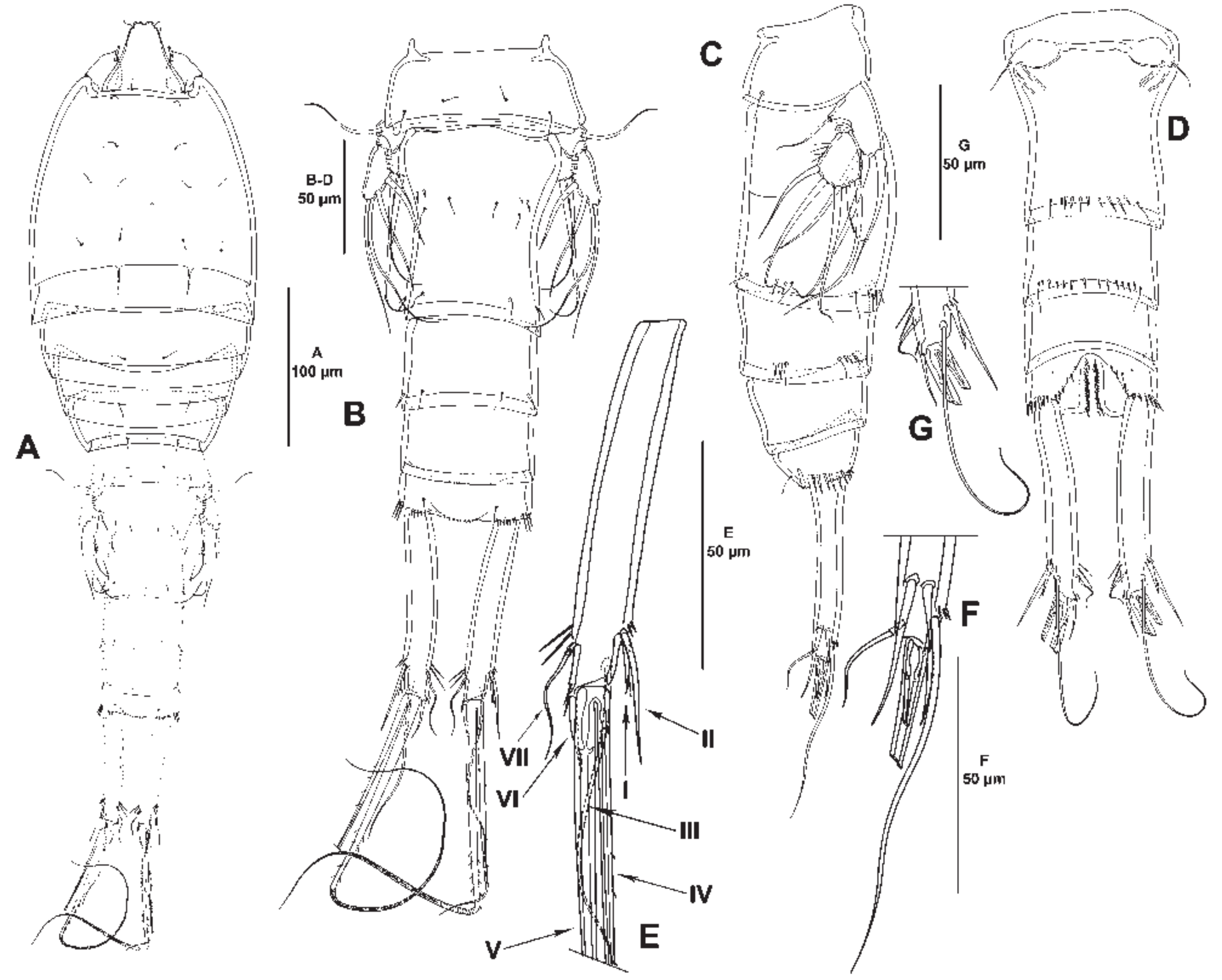

FIGURE 2. *Wellstenhelia euterpoides* **sp. nov.**, female: A, habitus, dorsal; B, urosome, dorsal; C, urosome, lateral; D, urosome, ventral (P5-bearing somite omitted); E, right caudal ramus, dorsal; F, distal part of left caudal ramus, lateral; G, distal part of left caudal ramus, ventral.

Rostrum (Fig. 3A) trapezoidal, not fused to cephalothorax, bifid, with two subdistal sensilla, and with a proximal dorsal pore.

Antennule (Fig. 3B) eight-segmented; all segments smooth, except for spinular row on first segment, the latter without pore. All setae smooth; second segment at least with one (some setae detached during dissection), third segment with one seta with fracture plane; seventh and eighth segment with two articulated setae. Armature formula: 1(1); 2(12?); 3(9); 4(4 + (1 + ae)), 5(2); 6(4); 7(4); 8(4 + acro). Acrothek consisting of two setae and one minute aesthetasc fused basally.

Antenna (Fig. 3C–D). Coxa short, with some outer long slender spinules, and some inner small ones (Fig. 3D). Allobasis with remain of original division between basis and first endopodal segment, as long as free endopodal segment, with long inner spinules proximally, and smaller ones close to base of exopod, with one pinnate abexopodal seta arising midway inner margin. Free endopodal segment elongate, with inner spinules as shown, with two outer subdistal frills; armature composed of two lateral spines and two accompanying slender setae, distally with one inner apical spine, three apical geniculate setae and one slender element, and one outer distal pinnate element fused basally to slender seta. Exopod three-segmented; third segment longest, about eight times as long as wide, and 1.3 times as long as first segment, second segment smallest; first and third segment with spinules as shown, second segment without spinular ornamentation; first and second segment with one seta, third segment with one proximal and three distal setae, none of which fused basally.

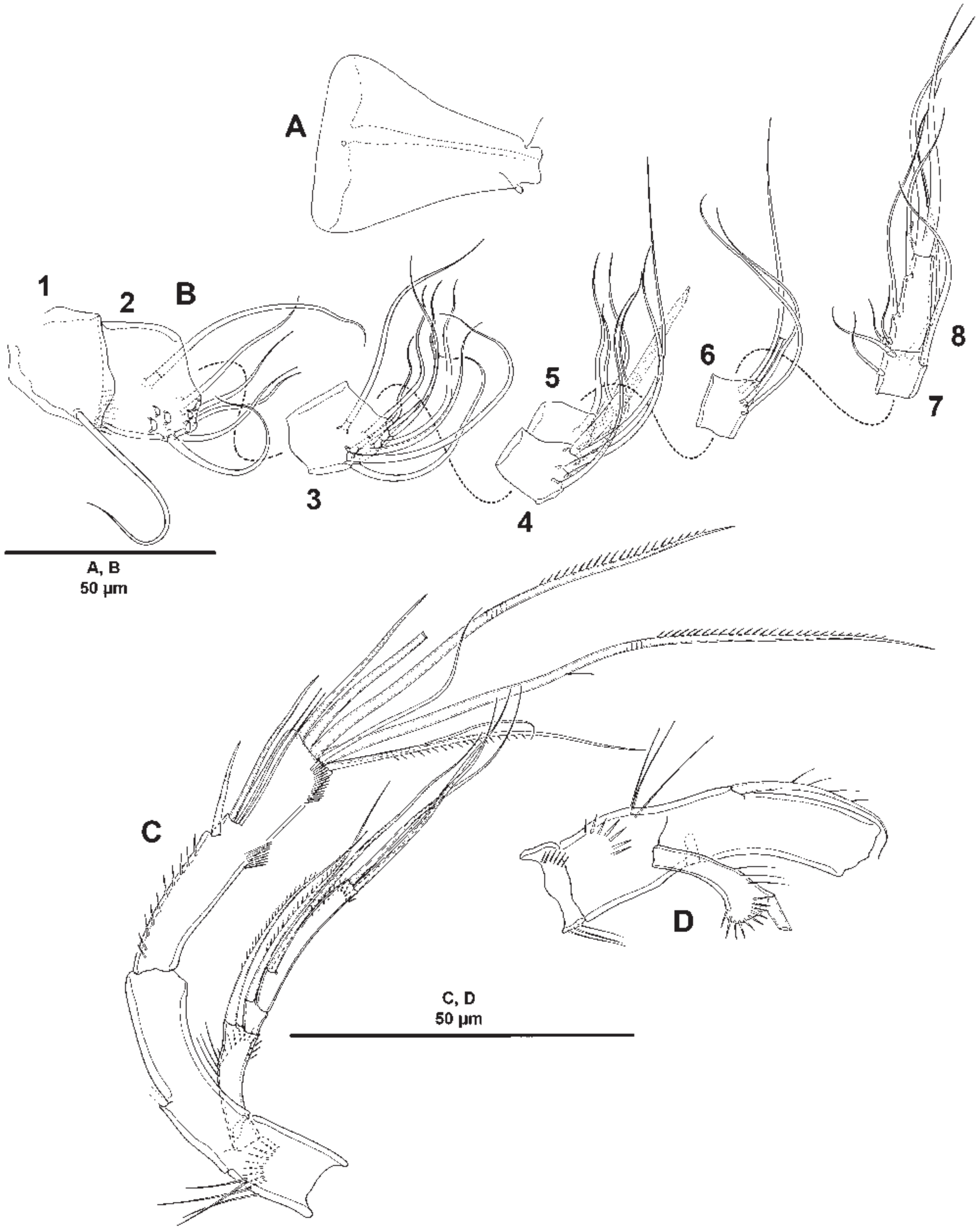

FIGURE 3. *Wellstenhelia euterpoides* **sp. nov.**, female: A, rostrum, dorsal; B, antennule, each actual segment numbered; C, antenna; D, coxa, allobasis and first exopodal segment of the antenna, another view.

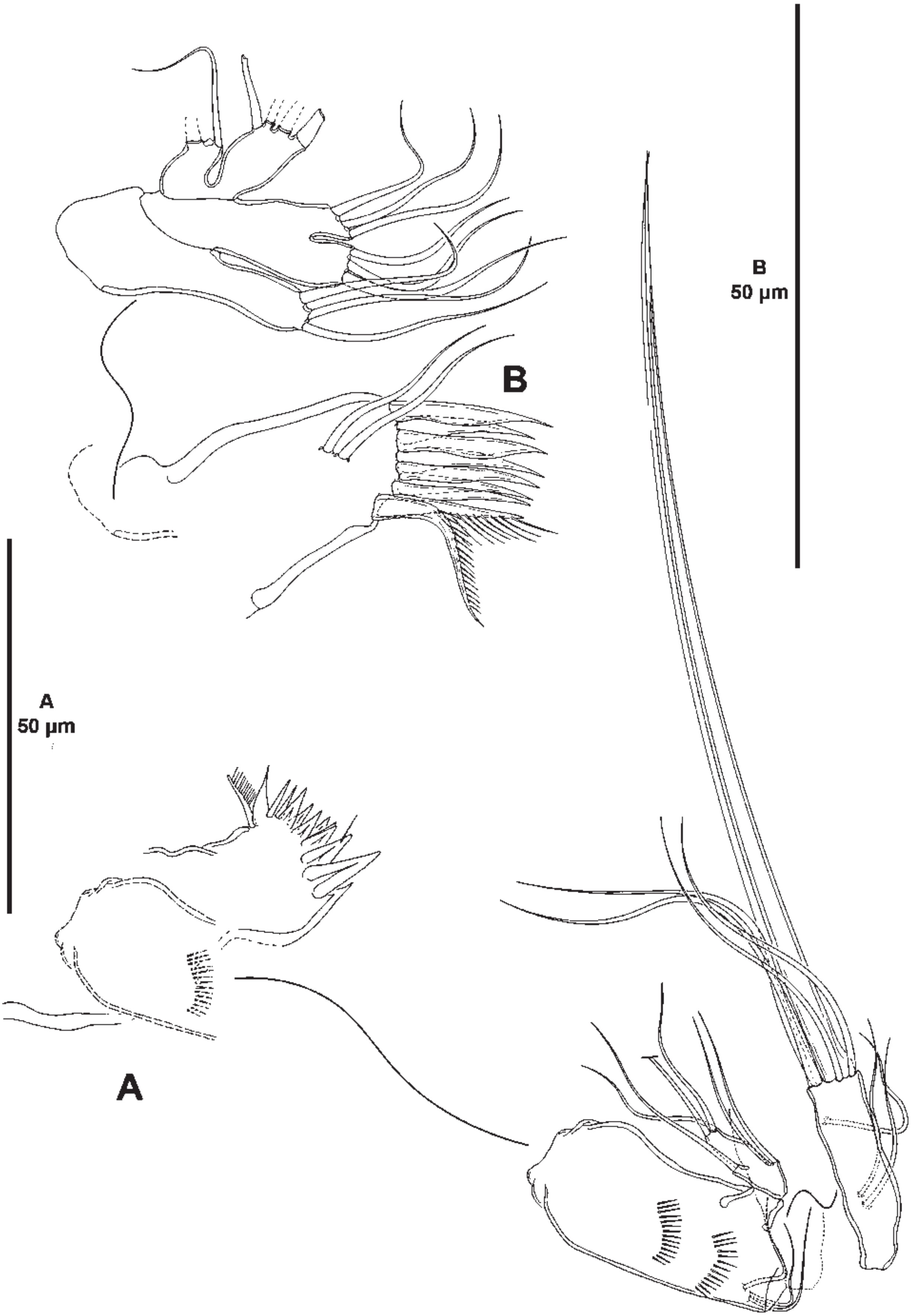

FIGURE 4. *Wellstenhelia euterpoides* **sp. nov.**, female: A, mandible; B, maxillule.

Mandible (Fig. 4A). Coxa relatively short. Gnathobase wide; ventral distal corner produced into small sharp semi-hyaline process; with two strong and several smaller teeth, two spinules, one pyriform spine, and one bipinnate seta. Basis with wide base, rather rectangular, with some medial and some subdistal spinules as shown, with three distal outer setae. Exopod arising from short pedestal, elongate, about three times as long as wide, and 0.4 times as long as basis, tapering distally, with three lateral and three apical slender setae none of which fused basally. Endopod recurved, twisted over exopod, with three lateral setae, and five distal elements (four slender setae and one long element fused to endopod and with hyaline flange).

Maxillule (Fig. 4B). Arthrite of praecoxa with two surface setae and eight distal elements one of which strongly spinulose, and one lateral spinulose recurved seta. Coxa with three setae. Basis with two endites, each apparently with three setae. Exopod and endopod fused basally, separated from basis, one-segmented; endopod larger than exopod, with four setae; exopod small, with two setae.

Maxilla (Fig. 5A). Large syncoxa with spinular ornamentation as shown; with three endites; proximal endite smallest, bilobate, each lobe with one naked and one pinnate seta; middle and distal endites elongate, the latter slightly longer, with two spinulose and one naked seta each. Basis drawn out into strong spinulose claw, additionally with strong spine and two slender setae. Endopod rather elongate, with five (or six?) slender setae.

Maxilliped (Fig. 5B) subchelate. Syncoxa elongate, rectangular; about 2.2 times as long as wide, with slender inner spinules, with two subdistal setae of which one spinulose and one bare, and one distal bare seta arising from long pedestal. Basis visibly shorter than syncoxa, oval, with slender outer spinules, with one anterior and one posterior inner spinular row as depicted; with two distal setae subequal in length. Endopod one-segmented, with one claw-like element and one seta.

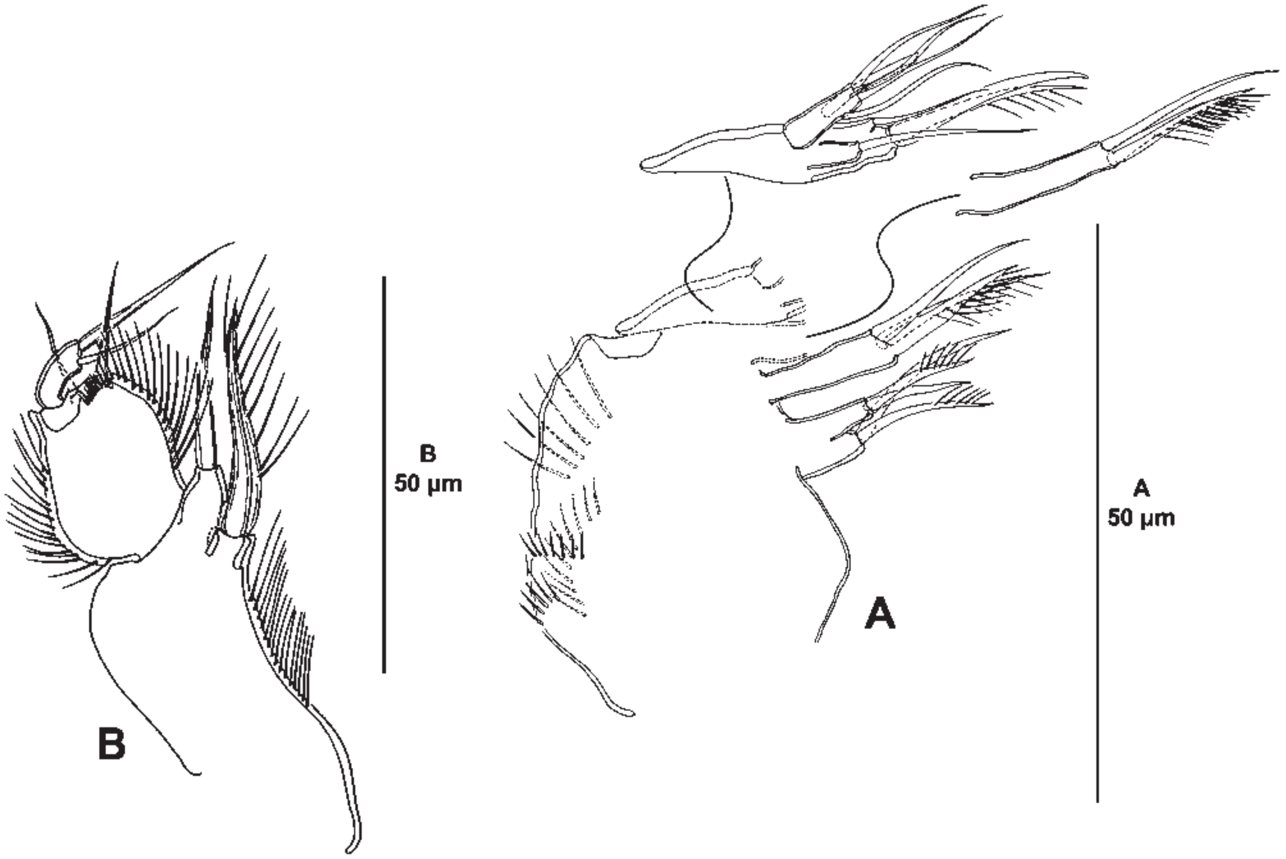

FIGURE 5. *Wellstenhelia euterpoides* **sp. nov.**, female: A, maxilla; B, maxilliped.

P1 (Fig. 6A). Intercoxal sclerite (not shown) transversely elongate, nearly straight, without surface ornamentation. Coxa massive, nearly as long as wide, with spinular ornamentation as shown. Basis with spinules proximally on inner margin, at base of inner and outer spines, and between rami. Exopod three-segmented, reaching distal third of ENP2; exopodal segments subequal in length; all segments without outer nor inner acute distal processes, no pores detected on exopodal segments; EXP1 and EXP2 with longitudinal row of outer spinules, EXP1 without,

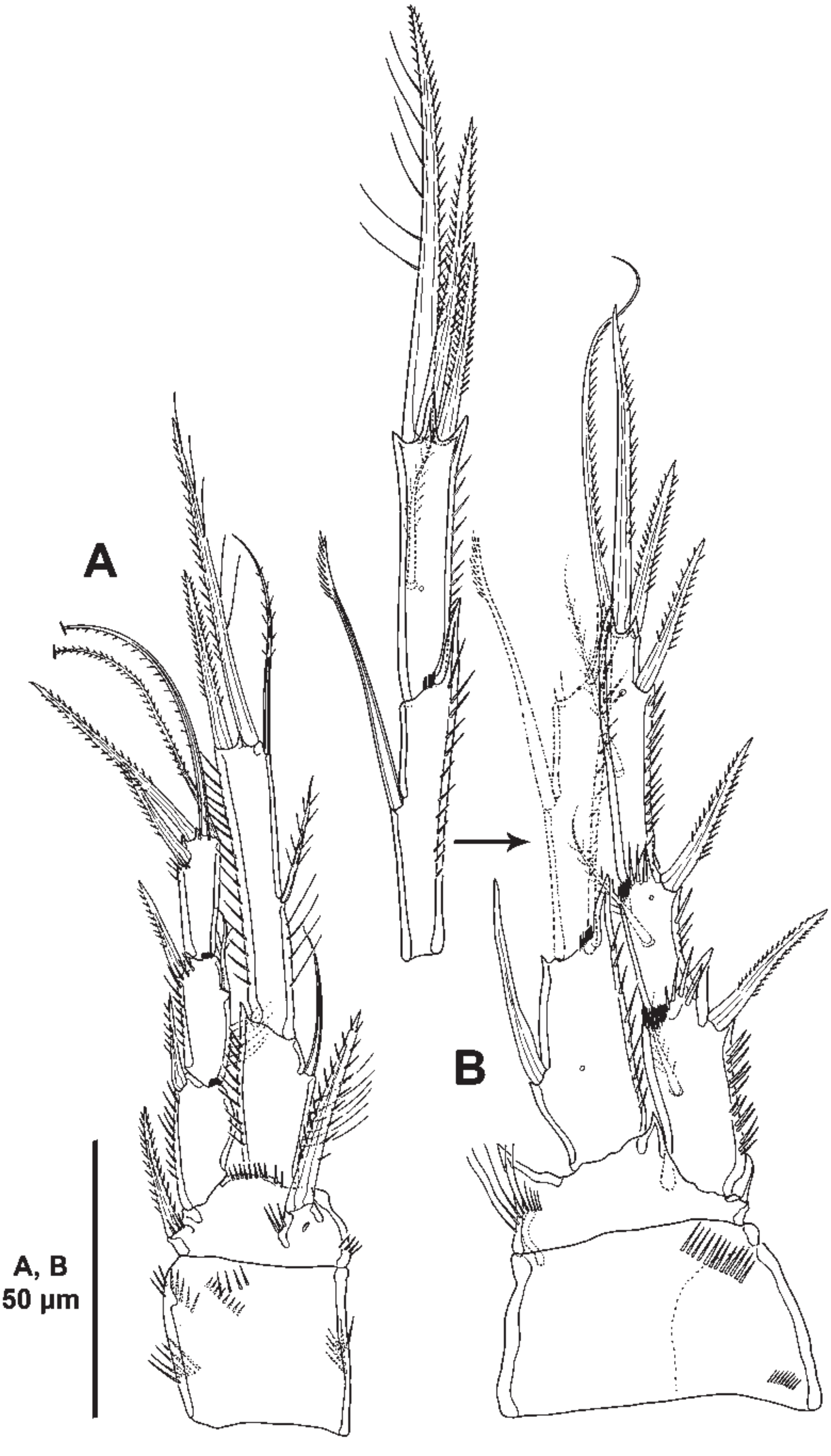

FIGURE 6. *Wellstenhelia euterpoides* **sp. nov.**, female: A, P1, anterior; B, P2, anterior.

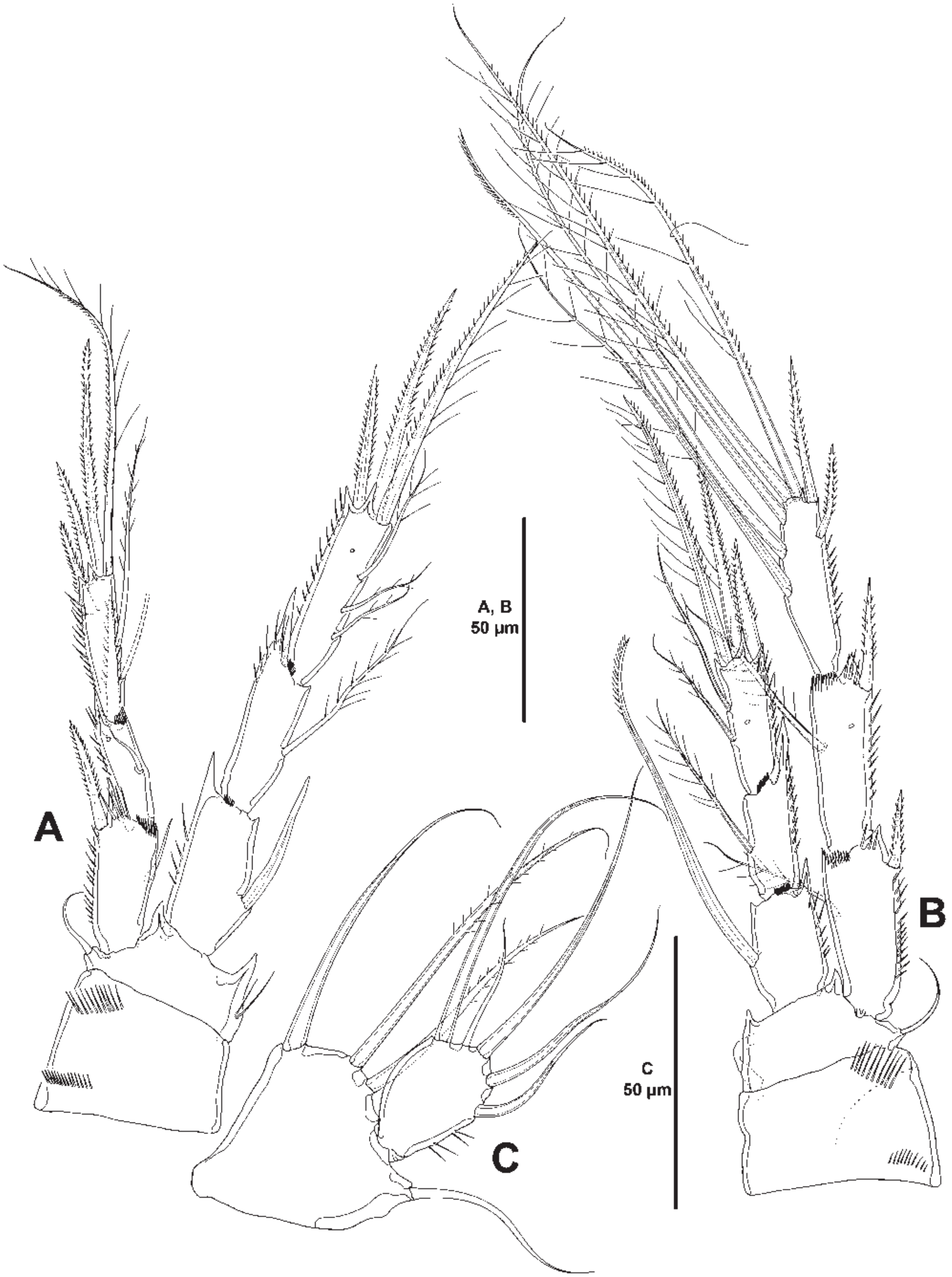

FIGURE 7. *Wellstenhelia euterpoides* **sp. nov.**, female: A, P3, anterior; B, P4, anterior; C, P5, anterior.

EXP2 with inner seta; EXP3 with some spinules at base of proximal outer element, with two outer spines and two apical setae. Endopod two-segmented, longer than exopod; no pores detected on exopodal segments; ENP1 with small outer acute process, with longitudinal row of outer spinules, and with one inner seta; ENP2 elongate, about twice as long as ENP1, with inner slender spinules proximally and with longitudinal row of stronger spinules along inner margin, with one inner proximal, one inner distal and one distal seta, and one outer distal spine.

P2–P3 (Figs. 6B, 7A). Intercoxal sclerite (not shown) not transversely elongate, trapezoidal, with strong pointed process on distal outer corners, without surface ornamentation. Coxa with outer spinular rows proximally and subdistally. Basis with outer seta (of P2 visibly shorter); with acute process at inner distal corner and between rami, the former larger; with slender long spinules on inner margin. Exopod three-segmented, reaching slightly beyond ENP2; EXP1 and EXP3 longest; EXP1 and EXP2 with outer acute distal process, with longitudinal row of outer spinules and with inner distal frill, with inner seta; EXP1 without, EXP2 with subdistal outer pore; EXP3 with outer spinules as shown, of P3 without, of P2 with medial pore on distal third, with one (P2) or two (P3) inner setae, with two apical elements, and two outer spines. Endopod three-segmented, longer than EXP; ENP1 shortest, ENP2 and ENP3 of about the same length; ENP1 and ENP2 with outer acute and inner small process distally, with longitudinal row of outer spinules, with small spinules at base of outer process; P2 ENP1 with, P3 ENP1 without pore, P2 ENP2 and P3 ENP2 without pore, P2 ENP3 and P3 ENP3 with medial subdistal pore; ENP1 with inner strong spine-like element, ENP2 with one inner seta as depicted, ENP3 with one (P2) or three (P3) inner setae, two apical elements and one outer apical spine.

P4 (Fig. 7B). Intercoxal sclerite (not shown) not transversely elongate, trapezoidal, with strong pointed process on distal outer corners, without surface ornamentation. Coxa and basis as in P3 but basis seemingly without inner ornamentation and inner process less developed. Exopod three-segmented, longer than endopod; exopodal segments of about the same length; EXP1 and EXP2 with outer acute distal process, with longitudinal rows of outer spinules and with inner distal frill, EXP1 without, EXP2 with outer subdistal pore, both segments with inner seta; EXP3 with small outer spinules, without pore, with three inner setae, two apical elements, and two outer spines. Endopod three-segmented, barely reaching beyond EXP2; ENP1 shortest, ENP2 and ENP3 of about the same length; ENP1 and ENP2 with outer acute and small inner process distally, with longitudinal row of outer spinules, with small spinules at base of outer process, without pore, inner element of ENP1 a long stiff element, ENP2 with inner seta; ENP3 with longitudinal row of outer spinules and with medial pore subdistally, with two inner setae, two apical elements and one outer spine.

Setal formula of swimming legs as follows:

	P1	P2	P3	P4
EXP	0,1,022	1,1,122	1,1,222	1,1,322
ENP	1,121	1,1,121	1,1,321	1,1,221

P5 (Fig. 7C). Baseoendopod pentagonal; endopodal lobe well-developed, reaching middle of EXP, with three setae. Exopod oval, 1.4 times as long as wide; with some outer small spinules proximally; with five setae, of which second innermost shortest.

P6 (Fig. 2D) a minute flap covering ventrolateral genital aperture; fused to somite; without surface ornamentation; with one slender seta.

Male. Unknown.

Genus *Wellstenvalia* gen. nov.

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Type species. *Wellstenvalia wellsi* **gen. et sp. nov.**

Etymology. The genus is dedicated to Prof. J. B. J. Wells for his contribution to the systematics and taxonomy of harpacticoid copepods. His last name is prefixed to an anagram of the generic names *Stenhelia* and *Delavalia*.

Diagnosis. Stenheliinae. Rostrum discrete, strongly bifid, with a proximal dorsal pore, without spinular ornamentation. Female antennule eight-segmented; first segment with proximal pore, with distal corner produced into blunt process; all setae smooth except for pinnate seta on first, second, and last segments; second segment with two, third segment with one seta with fracture plane; sixth segment with two, seventh segment with one articulated seta. Male antennule nine-segmented, haplocer, with geniculation between third and fourth, and sixth and seventh segments; first segment without pore, distal corner less produced than in female; seemingly none seta with fracture plane; eighth segment with two, ninth segment with one articulated seta; aesthetasc present on third, fifth, and last segments. Antenna with allobasis; exopod three-segmented, first and second segment with one, third segment with three setae; free endopodal segment with two lateral spines and two slender accompanying setae, distally with one inner apical spine, three apical geniculate setae and one slender element, and one outer distal pinnate element fused basally to one slender seta. Mandible with coxa relatively short; gnathobase without medial seta and with ventral distal corner produced into small sharp semi-hyaline process; basis with three distal outer setae; exopod arising from short pedestal, with six setae, endopod recurved, twisted over exopod, with three lateral setae, and five distal elements, of which longest element fused to endopod and with hyaline flange in middle part. Maxillulary basis with two endites; proximal endite with four, distal endite with three slender setae, exopod and endopod not fused, one-segmented, endopod with four, exopod with two setae. Maxilla with three endites; proximal endite with two, middle and distal endites with three elements each; basis drawn out into strong spinulose claw, additionally with one spine and two slender setae; endopod one-segmented, with six setae. Maxilliped subchelate; syncoxa with three, basis with two elements; endopod one-segmented, with one claw-like element and one seta. Female and male P1 with intercoxal sclerite transversely elongated and without surface ornamentation; exopod three- endopod two-segmented; armature formula of exopod/endopod 0,1,022/1,121. Female P2–P4 with three segmented rami; intercoxal sclerites with pointed distal processes; basis with inner acute pointed projection decreasing in size from P2 to P4; P2 ENP1 with inner strong element fused to segment, of P3 ENP1 discrete, of P4 ENP1 a long stiff seta; armature formula of exopod/endopod (P2) 1,1,123/1,1,121, (P3) 1,1,323/1,1,321, (P4) 1,1,323/1,1,221; male sexual dimorphism in P1 expressed in the relative length and width of EXP and ENP, and in the coarser spinular ornamentation; in P2 expressed in the somewhat shorter inner process of basis, ornamentation of setae and spines, and in the two-segmented ENP of which original division between ENP2 and ENP3 indicated by remains of distal outer and inner processes of former ENP2; in P3 expressed in the less developed inner process of basis, and in more slender setae on ENP3; in P4 expressed in the ornamentation of setae and spines and coarser outer spinules on EXP and ENP. Female P5 endopodal lobe with four setae of which outermost shortest and set closely to adjacent seta, innermost seta normal; exopod with five setae; male P5 EXP with one outer short spine, one medial long spine and one inner slender seta, both baseoendopods fused medially, each with one outer small seta and one inner long element. Female P6 a minute flap without surface ornamentation, with one slender seta; male P6 pair asymmetric, one of them functional and separated from somite, the other fused and not functional, each with one outer seta and one inner spine. Caudal rami elongate, about five times as long as wide and nearly four times as long as anal somite; with seven elements; seta I minute, ventral to seta II, both arising laterally on distal third, setae IV and V not fused, the former without, the latter with fracture plane.

Wellstenvalia wellsi **sp. nov.**

(Figs. 8–19)

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Type locality. Off San Pablo Bay, Baja California Sur (Eastern Tropical Pacific), Mexico; Talud XV cruise, sampling station 24 (27.11806°N, 114.6008°W); depth, 1039 m; organic carbon content, 3.26%; organic matter content, 5.60%; sand 35.53%; clay, 7.95%; silt, 56.52%.

Other localities. Off Todos Santos/El Pescadero, Baja California Sur (Eastern Tropical Pacific), Mexico; Talud XV cruise, sampling station 5D (23.295°N, 110.3642°W); depth, 665 m; organic carbon content, 5.83%; organic matter content, 10.03%; sand 11.04%; clay, 5.99%; silt, 82.96%.

Off La Bocana, Baja California Sur (Eastern Tropical Pacific), Mexico; Talud XV cruise, sampling station 20 (26.54278°N, 113.93889°W); depth, 479 m; organic carbon content, 3.18%; organic matter content, 5.47%; sand 47.08%; clay, 7.75%; silt, 45.16%.

San Isidro Basin, off west coast of Baja California (Eastern Tropical Pacific), Mexico; Talud XVIB cruise, sampling station 21 (30.92472°N, 116.8267°W); depth, 2037 m; organic carbon content, 2.21%; organic matter content, 3.81%; sand, 1.08%; clay, 12.54%; silt, 86.38%.

Guaymas Basin, between San Pedro Nolasco Island and Tortuga Island, Gulf of California, Mexico; Talud X cruise, sampling station 15 (27.7°N, 111.6333°W); depth, 1570 m; organic carbon content, 4.48%; organic matter content, 8.37%; sand, 4.49%; clay, 11.96%; silt, 84%.

Guaymas Basin, off Santa Inés Bay, Gulf of California, Mexico; Talud X cruise, sampling station 17 (27.16444°N, 111.7842°W); depth, 1332 m; organic carbon content, 4.76%; organic matter content, 8.19%; sand, 3.17%; clay, 10.33%; silt, 88.09%.

Off Sinaloa State, Gulf of California, Mexico; Talud cruise IV, sampling station 26 (24.93333°N, 109.0692°W); depth, 1235 m; organic carbon content, 4.08%.

Specimens examined. From the type locality. Adult female holotype preserved in alcohol (EMUCOP-010812-02), adult male allotype preserved in alcohol (EMUCOP-010812-03), 28 paratypes (two adult females, three adult males, one CII, nine CIII, seven CIV, and six CV) preserved in alcohol (EMUCOP-010812-04), two dissected male paratypes (EMUCOP-010812-05, EMUCOP-010812-06), one dissected female paratype (EMUCOP-010812-07), and one dissected aberrant female paratype (EMUCOP-010812-08); August 1, 2012; coll. S. Gómez.

From other localities. One dissected female paratype (EMUCOP-050812-04) from sampling station 5D (Talud XV cruise; August 5, 2012; coll. S. Gómez), one CV paratype preserved in alcohol (EMUCOP-020812-06) from sampling station 20 (Talud XV cruise; August 2, 2012; coll. S. Gómez), one female paratype preserved in alcohol (EMUCOP-280514-01) from sampling station 21 (Talud XVIB cruise; May 28, 2014; coll. S. Gómez), one dissected male paratype (EMUCOP-110207-03) from sampling station 15 (Talud X cruise; February 11, 2007; coll. S. Gómez), one female paratype preserved in alcohol (EMUCOP-120207-04) from sampling station 17 (Talud X cruise; February 12, 2007; coll. S. Gómez), one CIV paratype preserved in alcohol (EMUCOP-260800-01) from sampling station 26 (Talud IV cruise; August 26, 2000; coll. S. Gómez).

Two adult males from the type locality, one female from sampling station 21 (Talud XVIB cruise; May 28, 2014; coll. S. Gómez), and one CI from sampling station 15 together with one CIII and one CV from station 17 (Talud X cruise; February 11 and 12, 2007, respectively; coll. S. Gómez) were used for molecular analyses without satisfactory results.

Etymology. The species was named in honour to Prof. J. B. J. Wells for his contribution to the systematics and taxonomy of harpacticoid copepods. It is a noun in the genitive case.

Description of female. Total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 690 µm to 820 µm (mean = 764 µm; *n* = 5); habitus pyriform, widest at posterior end of cephalothorax, tapering posteriad (Fig. 8A); cephalothorax/body length ratio, 0.32.

Prosome consisting of cephalothorax with fused first pedigerous somite, and second to fourth free pedigerous somites. Cephalothorax about as long as wide, with surface sensilla as shown (Fig. 8A), hyaline fringe broad and smooth. Free pedigerous somites without expansions laterally nor dorsally and without spinular ornamentation; integument smooth, weakly sclerotized; hyaline fringe of second and third pedigerous somites broad and smooth, of fourth pedigerous somite visibly narrower; width of second to fourth pedigerous somites decreasing progressively, with few surface sensilla (Fig. 8A).

Urosome (Figs. 8A, 9A, C) consisting of fifth pedigerous somite (first urosomite), genital double-somite (genital—second urosomite—and third urosomites fused), two free urosomites, and anal somite. Urosomites without expansions laterally nor dorsally; integument weakly sclerotized.

Fifth pedigerous somite visibly narrower than preceding somites; with surface sensilla as shown (Figs. 8A, 9A); without spinular ornamentation; hyaline fringe narrow.

Second and third urosomites completely fused forming genital double-somite, without any trace of division; as long as wide, widest part measured in proximal third close to P6; with few sensilla dorsally (Fig. 8A), laterally (Fig. 9A) and ventrally (Fig. 9C), with short spinular row laterally (Fig. 9A), and with transverse spinular row ventrally (Fig. 9C); posterior hyaline fringe broad and smooth. Genital complex (Fig. 9C) hardly distinguishable; copulatory pores not exposed; paired genital apertures located ventrolaterally and covered by P6.

Fourth urosomite with few sensilla dorsally (Fig. 8A), laterally (Fig. 9A) and ventrally (Fig. 9C); with some lateral spinules (Fig. 9A) and a ventral spinular row (Fig. 9C).

Fifth urosomite without sensilla nor lateral spinules (Figs. 8A, 9A); ventral row of spinules shorter than in preceding somite (Fig. 9C).

Anal somite three times as wide as long (Fig. 8B); with spinules around joint of caudal rami (Figs. 8B, 9A, C); ventrally (Fig. 9C) with spinules along each side of medial cleft and with two pores. Anal operculum rather straight, flanked by one sensillum on each side, posterior margin with transverse row of small spinules (Figs. 8B, 9A).

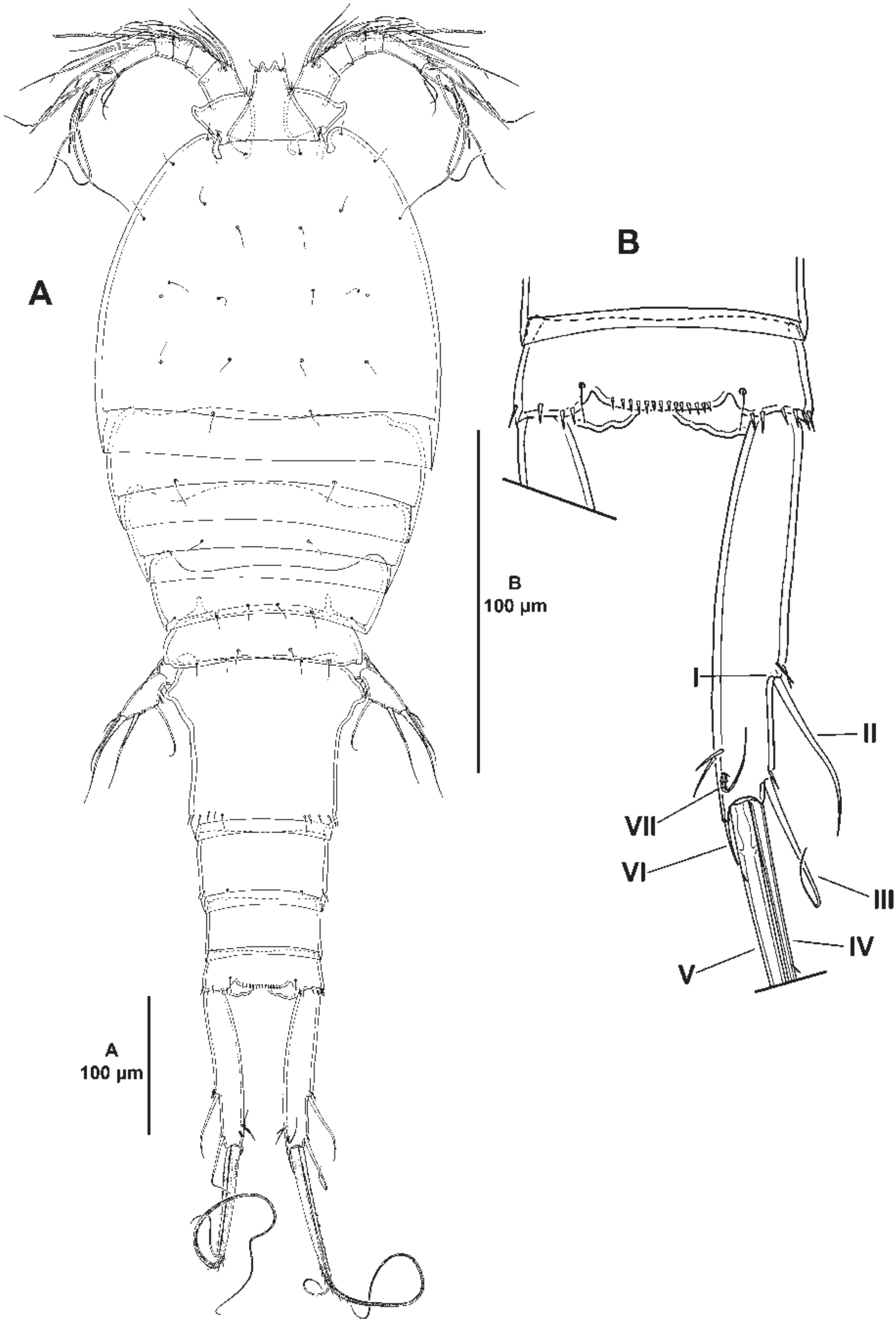

FIGURE 8. *Wellstenvalia wellsi* **sp. nov.**, female: A, habitus, dorsal (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10581); B, anal somite and caudal rami, dorsal.

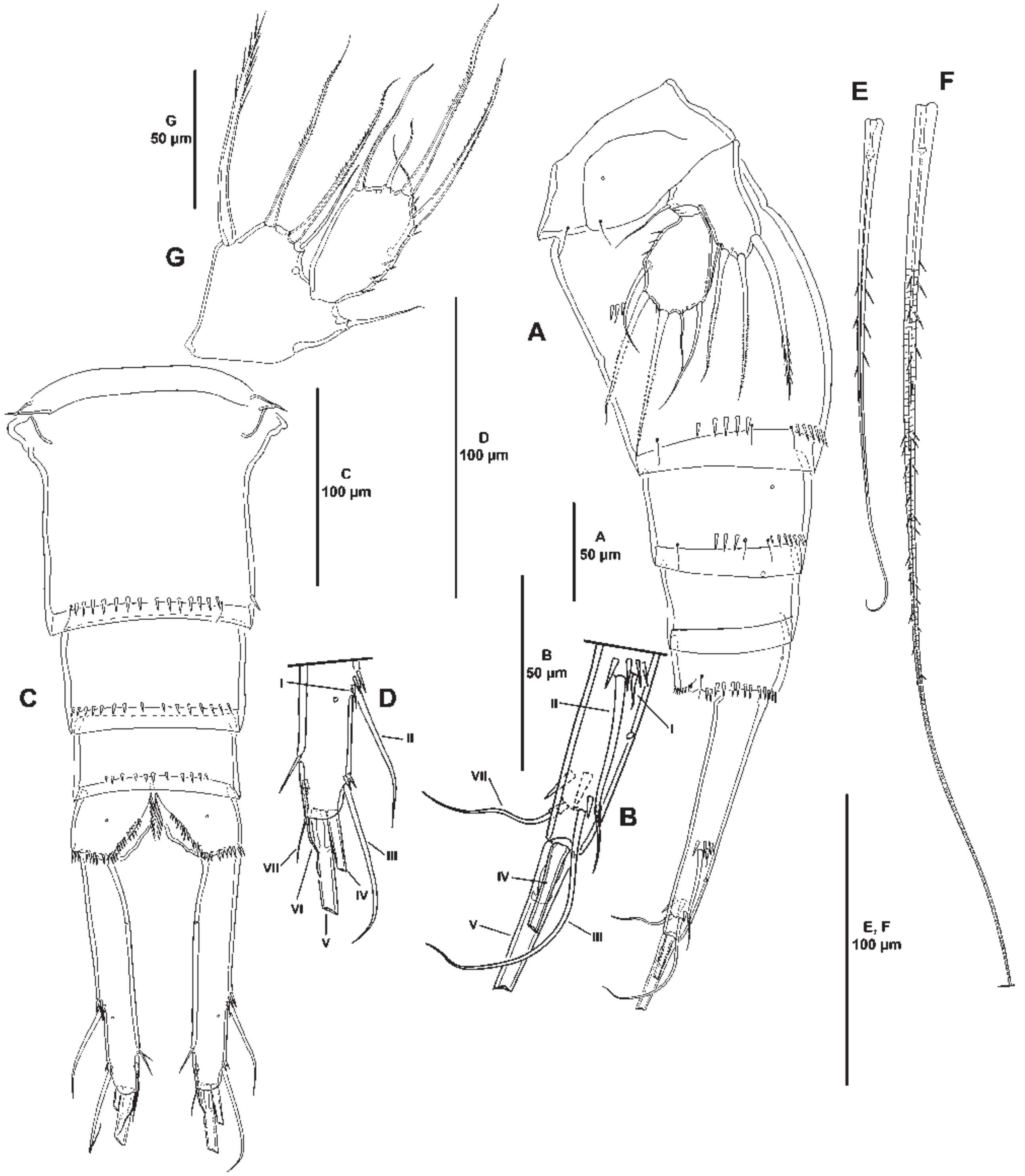

FIGURE 9. *Wellstenvalia wellsi* **sp. nov.**, female: A, urosome, lateral; B, distal part of right caudal ramus, lateral; C, urosome, ventral, P5-bearing somite omitted; D, distal part of left caudal ramus, ventral; E, left caudal seta IV, lateral; F, left caudal seta V, lateral; G, P5.

Caudal rami elongate, about five times as long as wide (Figs. 8A, B, 9A, C) and nearly four times as long as anal somite; each ramus with one inner and one ventral pore, the former in proximal third of ramus, the latter in distal third (Fig. 9C); with small spinules at base of setae I and II, and III (Fig. 9A–D); with seven elements (Figs. 8B, 9B, D); seta I minute, ventral to seta II, both arising laterally on distal third, the latter reaching slightly beyond posterior margin of ramus; seta III subdistal, arising laterally, slightly longer than seta II; seta IV arising at outer distal corner, without fracture plane, visibly slenderer than and about half as long as seta V, the latter rat-like, with fracture plane, both with outer pinnae (Fig. 9E–F); seta VI issuing at inner distal corner; dorsal seta VII triarticulate at base, situated subdistally close to inner margin.

Rostrum (Fig. 10A) trapezoidal, not fused to cephalothorax, reaching distal margin of second antennulary segment, strongly bifid, with two subdistal sensilla and with a proximal dorsal pore.

Antennule (Fig. 10A) eight-segmented; all segments smooth, except for spinular row on first segment, the latter without pore and with outer distal corner produced into blunt process. All setae smooth except for pinnate seta on first, second, and last segments; second segment with two, third segment with one seta with fracture plane; sixth segment with two, seventh segment with one articulated seta. Armature formula: 1(1); 2(9); 3(8); 4(5 + (1 + ae)), 5(2); 6(4); 7(4); 8(3 + acro). Acrothek consisting of two setae and one slender aesthetasc fused basally.

Antenna (Fig. 10B). Coxa short, with some outer spinules. Allobasis as long as free endopodal segment, with small outer spinules proximally, with proximal and medial longitudinal row of inner spinules, with one pinnate abexopodal seta arising midway inner margin. Free endopodal segment elongate; inner margin with two sets of proximal and medial spinules, with two outer subdistal spinular rows; armature composed of two lateral spines and two accompanying slender setae, distally with one inner apical spine, three apical geniculate setae and one slender element, and one outer distal pinnate element fused basally to slender seta. Exopod three-segmented; first segment longest, about five times as long as wide, with lateral and apical spinules as shown, with one bipinnate long seta; second segment shortest, without spinular ornamentation, with one long bipinnate seta; third segment slightly shorter than first segment, with one medial and one subdistal row of spinules, with one proximal bipinnate seta and three bare elements distally none of which seems to be fused basally.

Mandible (Fig. 11A–C). Coxa relatively short. Gnathobase wide; ventral distal corner produced into small sharp semi-hyaline process; with two strong and several smaller bicuspidate teeth, some spinules, and one bipinnate seta accompanied by strong element. Basis with wide base, tapering distally, with some medial and some subdistal spinules close to outer margin, with three subdistal outer setae. Exopod (Fig. 11C) arising from short pedestal, elongate, tapering distally; about three times as long as wide, and 0.4 times as long as basis; with two outer, two inner, and two apical slender setae, the latter fused basally. Endopod (Fig. 11B) recurved, twisted over exopod; with three lateral setae, and five distal elements (two slender setae and two strong elements, and longest element fused to endopod and with hyaline flange in middle part).

Maxillule (Fig. 11D–E). Arthrite of praecoxa (Fig. 11D) with two surface setae and nine distal elements, one of which a small seta arising next to ventralmost spine, one spinulose dorsal spine, and one lateral spinulose recurved seta. Coxa with arched spinular row and three setae (Fig. 11E). Basis (Fig. 11E) with two endites; proximal endite with four, distal endite with three slender setae. Exopod and endopod not fused neither to each other nor to basis, one-segmented; endopod larger than exopod, with four setae; exopod small, with two setae.

Maxilla (Fig. 11F–G). Large syncoxa seemingly without spinular ornamentation; with three endites; proximal endite smallest, bilobate, each lobe with two setae as shown; middle and distal endites elongate, the latter slightly longer, with three spinulose elements each. Basis (Fig. 11F–G) drawn out into strong spinulose claw, additionally with strong spinulose spine and two slender setae. Endopod (Fig. 11G) small, 1.5 times as long as wide, with six slender setae (one arising basally, two medially, and three apically).

Maxilliped (Fig. 11H–I) subchelate. Syncoxa rectangular, about 1.5 times as long as wide; with slender inner spinules; with one bare and two spinulose strong elements, of which bare seta and one spinulose element at the same level, the other arising distally from long pedestal (see also Fig.11I). Basis slightly shorter than syncoxa, oval; with slender outer spinules, and with one anterior and one posterior inner spinular row as depicted; with two slender distal setae, one of which visibly longer (see also Fig. 11I). Endopod (see also Fig. 11I) one-segmented, with one claw-like element and one seta.

P1 (Figs. 12A, 14A). Intercoxal sclerite transversely elongate, nearly straight, without surface ornamentation (Fig. 14A). Coxa massive; 1.4 times as long as wide; with small outer spinules, and with longer spinules on distal outer corner and medially close to basis. The latter with inner and outer spine; with small spinules at the base of the former, and with strong spinules at the base of the latter; with strong spinules close to inner proximal corner and with minute spinules between rami. Exopod three-segmented, as long as ENP; EXP2 longest, EXP3 shortest; all segments without outer nor inner acute distal processes; EXP1 with transverse rows of outer spinules medially and subdistally, with additional transverse spinular row medially on proximal third and distally close to EXP2, without inner armature; EXP2 with minute spinules midway outer margin and distally close to EXP3, with inner seta; EXP3 with some minute outer spinules, with two distal setae and two outer spines. Endopod two-segmented; segments without inner nor outer acute distal processes; ENP1 reaching middle of EXP2, 2.8 times as long as wide, and as long as ENP2, with long inner spinules and with longitudinal row of outer spinules, with one inner seta; ENP2 slenderer than ENP1, 4.3 times as long as wide, with one inner distal seta arising at proximal fourth, one inner distal seta, one apical element, and one outer spine.

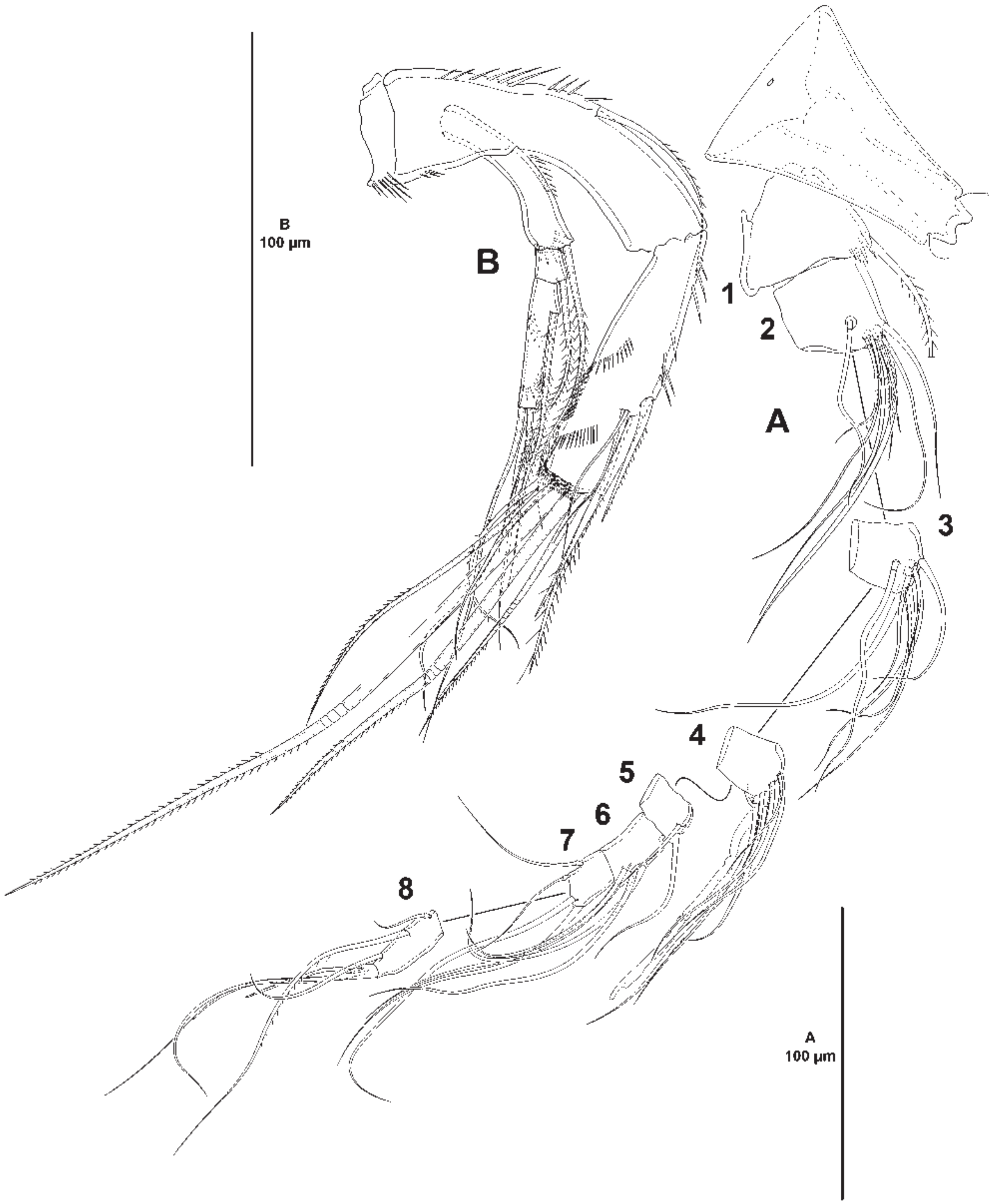

FIGURE 10. *Wellstenvalia wellsi* **sp. nov.**, female: A, rostrum and antennule, each actual antennulary segment numbered (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10588); B, antenna (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10580).

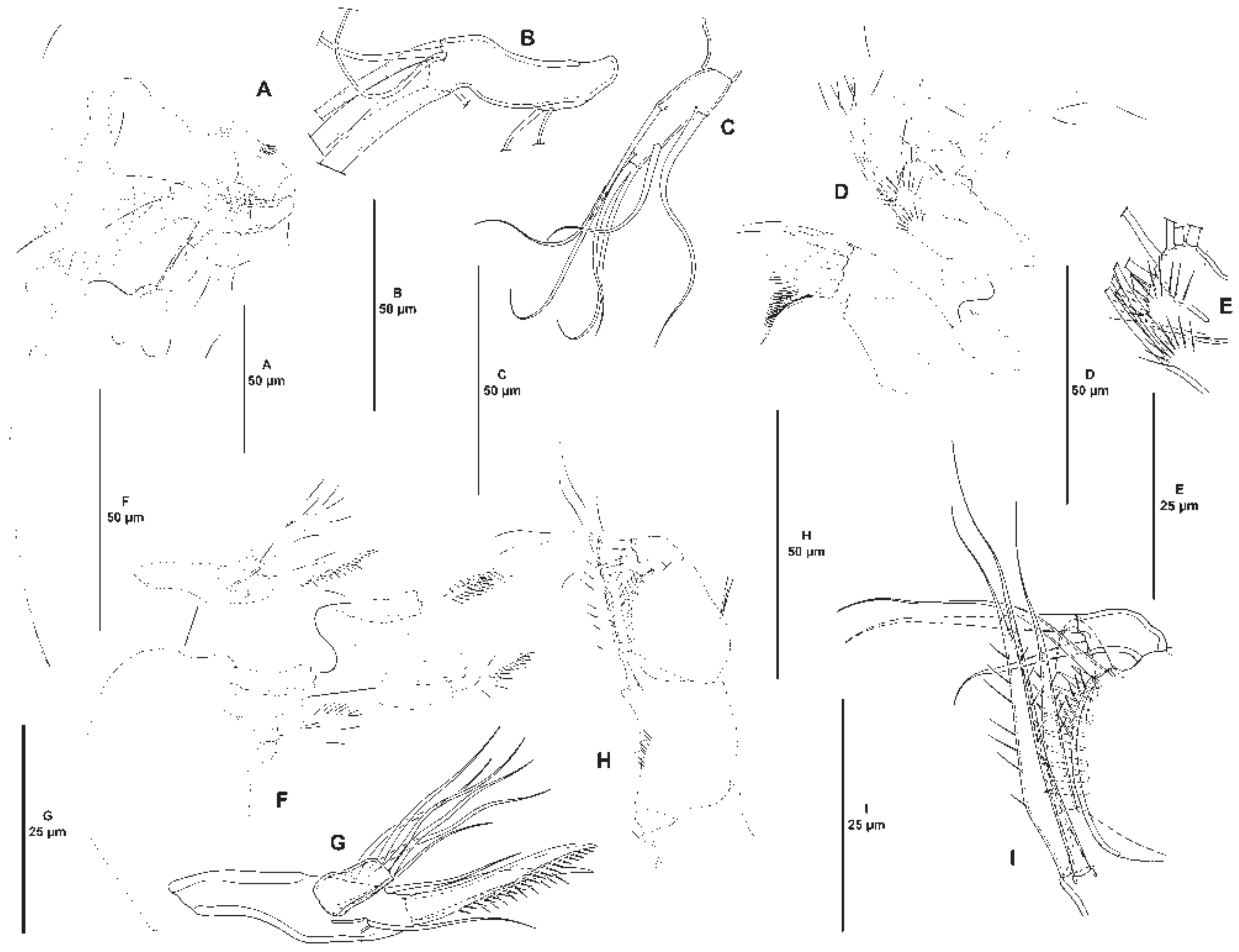

FIGURE 11. *Wellstenvalia wellsi* **sp. nov.**, female: A, mandible (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10582); B, endopod of mandible; C, exopod of mandible; D, maxillule; E, distal part of coxal endite and basis of maxillule showing armature; F, maxilla; G, allobasis and endopod of maxilla showing armature; H, maxilliped (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10583); I, inner distal corner of syncoxa, inner margin of basis, and endopod showing armature.

P2 (Figs. 12B, 14B). Intercoxal sclerite not transversely elongate; trapezoidal; with strong pointed process on distal outer corners; without surface ornamentation (Fig. 14B). Coxa (not shown) as in P3. Basis with outer spine and strong acute inner process, the latter reaching middle of ENP1 and with slender spinules at its base. Exopod three-segmented, reaching slightly beyond ENP2; EXP2 shortest, EXP3 longest; EXP1 and EXP2 with outer acute distal process, with longitudinal row of outer spinules and with inner distal frill, with inner seta, EXP1 without, EXP2 with subdistal outer pore; EXP3 with small outer spinules proximally, with medial pore on distal third, with one inner and two apical setae, and three outer spines. Endopod three-segmented, longer than EXP; ENP1 and ENP2 subequal in length, ENP3 longest; ENP1 and ENP2 with outer acute and inner small process distally, with longitudinal row of small spinules, with small spinules at base of outer process and with inner distal frill, ENP1 with, ENP2 without medial pore, inner element of ENP1 fused to segment forming strong spike, ENP2 with inner seta; ENP3 with longitudinal row of outer spinules and with medial pore subdistally, with one inner seta, two apical elements and one outer spine.

P3 (Figs. 13A, 14C). Intercoxal sclerite not transversely elongate, trapezoidal, wider than in P2; with strong pointed process on distal outer corners, without surface ornamentation (Fig. 14C). Coxa squared, with small spinules close to proximal outer corner and with longer spinules close to inner and outer distal corners, with distal outer pore. Basis with outer seta, with pointed inner process smaller than in P2 and with slender spinules at its base, with minute spinules at the base of ENP. Exopod three-segmented, reaching proximal third of ENP3; EXP2 shortest, EXP3 longest; EXP1 and EXP2 with outer acute distal process, with longitudinal row of outer spinules and with inner distal frill, EXP1 without, EXP2 with outer subdistal pore, both segments with inner seta; EXP3 with small outer spinules proximally, without pore, with three inner setae, two apical elements, and three outer spines. Endopod three-segmented, longer than EXP; ENP1 and ENP2 subequal in length, ENP3 longest; ENP1 and ENP2 with outer acute and small inner process distally, with longitudinal row of small spinules, with small spinules at base of outer process and with inner distal frill, ENP1 with, ENP2 without medial pore, inner element of ENP1 a strong spine, ENP2 with inner seta; ENP3 with longitudinal row of outer spinules and medial pore subdistally, with three inner setae of which distalmost thicker and spinulose, with two apical elements and one outer spine.

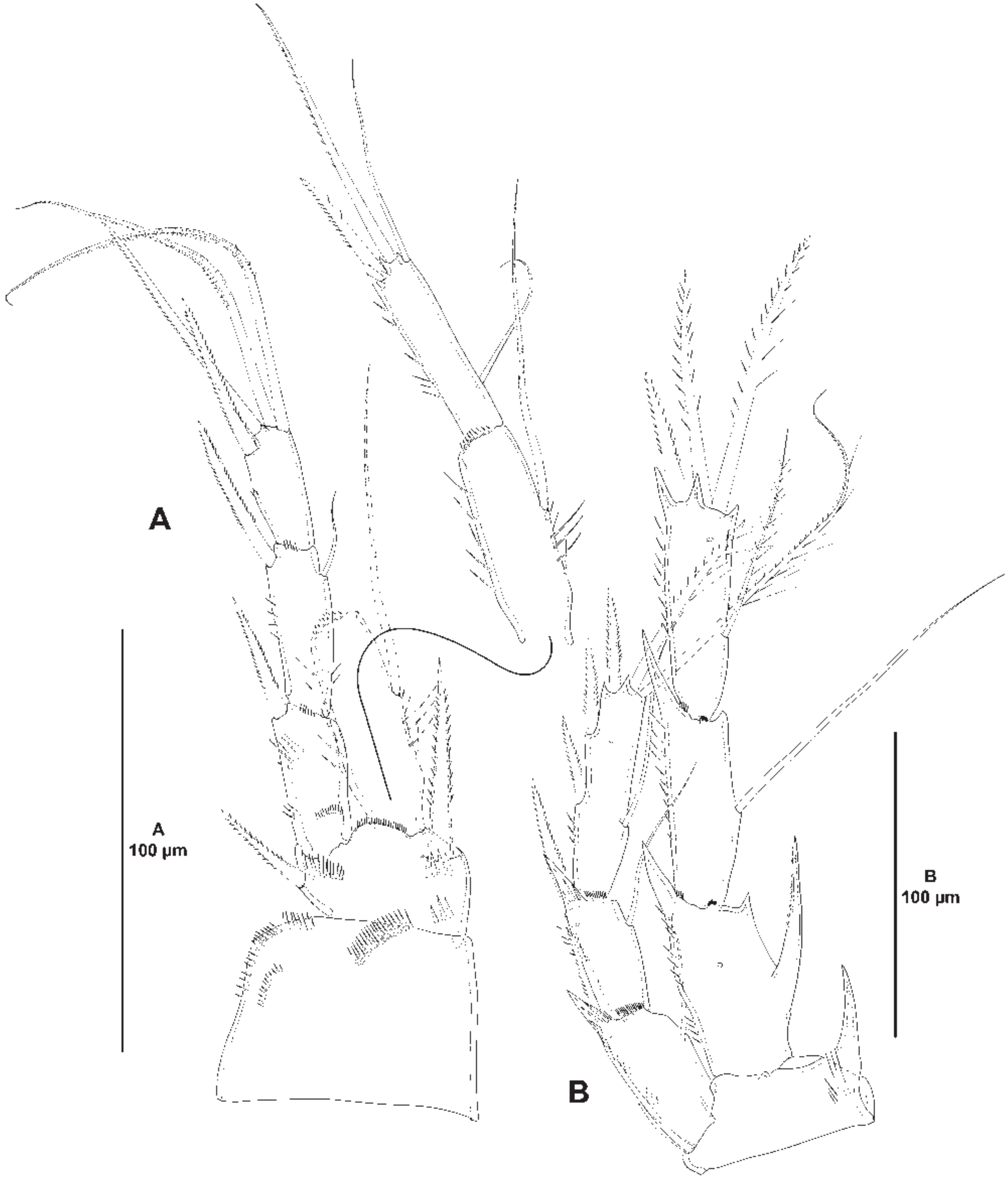

FIGURE 12. *Wellstenvalia wellsi* **sp. nov.**, female: A, P1, anterior (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10584); B, P2, anterior (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10585).

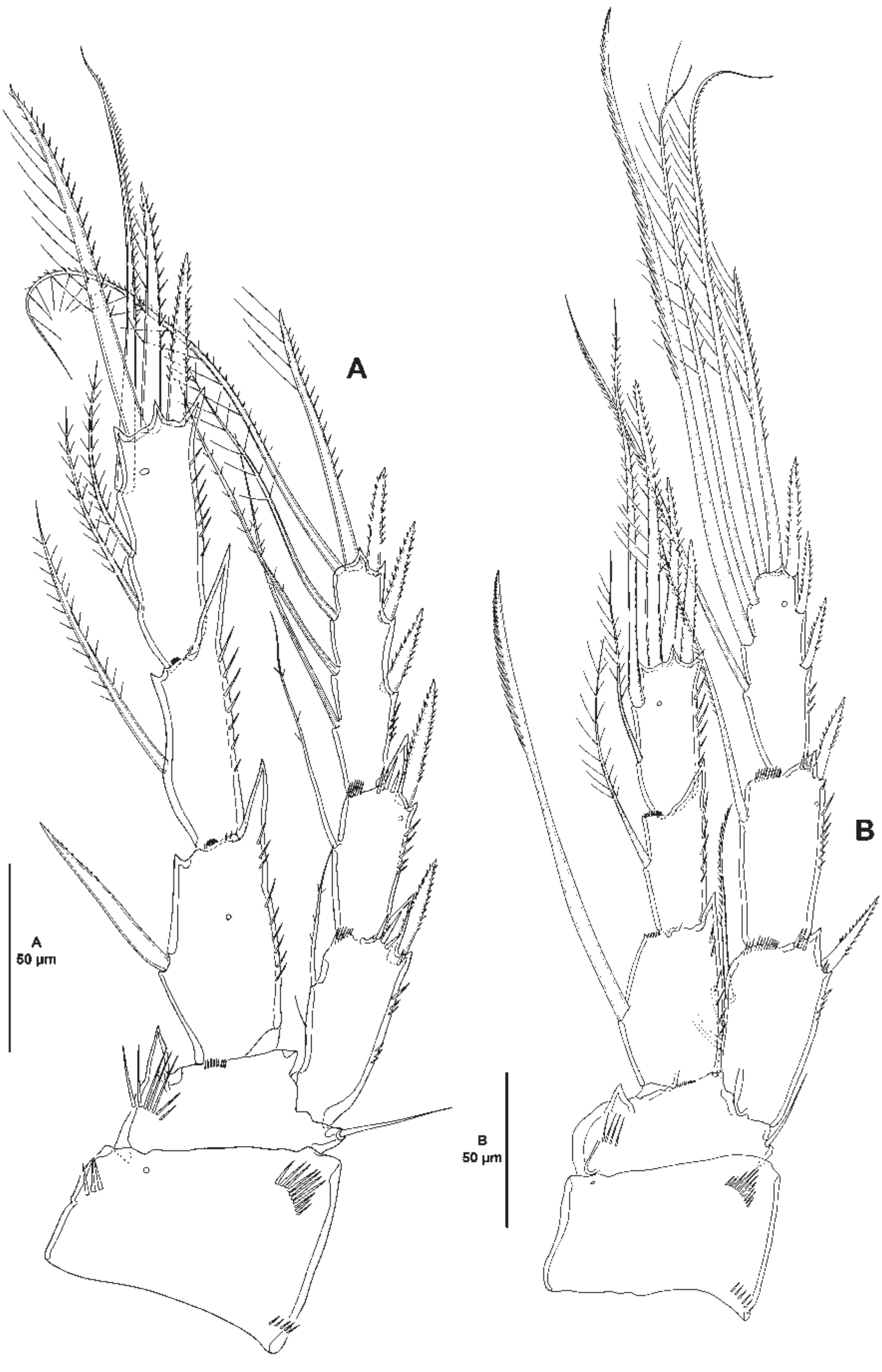

FIGURE 13. *Wellstenvalia wellsi* **sp. nov.**, female: A, P3, anterior (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10586); B, P4, anterior (microphotograph available in http://metadata.icmyl.unam.mx/handle/20.500.12201/10587).

P4 (Figs. 13B, 14D). Intercoxal sclerite not transversely elongate, trapezoidal, smaller than in P3, with strong pointed process on distal outer corners, without surface ornamentation (Fig. 14D). Coxa squared, ornamented as in P3 except for lack of inner spinular ornamentation, with distal outer pore. Basis as in P3, but inner process smaller. Exopod three-segmented, 1.3 times as long as ENP; EXP1 and EXP2 subequal in length, EXP3 slightly longer; EXP1 and EXP2 with outer distal process less developed than in P3, with longitudinal row of outer spinules and with inner distal frill, EXP1 without, EXP2 with outer subdistal pore, both segments with inner seta; EXP3 with small outer spinules proximally, with medial pore subdistally, with three inner setae of which medial element visibly thicker and with inner margin strongly serrate, two apical elements, and three outer spines. Endopod three-segmented, shorter than EXP; ENP1 and ENP3 subequal in length, ENP2 shortest; ENP1 and ENP2 with outer acute and small inner process distally, with outer longitudinal row of small spinules and with inner distal frill, without pore, ENP1 with inner long element with distal third serrate, ENP2 with inner slender seta; ENP3 with longitudinal row of outer spinules and medial pore subdistally, with two inner setae of which distalmost thicker, with two apical elements and one outer spine.

Setal formula of swimming legs as follows:

	P1	P2	P3	P4
EXP	0,1,022	1,1,123	1,1,323	1,1,323
ENP	1,121	1,1,121	1,1,321	1,1,221

P5 (Fig. 9G). Baseoendopod pentagonal, reaching proximal third of EXP; with four setae, of which outermost shortest and set closely to adjacent seta, the latter and medial setae bipinnate, innermost seta thickest and strongly spinulose. Exopod oval, 1.7 times as long as wide, with some outer small spinules and one distal pore, with five setae of which second innermost shortest.

P6 (Fig. 9C) minute flap covering ventrolateral genital aperture, fused to somite, without surface ornamentation, with one slender seta.

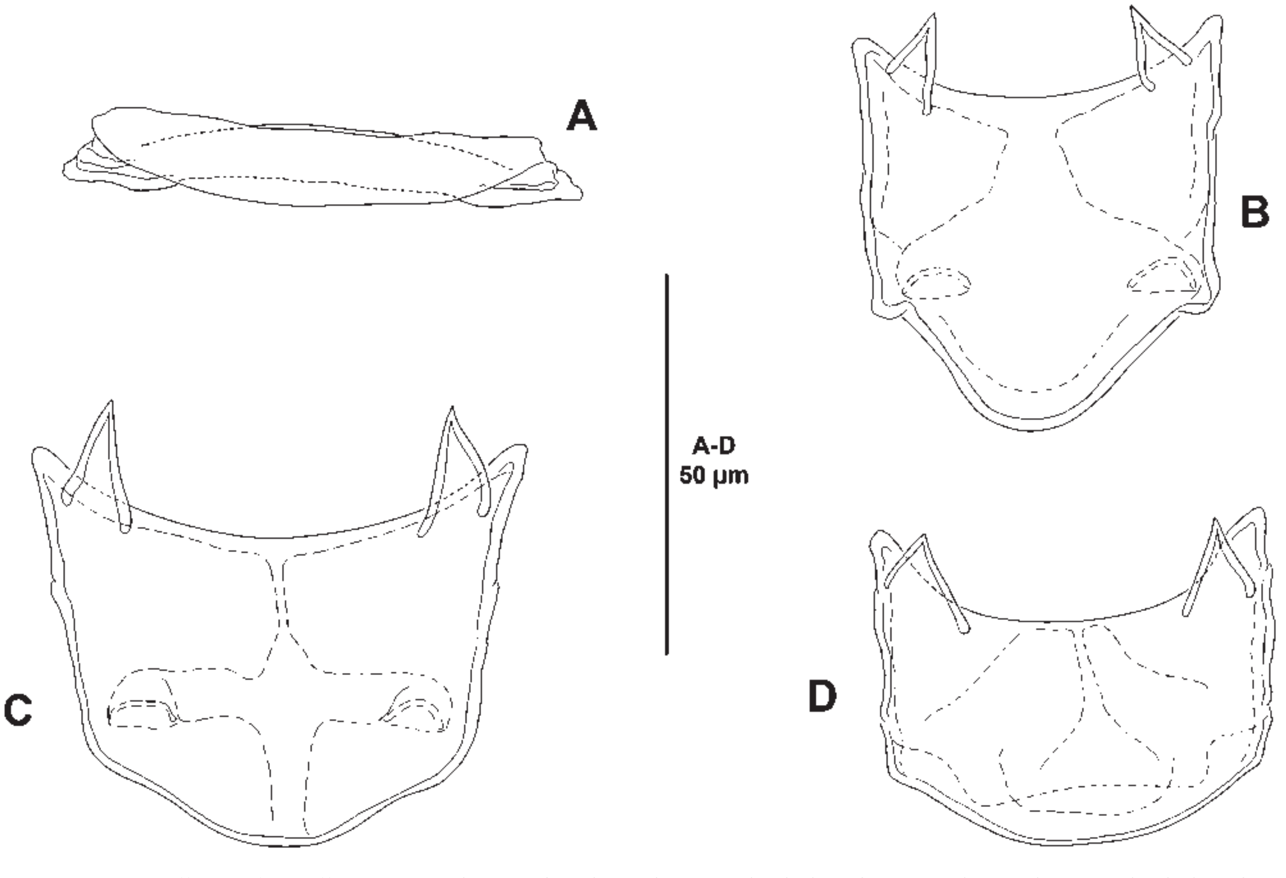

FIGURE 14. *Wellstenvalia wellsi* **sp. nov.**, aberrant female: A, intercoxal sclerite of P1, anterior; B, intercoxal sclerite of P2, anterior; C, intercoxal sclerite of P3, anterior; D, intercoxal sclerite of P4, anterior.

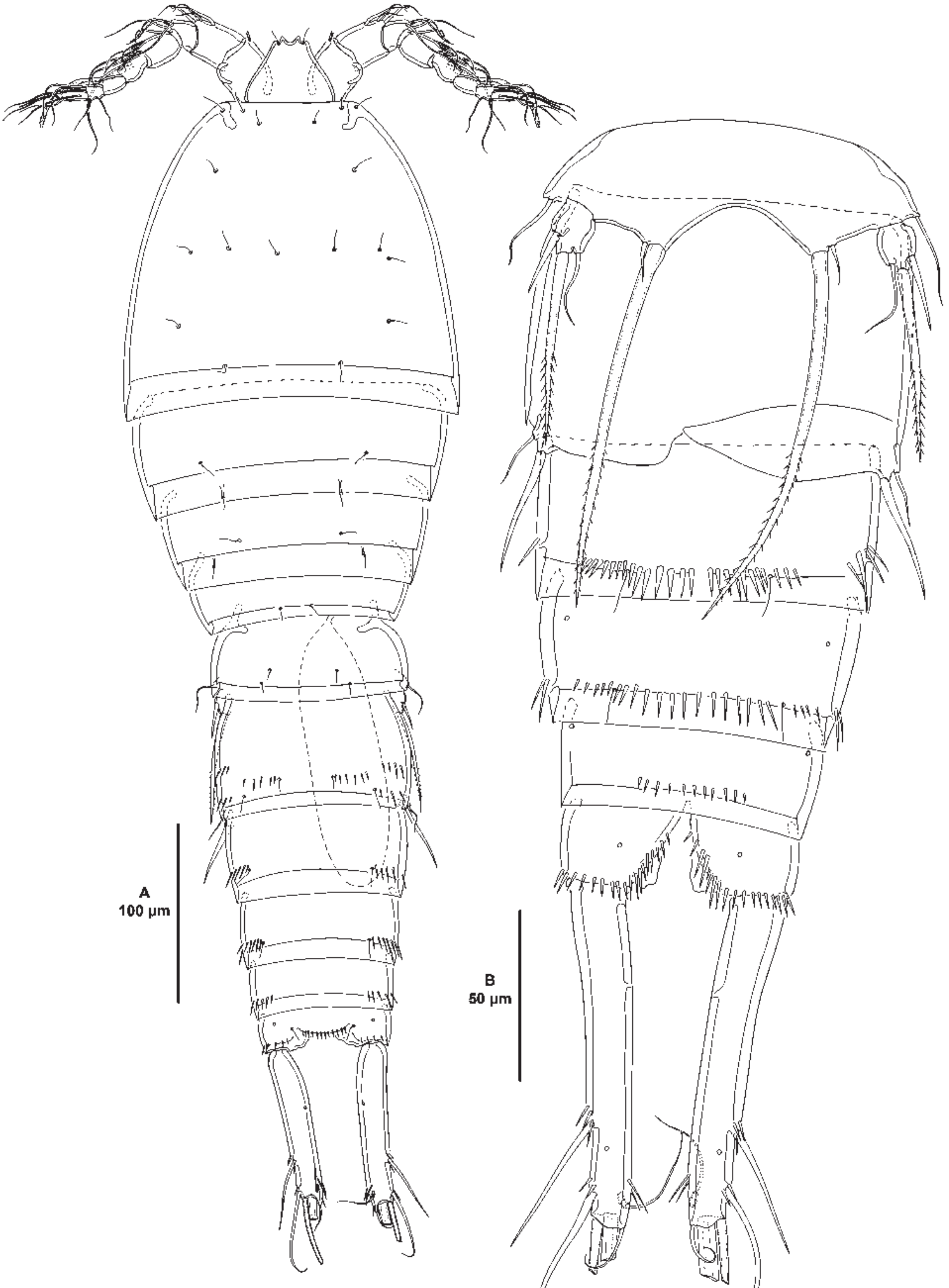

FIGURE 15. *Wellstenvalia wellsi* **sp. nov.**, male: A, habitus, dorsal; B, urosome, ventral.

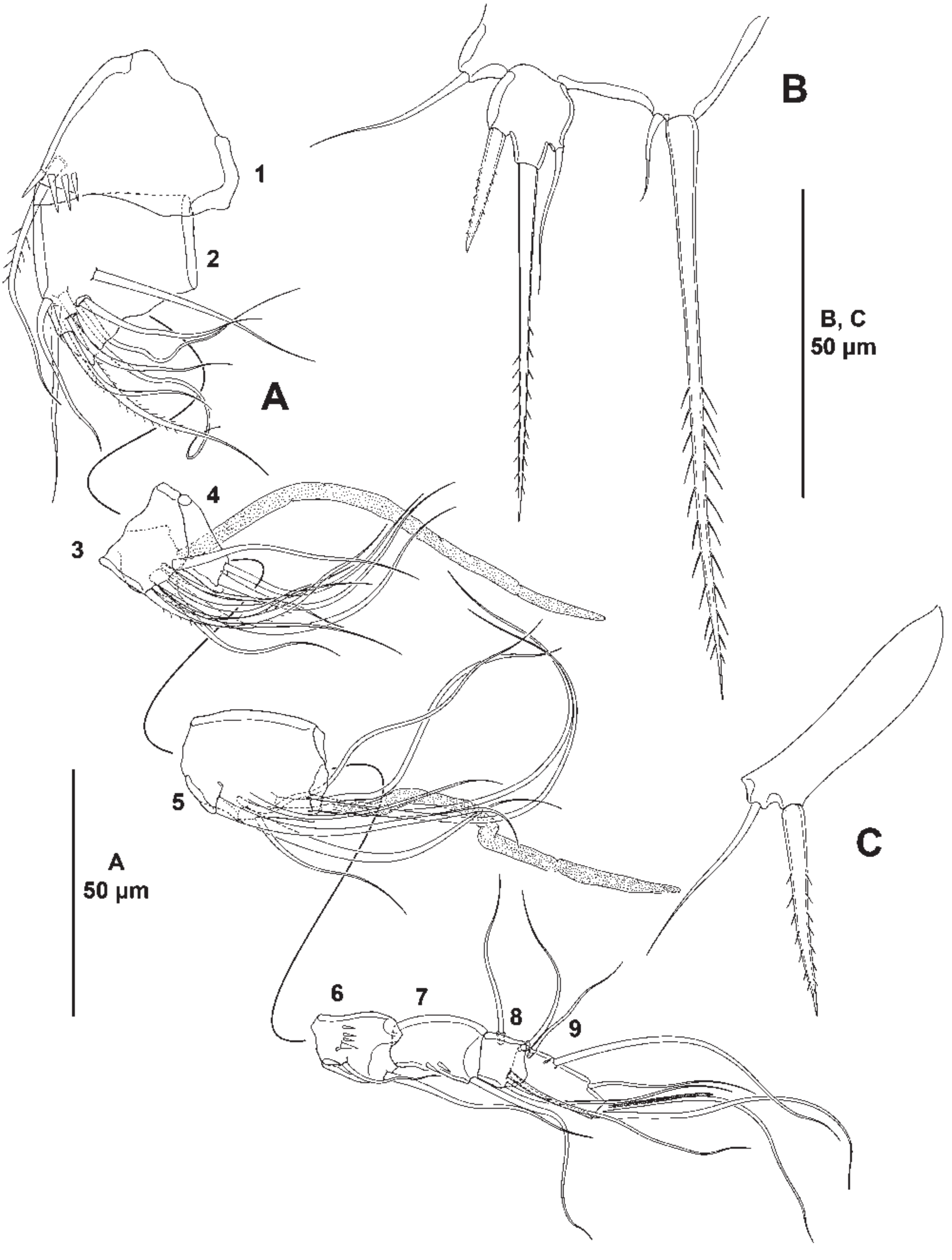

FIGURE 16. *Wellstenvalia wellsi* **sp. nov.**, male: A, antennule, each actual segment numbered; B, P5; C, P6.

Description of male. Total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 541 μm to 700 μm (mean = 645 μm; *n* = 8); general shape of habitus (Fig. 15A) as in female. Pedigerous somites largely as in female except for narrower male fifth pedigerous somite. Genital somite with dorsal and laterodorsal rows of spinules and with posterior sensilla. Third and fourth urosomites with laterodorsal and ventral spinules, and with posterior sensilla. Fifth urosomite with laterodorsal spinules, with short ventral row of spinules, without sensilla.

Anal somite and caudal rami (Fig. 15A–B), and rostrum (not shown) as in female.

Antennule (Fig. 16A) nine-segmented, haplocer, with geniculation between third and fourth, and sixth and seventh segments; distal corner of first segment less produced than in female, without pore. All segments smooth except for some spinules on first, sixth and seventh segments. All setae smooth except for one pinnate seta on first and second segments; seemingly none seta with fracture plane; eighth segment with two, ninth segment with one articulated seta. Aesthetasc present on third, fifth, and last segments. Armature formula: 1(1); 2(9); 3(8 + ae); 4(2); 5(7 + (1 + ae)), 6(2); 7(1); 8(4); 9(3 + acro). Acrothek consisting of two setae fused basally to aesthetasc.

Antenna, mandible, maxillule, maxilla and maxilliped (not shown) as in female.

P1 (Fig. 17A) largely as in female. Sexual dimorphism expressed in the relatively shorter EXP (ENP 1.3 times as long as EXP), more robust ENP1 (2.3 times as long as wide), longer and slender ENP2 (1.5 times as long as ENP1, and 7.3 times as long as wide), stronger spinules on ENP1 and ENP2, and in the ornamentation of some setae (with setules) and outer spines (spinules coarser).

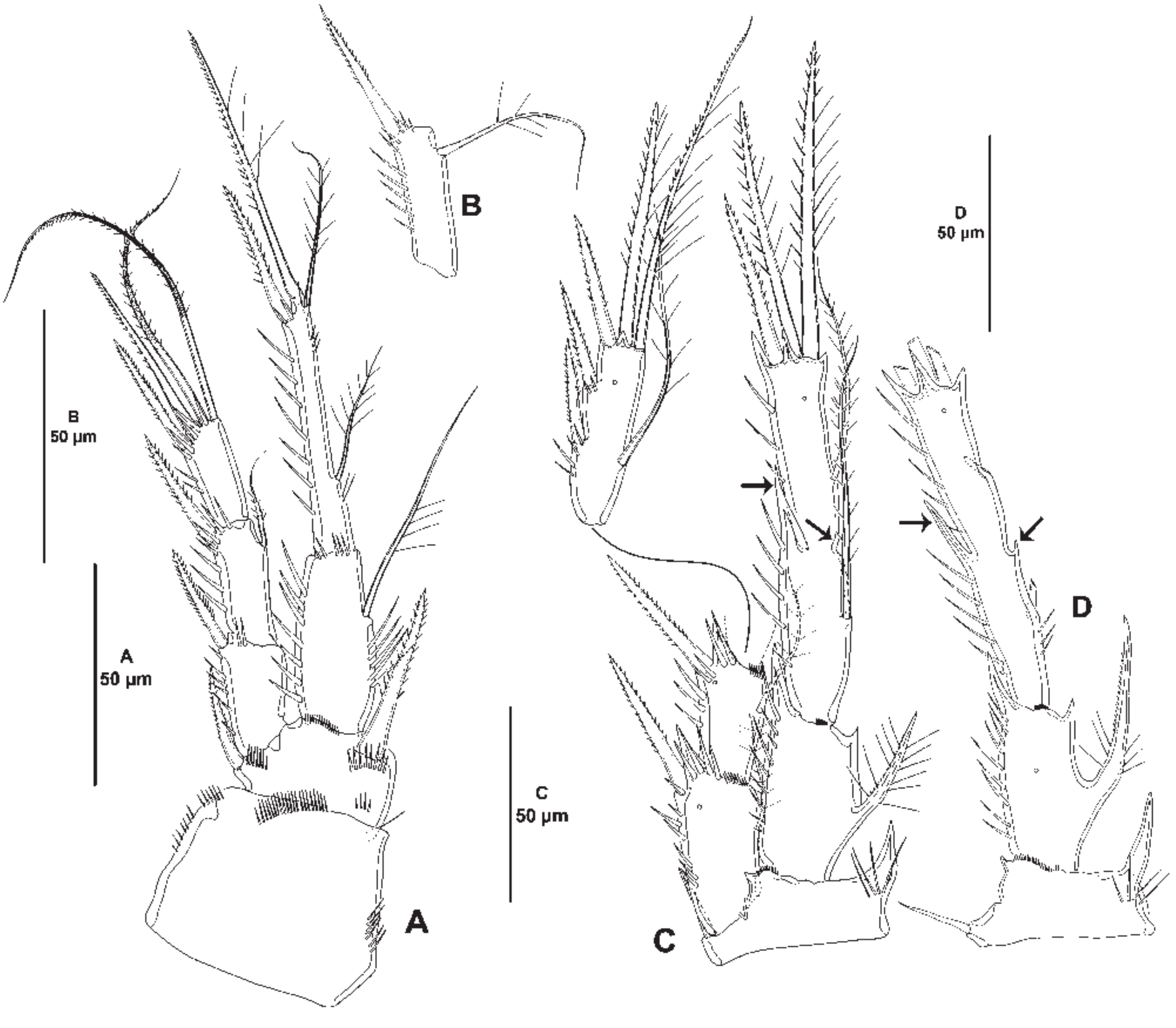

FIGURE 17. *Wellstenvalia wellsi* **sp. nov.**, male: A, P1, anterior; B, male P1 EXP2 showing variability in length of inner seta; C, P2, anterior; D, P2 ENP showing variability in remains of the original division between ENP2 and ENP3.

P2 (Fig. 17B–D). Basis as in female, except for comparatively shorter inner acute process. EXP largely as in female, except for ornamentation of setae and outer spines, and stronger outer spinules. ENP1 as in female, except for stronger outer spinules and for setules on inner spike; ENP2 and ENP3 fused forming a long and slender segment, 5.4 times as long as broad, outer spinules stronger than in female; original division between ENP2 and ENP3 indicated by remains of distal outer and inner processes of former ENP2 (arrowed in Fig. 17C–D).

P3 (Fig. 18A). Basis largely as in female, except for less developed inner process. ENP as in female except for ornamentation of armature complements, for slenderer subdistal inner seta, and for stronger outer spinules. EXP as in female except for stronger outer spinules.

P4 (Fig. 18B) largely as in female except for ornamentation of some armature complements, relative length of outer spinules of EXP, and stronger outer spinules on both rami.

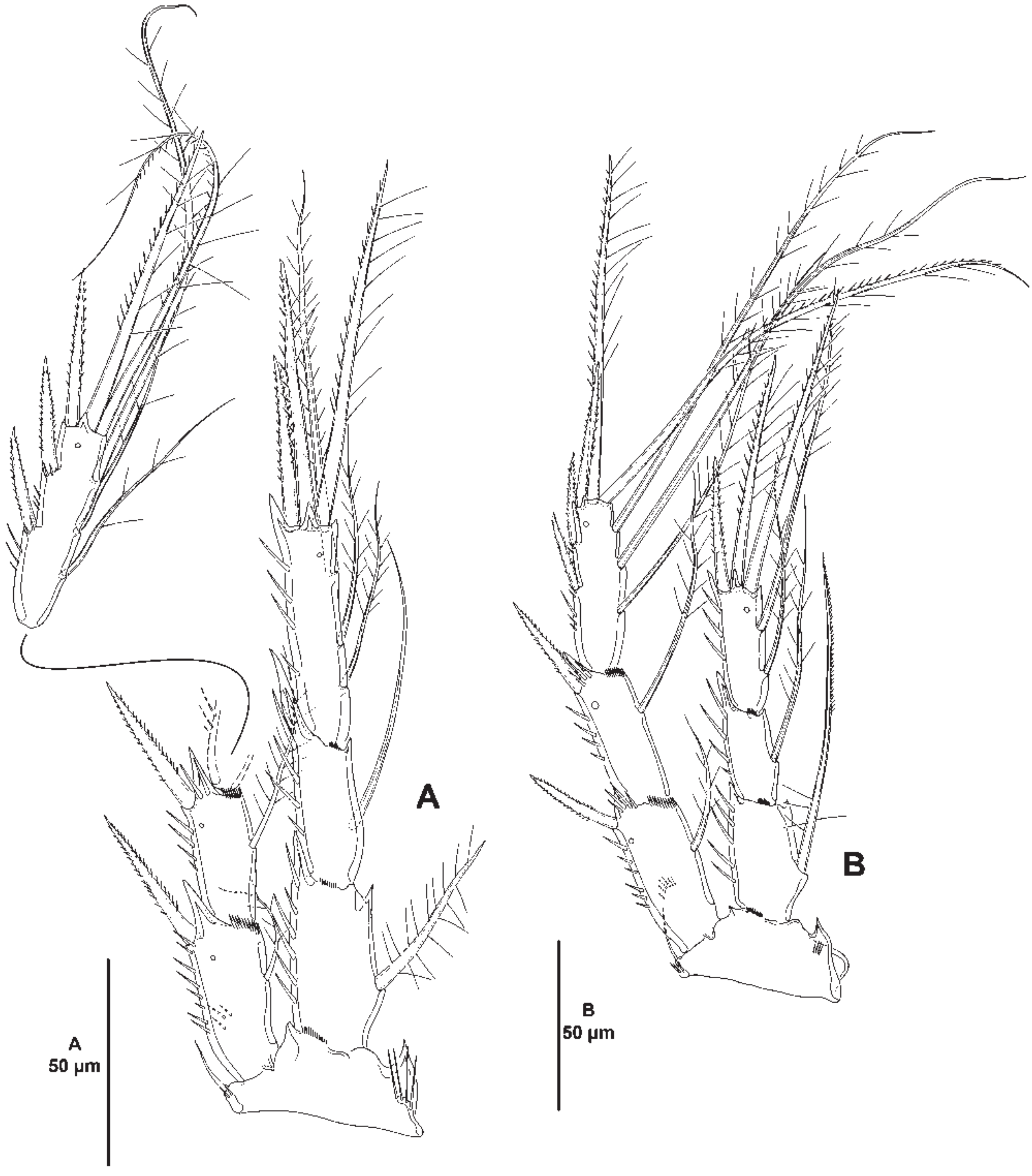

FIGURE 18. *Wellstenvalia wellsi* **sp. nov.**, male: A, P3, anterior; B, P4, anterior.

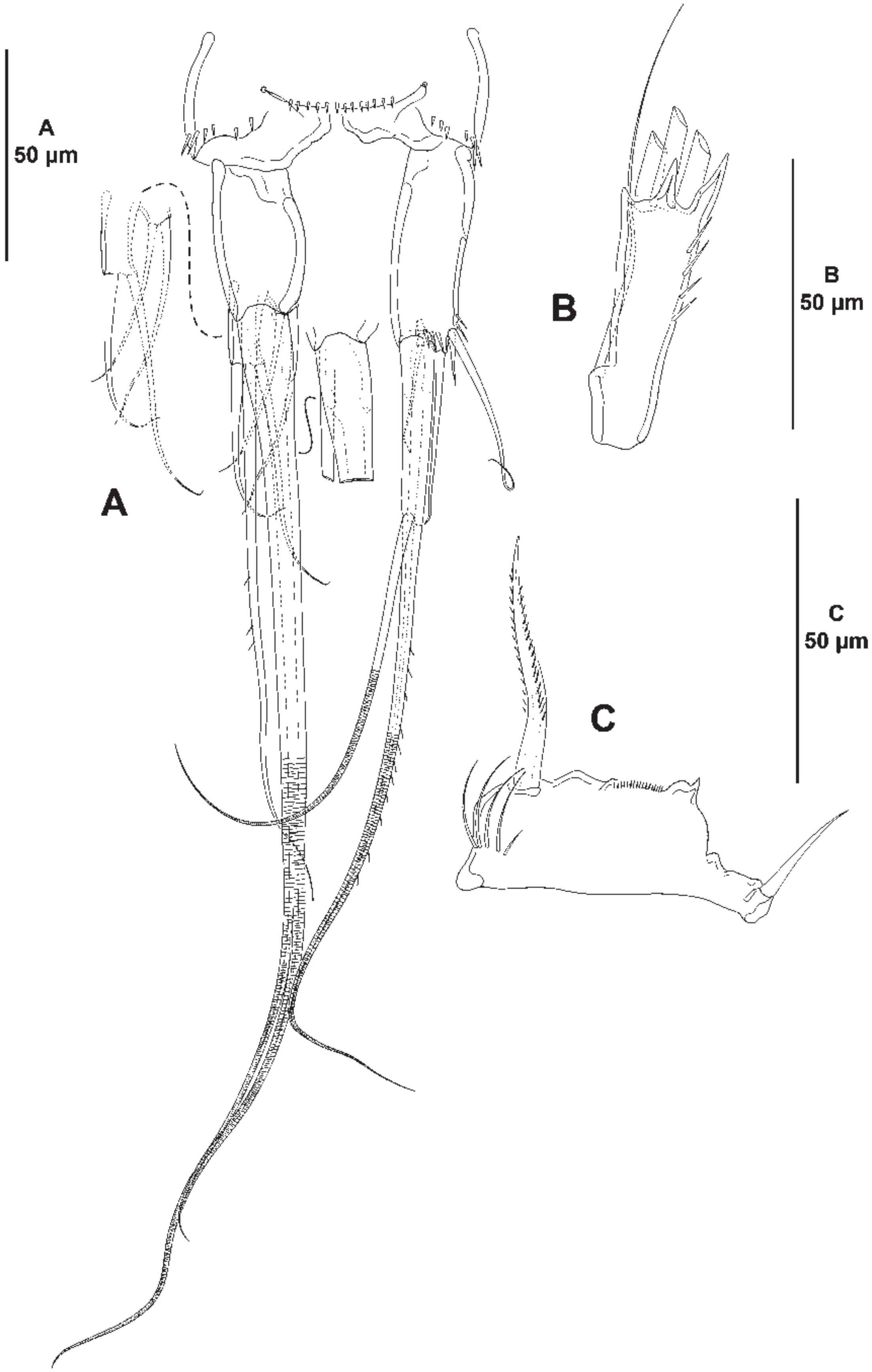

FIGURE 19. *Wellstenvalia wellsi* **sp. nov.**, aberrant female: A, anal somite and caudal rami; B, right P2 ENP3; C, basis of right P2.

P5 (Figs. 15B, 16B) dimorphic. EXP small, oval, with three elements as depicted. Baseoendopods fused medially forming a continuous plate, each endopodal lobe with one inner long pinnate seta and one outer small element.

P6 (Figs. 15B, 16C) dimorphic. Both legs separated, only one of them functional, the other fused to somite, with one outer seta and one inner spine each.

Variability. The outermost seta of the female P5 endopodal lobe of paratype EMUCOP-050812-04 from sampling station 5D (Talud XV cruise) does not reach the insertion level of innermost seta of EXP. Only a small notch and a well-developed outer process remain marking the original division between ENP2 and ENP3 of the male P2 (Fig. 17C) in some specimens from sampling station 24 (Talud XV cruise), while the original division between these two segments is marked by a less developed outer process and an inner small pointed projection (Fig. 17D) in some males from the same sampling station and from sampling station 15 (Talud X cruise); also, the length of the inner seta on P1EXP2 (compare Figs. 17B and A) and the length of the inner spike on P2ENP1 (compare Figs. 17C and D) may vary in length. One female (EMUCOP-010812-08) showed aberrant caudal rami (Fig. 19A), possesses two inner setae on left P1 ENP2, the inner seta on right P2 ENP3 is inserted more proximally (Fig. 19B), possesses one inner spine on the basis of right P2 (Fig. 19C), and the basis of left P2 lacks the inner process.

Remarks and discussion

Justification of *We. euterpoides* sp. nov. and *Wellstenvalia* gen. nov., and some comments on the relationships of the new genus within the subfamily Stenheliinae.

Delavalia is the most species-rich and morphologically diverse genus within the subfamily Stenheliinae. The monophyly of the genus is far from resolved. Willen (2000) recognized eight apomorphic character states towards the monophyly of Stenheliinae, and questioned the monophyly of the genus *Delavalia*. Willen (2002) commented on the probable paraphyly of *Delavalia* and reinstated the genus *Melima*. In their paper Mu & Huys (2002) abandoned the subgeneric classification of the genus *Stenhelia*, redefined the latter and gave the subgenus *Stenhelia* (*Delavalia*) full generic rank. In the same paper, Mu & Huys (2002) created the genus *Anisostenhelia* for *Stenhelia* (*Stenhelia*) *asetosa* Thistle & Coull, 1979, reinstated the genus *Beatricella* for *Delavalia aemula* Scott, 1893, reallocated *Stenhelia* (*Stenhelia*) *diegensis* Thistle & Coull, 1979 to *Delavalia*, and created the genus *Hicksia* Mu & Huys, 2002 for *S. xylophila* Hicks, 1988. Later, Özdikmen (2009) proposed to replace the genus name *Hicksia* for *Muohuysia*.

In their analysis on the affinities of *Mu. xylophila* (Hicks, 1988), Mu & Huys (2002) commented on the close relationship between the former and *D. bocqueti* (Soyer, 1971) and *D. hanstroemi* (Lang, 1948) as evidenced by the presence of a stout spine on P2–P3 ENP1 and a long falciform element of P4 ENP1 in these three species (the relationships between *D. bocqueti* and *D. hanstroemi* had already been noted by Soyer (1971)). Mu & Huys (2002) hypothesized on the sistergroup relationship between the *D. hanstroemi*-*D. bocqueti* lineage and *Mu. xylophila*, and suggested that they might have derived from a common ancestor which already displayed the spinous modifications of P2–P4 ENP and had lost one of the endopodal setae on the female P5. According to Mu & Huys (2002) the two-segmented condition of the P1 ENP of the *D. hanstroemi*-*D. bocqueti* lineage evolved independently of that in other *Delavalia* species, thus supporting the polyphyletic status of *Delavalia*.

Probably unaware of Mu & Huys' (2002) study, Willen (2003) proposed six groups/subgroups for several species of *Delavalia*. Dahms *et al.* (2005) proposed some apomorphies for *Delavalia* and *Pseudostenhelia* (Dahms *et al.* 2005: 12, table 2), and for Stenheliinae (Dahms *et al.* 2005: 12, table 3) based on naupliar morphology, as well as a list of some characters shared by *Stenhelia*, *Delavalia*, and *Pseudostenhelia* (Dahms et al 2005: 13). Huys & Mu (2008) discussed Willen's (2002) and Dahms *et al.*'s (2005) list of apomorphies, and presented a subdivision of the genus *Delavalia* without mention of Willen's (2003) subdivision.

In a recent attempt towards redefining the genus *Delavalia*, Karanovic & Kim (2014) proved the polyphyly of the genus and proposed the genus *Wellstenhelia* for its type species *We. calliope*, and *We. clio, We. erato*, *We. euterpe*, *We. melpomene, We. qingdaoensis*, *We. hanstroemi*, and *We. bocqueti*. Additionally, they proposed two other genera with two-segmented P1 ENP and with normal inner setae on P2–P3 ENP1, *i.e.* (1) *Willenstenhelia* for its type species *Wi. thalia* Karanovic & Kim, 2014, *Wi. minuta* (Scott, 1902) (= *D. minuta* Scott, 1902), *Wi. unisetosa* (Wells, 1967) (= *Stenhelia* (*Delavalia*) *unisetosa* Wells, 1967), *Wi. urania* Karanovic & Kim, 2014 and *Wi. terpsichore* Karanovic & Kim, 2014, and (2) *Itostenhelia* for *I. polyhymnia* Karanovic & Kim, 2014 and *I. golikovi* (Chislenko, 1978) (= *Stenhelia* (*Delavalia*) *golikovi* Chislenko, 1978). More recently, Gómez (2020) added *Wi. reducta* Gómez, 2020 to the species of *Willenstenhelia*, and proposed a new genus, *Lonchoeidestenhelia* Gómez, 2020 for *L. prote* Gómez, 2020. As a result of all these contributions, the subfamily Stenheliinae is currently composed of fourteen genera: *Anisostenhelia*, *Beatricella*, *Cladorostrata*, *Delavalia*, *Itostenhelia*, *Lonchoeidestenhelia*, *Melima*, *Muohuysia*, *Onychostenhelia*, *Pseudostenhelia*, *Stenhelia*, *Wellstenhelia*, *Wellstenvalia* **gen. nov.**, and *Willenstenhelia.*

Karanovic & Kim (2014) adopted Mu & Huys' (2002) hypothesis regarding the sistergroup relationship between *Wellstenhelia* (which includes Mu & Huys' (2002) *D. hanstroemi*-*D. bocqueti* lineage) and *Muohuysia*, and supported Mu & Huys' (2002) view that, being *Mu. xylophila* (not *Muohuysia hylophila* as in Karanovic & Kim (2014: 91)) the only other stenheliin with curved spiniform elements on P2–P3 ENP1 but also with a three-segmented P1 ENP, the two-segmented P1 ENP of *Wellstenhelia* (but also of *Itostenhelia* and *Willenstenhelia* (Karanovic & Kim 2014: 88)), could have had evolved independently in some other species of *Delavalia*.

Karanovic & Kim (2014) proposed the genus *Wellstenhelia* based on four apomorphies, but as shown below, the presence of a very strong curved seta on P2–P3 ENP1 is shared by a core group of genera including *Muohuysia*, *Wellstenhelia*, and *Wellstenvalia* **gen. nov.**, (the *MWW* lineage) and a sistergroup relationship between them is hypothesized (see also Mu & Huys 2002; Karanovic & Kim 2014). Moreover, within that lineage, only *Wellstenhelia* and *Wellstenvalia* **gen. nov.** (the *WW* lineage) display the combination of a two-segmented endopod of P1 and the presence of a strong inner spine-like element on P2–P3 ENP1, being the lack of armature on the male P5 endopodal lobe one potential apomorphy for *Wellstenhelia* (see below). The new species, *We. euterpoides* **sp. nov.**, clearly belongs to the *WW* lineage on account of a two-segmented P1 ENP and presence of a strong spine-like inner element on P2–P3 ENP1, and was allocated into *Wellstenhelia* based on the presence of three setae only on the baseoendopod of the female P5. The latter seems to be synapomorphic for *We. euterpoides* **sp. nov.** and *We. euterpe*, and a close relationship between them is hypothesized. As noted below, Karanovic & Kim (2014) described the mandible of all the species of *Wellstenhelia* with a medial seta on the cutting edge and seems to be another probable apomorphy for the genus. The lack of the medial seta on the cutting edge of the mandible of *Wellstenhelia euterpoides* **sp. nov.** is considered here a secondary loss. Karanovic & Kim (2014) diagnosed the genus *Wellstenhelia* with a non-prehensile maxilliped with two seta-like endopodal elements of which the distalmost is homologous to the endopodal claw in the subchelate maxilliped of most harpacticoids. However, the apical endopodal element in the South Californian species is clearly stronger and stiffer than the accompanying seta, giving the maxilliped a subchelate appearance. The South Californian species can be readily separated from all its other congeners and especially from *We. euterpe* by the armature of P2–P4 EXP3 (with three outer spines in *We. euterpe* and in all other species of the genus, but with two outer spines only in the new species), armature complement of the female P5 EXP (with six setae in *We. euterpe* and in all other species of the genus, but five setae only in *We. euterpoides* **sp. nov.**), and length of the caudal rami (1.7 times as long as wide in *We. euterpe*, but 6.4 times as long as wide in *We. euterpoides* **sp. nov.**). Interestingly, some other stenheliins (*e.g. Melima*) possess two outer spines only on P2–P4. This character state seems to have evolved independently in several lineages.

The inner strong element of P2 ENP1 is not fused to the supporting segment in *Wellstenhelia* (the P2 ENP of *We. melpomene* remains unknown) nor in *Muohuysia*. The fusion of the inner strong element of P2 ENP1 in *Wellstenvalia* **gen. nov.** seems to be autapomorphic for this genus.

Huys & Mu (2008) drew attention to a core group of Stenheliinae (*Onychostenhelia*, *Cladorostrata*, and *Delavalia*) but also *Pseudostenhelia* (see Gómez 2021) sharing a synapomorphic confluent maxillulary exopod and endopod not fused to the supporting basis. The confluent maxillulary rami separated from the basis has been observed also in *Wellstenhelia* (Karanovic & Kim 2014). Note that in the text description of *We. qingdaoensis*, Ma & Li (2011) described the maxillulary rami as confluent but separated from the basis, but in their figure 3D (Ma & Li 2011: 1090) they showed both rami discrete, not fused to the supporting basis; Karanovic & Kim (2014) re-described the maxillulary rami of the species as confluent but separated from the basis. The significance of this condition in the maxillulary rami is not clear. Huys & Mu (2008) suggested that it could be a strong synapomorphy for *Onychostenhelia*, *Cladorostrata* and *Delavalia*, but its presence in *Pseudostenhelia*, and *Wellstenhelia* renders its synapomorphic status doubtful unless convergent evolution is assumed. The confluent maxillulary rami fused to the supporting basis observed for *Willenstenhelia* (Karanovic & Kim 2014) seems to be autapomorphic for this genus. Note that in their written description, Ma & Li (2018) described the maxillulary endopod and exopod of *Wi. mirabilipes* fused basally and separated from the supporting basis, but in their figure they (Ma & Li 2018: 198, fig. 4) showed the endopod and exopod of the maxillule not fused basally and separated from the supporting basis. The condition of the maxillulary rami of *Wi. mirabilipes* is considered here doubtful and needs confirmation. The discrete maxillulary exopod and endopod not fused to the basis seems to be a strong synapomorphy for a core group composed of *Stenhelia*, *Beatricella*, *Melima*, *Anisostenhelia*, and *Muohuysia* (Huys & Mu 2008), and seems to have appeared independently also in *Itostenhelia* (Karanovic & Kim 2014) and *Wellstenvalia* **gen. nov.**

The lateral caudal setae I and II are located subdistally close to the outer corner in most stenheliin species, and a more proximal position of these setae has been observed only in few *Delavalia* species (*e.g. D. arctica* Scott, 1899 and *D. intermedia*). Caudal lateral setae I and II are situated subdistally in *Stenhelia*, *Anisostenhelia*, *Beatricella*, *Muohuysia*, *Wellstenhelia*, *Itostenhelia*, *Lonchoeidestenhelia*, and *Willenstenhelia*, and the more proximal situation of these setae in *Wellstenvalia* **gen. nov.—**just below the middle of each caudal ramus—, is another potential apomorphy for the new genus.

Relationships of *Wellstenvalia* gen. nov.

Mu & Huys (2002: 197) proposed seven synapomorphies supporting a sistergroup relationship between *Anisostenhelia*, with its only species *A. asetosa* (Thistle & Coull, 1979), and the genus *Stenhelia*. They noticed that *Beatricella* does not display any of the seven synapomorphies supporting the sistergroup relationship between *Stenhelia* and *Anisostenhelia*, but that the lack of an inner seta on P1 EXP2 could be a potential synapomorphy for *Beatricella*, *Stenhelia* and *Anisostenhelia* (but see Gómez 2021), and also for *Lonchoeidestenhelia* (Gómez, 2020). Amongst the seven synapomorphies supporting a sistergroup relationship between *Anisostenhelia* and *Stenhelia* proposed by Mu & Huys (2002: 197), the synapomorphic male P5 exopod with two outermost elements modified into spines (see Mu & Huys (2002: 200, fig. 14G)), which is also present in *Lonchoeidestenhelia* (see Gómez, 2020), stands out. Two outer spines on the male P5 EXP are present also in *Itostenhelia* (in this genus the second outermost spine is fused to supporting exopod) and in some species of *Delavalia* (*e.g. D. mixta* (Wells & Rao, 1987) and *D. latioperculata* (Itô, 1981)). The presence of two spines on the male P5 EXP of *Willenstenhelia* is not conclusive. Hence, the (syn-)apomorphic status of the male P5 exopod with two outermost elements modified into spines for *Anisostenhelia* and *Stenhelia,* and also *Lonchoeidestenhelia*, seems questionable.

Mu & Huys (2002) noticed that *Beatricella* has a more primitive armature formula of swimming legs with two inner setae on P2 EXP3 (armature formula 223) and three inner setae on P3 EXP3 (armature formula 323), that the second innermost seta on the P5 BENP is not modified, and that the inner element on the male P6 is small and setiform. Mu & Huys (2002: 201) justified the exclusion of *S. asetosa* from *Stenhelia*, and its inclusion in their newly erected genus *Anisostenhelia*, arguing that *S. asetosa* could not be accommodated in *Stenhelia* because of the unmodified endopodal spine in the P5 of both sexes. Although its significance is not clear, it is noteworthy that *Beatricella*, *Anisostenhelia,* the *MWW* lineage, *Lonchoeidestenhelia*, and *Itostenhelia* and *Willenstenhelia* share the unmodified endopodal element of P5.

Additionally, Mu & Huys (2002: 203) presented three apomorphies for *Beatricella*. The male P2 ENP2 drawn out into sigmoid process finely pinnate and outer margin with row of long spinules is unique to *Beatricella*, but the apomorphic status of the long stout seta on P4 ENP1 is not clear. This seta reaches well beyond P4 EXP3 in *B. aemula*, but a similar though somewhat shorter element is common to other genera and species (*e.g.* some species of *Delavalia* such as *D. acutirostris* (Willey, 1935), *D. clavus* (Wells & Rao, 1987), *D. confluens* (Lang, 1965), *D. diegensis*, etc., *Muohuysia*, *Wellstenhelia*, *Itostenhelia*, *Wellstenvalia* **gen. nov.**, and *Willenstenhelia*). Also, the fused male P5 EXP and BENP with outermost element modified into a strong spine is common to a larger group of species of Willen's (2003) *normani*-group and some other species outside that group. This seems to render Mu & Huys' (2002: 203) hypothesis about the apomorphic status of this character for *Beatricella*, and Willen's (2003: 1706) hypotheses about the autapomorphic status of this character for her *normani*-group, doubtful.

The relationships between either *Stenhelia*-*Anisostenhelia*-*Lonchoeidestenhelia* or *Beatricella* and the *MWW* lineage is not clear. However, the primitive armature formula of P2 EXP3 (223) and P3 EXP3 (323) of *Beatricella vs* the armature formula of P2 EXP3 (123) and P3 EXP3 (223) of *Stenhelia, Anisostenhelia,* and *Lonchoeidestenhelia,* seems to support a closer relationship between the former and the *MWW* lineage (armature formula of P2 EXP3, 223, except for *Wellstenvalia* (123) and *We. euterpoides* **sp. nov.** (122); armature formula of P3 EXP3, 323, except for *We. melpomene* (223), and *We. euterpoides* **sp. nov.** (222)). *Wellstenvalia* **gen. nov.** shares the reduction in inner armature of P2 EXP3 from two to one seta with *Stenhelia, Lonchoeidestenhelia,* and *Anisostenhelia*, but also with *We. euterpoides* **sp. nov.**, but the loss of one inner seta on P2 EXP3 of *Wellstenvalia* **gen. nov.** and *We. euterpoides* **sp. nov.** could be attributed to a secondary loss. *Stenhelia, Lonchoeidestenhelia,* and *Anisostenhelia*, *Beatricella*, *Muohuysia*, and *Willenstenhelia* and *Itostenhelia* share the presence of two inner setae on P2 ENP2. Amongst the species of *Wellstenhelia*, two inner setae on P2 ENP2 are present only in *We. hanstroemi* and *We. melpomene*. Karanovic & Kim (2014) questioned the presence of two setae instead of only one element on P2 ENP2 of these two species arguing that these would be the only species of *Wellstenhelia* with such armature complement and that neither Lang (1948) nor Kornev & Chertoprud (2008) seem to have studied this appendage in detail. The reduced inner armature on P3 EXP3 from three to two is present in *We. melpomene* but also in *We. euterpoides* **sp. nov.**, and is also shared with *Stenhelia, Lonchoeidestenhelia,* and *Anisostenhelia*, and *Willenstenhelia*, pointing to a probable close relationship between these genera. Also, *Anisostenhelia* and *Willenstenhelia* are the only genera without inner seta on P2–P4 EXP1 supporting a probable relationship between them.

The anal operculum of stenheliins has received little attention. It is present and well developed in *Lonchoeidestenhelia*, *Beatricella* (Mu & Huys 2002)*, Muohuysia* (Mu & Huys 2002), *Itostenhelia* (Karanovic & Kim 2014), *Willenstenhelia* (Karanovic & Kim 2014), *Wellstenvalia* **gen. nov.,** and most species of *Delavalia*. It is very small in *Melima* (Willen 2002, 2003) and *Pseudostenhelia* (Willen 2003)—the anal operculum is very short or inconspicuous in *P. wellsi* Coull & Fleeger, 1977 (Coull & Fleeger 1977; Gómez 2021), and its size and shape is not conclusive in *P. prima* Wells, 1967 and *P. secunda* Wells, 1971 (Wells 1967, 1971)—. Willen (2003: 1703) hypothesized on a modified anal operculum (large and strongly sclerotized plate covering much of the anal somite and reaching to its distal margin or beyond) as a strong autapomorphy for her group A of species of *Delavalia*. The presence of such a well-developed anal operculum could point to a close relationship between *Beatricella, Muohuysia*, *Itostenhelia*, *Willenstenhelia*, and *Wellstenvalia* **gen. nov.** In contrast, according to Willen (2003), many stenheliin species including *Melima*, *Pseudostenhelia* and some species of *Delavalia* (the disparity in the shape of the anal operculum in *Delavalia* could be indicative of its polyphyletic status) display a plesiomorphic anal operculum (semicircular, relatively small, weakly chitinized and flanked by a sensillum on each side). The anal operculum is also very short or inconspicuous in *Wellstenhelia* (Karanovic & Kim 2014) and *We. qingdaoensis* (Karanovic & Kim 2014; Ma & Li 2011), and is completely absent in *Stenhelia* and *Anisostenhelia* (Mu & Huys 2002), and *Onychostenhelia* (Huys & Mu 2008).

The caudal seta I seems to be transformed into a spine in *Stenhelia*. It is also a spine in *Anisostenhelia*, *Lonchoeidestenhelia*, *Cladorostrata*, *Itostenhelia*, most species of *Wellstenhelia* (*We. bocqueti*, *We. calliope*, *We. erato*, *We. euterpe*, *We. euterpoides* **sp. nov.**, *We. qingdaoensis*), and in *Me. papuaensis* Willen, 2002 (the condition of this seta is unknown for the rest of the species of *Melima*). The shape of caudal seta I is not clear for *We. hanstroemi*, *We. melpomene* and *Mu. xylophila*. The condition of this seta in *Beatricella* is not conclusive, but it is probably a spine. On the contrary, caudal seta I is a relatively long seta (most probably plesiomorphic) in *Pseudostenhelia* and *Onychostenhelia*, but a very small seta in *We. clio*, *Wellstenvalia* **gen. nov.** and *Willenstenhelia* (it is a very small seta in *Wi. thalia* (Karanovic & Kim 2014: 77, fig. 49) and *Wi. mirabilipes* Ma & Li, 2018 (Ma & Li 2018: 196, fig 2b); this seta has not been described for *Wi. urania* and *Wi. terpsichore*, but it is probably a small seta). The shape of caudal seta I of *Delavalia* has received little attention and its morphology is not conclusive for most species. However, this seta seems to vary from a stout spine (*e.g. D. adriatica* (Marinov & Apostolov, 1981), *D. bermudensis* (Coull, 1969), *D. breviseta* (Wells & Rao, 1987), *D. elisabethae* (Por, 1960), and *D. gundulae*), to a well-developed (*e.g. D. arenicola* (Wilson, 1932), and *D. latipes* (Lang, 1965)) or very small seta (*e.g. D. clavus*, and *D. paraclavus* (Wells & Rao, 1987)). The significance of the reduction of this element to a very small seta located ventral to caudal seta II is not clear, but could indicate some relationship between *Wellstenvalia* **gen. nov.**, *We. clio*, and *Willenstenhelia*.

Redefinition of *Wellstenhelia*

According to Karanovic & Kim (2014), the genus *Wellstenhelia* is supported by the following apomorphies: 1) presence of a very strong curved seta on P2–P3 ENP1, 2) male sexual dimorphism expressed in the slenderness of some setae on P3 and P4, 3) male P5 EXP with three setae, of which the innermost strongest, and 4) lack of armature on the male P5 endopodal lobe. However, the independent origin (convergence) of the two-segmented P1 ENP in the *WW* lineage and some species of *Delavalia*, and the sistergroup relationship between the *WW* lineage and *Muohuysia* based on the shared inner strong curved element on P2–P3 ENP1, render such strong element synapomorphic for the *MWW* lineage. Similarly, the male sexual dimorphism expressed in the slenderness of some setae on P3 and P4 seems to be synapomorphic for the *WW* lineage (such dimorphism has not been reported for *Muohuysia*). The apomorphic status of the male P5 EXP for *Wellstenhelia* (with three setae of which the innermost is the strongest) in Karanovic & Kim (2014: 90) is actually a synapomorphy for the *WW* lineage. Although the males of *We. euterpe*, *We. melpomene*, *We. hanstroemi*, and *We. bocqueti* remain unknown, the only true apomorphy for *Wellstenhelia* seems to be the lack of armature on the male P5 endopodal lobe.

Even though Ma & Li (2011) did not mention or illustrate any seta on the cutting edge of the mandible, Karanovic & Kim (2014) re-described the mandible of *We. qingdaoensis* with a medial seta on the cutting edge. This seta is present in all the species attributed so far to *Wellstenhelia* (Karanovic & Kim 2014). This seta seems to be unique and constitutes a potential synapomorphy for some species of that genus.

Stenhelia, *Lonchoeidestenhelia*, *Anisostenhelia*, *Beatricella*, *Muohuysia*, *Wellstenvalia* **gen. nov.**, and *Melima* display subchelate maxillipeds with a one-segmented endopod armed with an apical claw and a seta. *Wellstenhelia*, *Itostenhelia*, and *Willenstenhelia* possess non-prehensile maxillipeds. The maxilliped of *Wellstenhelia* and *Itostenhelia* possesses a small one-segmented endopod with two setae, of which the apicalmost is homologous to the endopodal claw of the other seven genera with subchelate maxillipeds. The apicalmost element of the maxillipedal endopod of *We. euterpoides* **sp. nov.** is visibly stronger than the accompanying subordinate seta giving the maxilliped a subchelate prehensile appearance. The maxillipedal endopod is incorporated into the basis in *Willenstenhelia*, but the endopodal elements are still discernible. Some *Delavalia* species possess non-prehensile maxillipeds (*e.g. D. andamanica* (Rao, 1993), *D. breviseta*, *D. clavus*, *D. elisabethae*, *D. hirtipes* (Wells & Rao, 1987), *D. latioperculata*, *D. madrasensis* (Wells, 1971), *D. mixta*, *D. oblonga* (Lang, 1965), *D. palustris* Brady, 1869, *D. paraclavus*, *D. schminkei* (Willen, 2002), *D. stephensoni* (Greenwood & Tucker, 1984) and *D. valens* (Wells & Rao, 1987)). The phylogenetic importance of the subchelate or non-prehensile maxilliped in *Delavalia* species is not well-understood, but this, and the disparity in morphology of the dimorphic male P2 ENP, swimming leg armature pattern, P5 setation and segmentation, caudal ramus shape, morphology of P1, and anal operculum supports the di- or polyphyletic status of the genus (Mu & Huys 2002). Mu & Huys (2002) suggested that the *D. hanstroemi*-*D. bocqueti* lineage (included in *Wellstenhelia*) and *Mu. xylophila* might have derived from a common ancestor which already displayed the spinous modifications of P2–P4 ENP and had lost one of the endopodal setae on the female P5. It is conceivable that such common ancestor also displayed a three-segmented P1 ENP and a subchelate maxilliped. This would imply that the non-prehensile condition of the maxilliped in some *Delavalia* species evolved independently of that in *Wellstenhelia*, *Itostenhelia*, and *Willenstenhelia*, supporting the potential synapomorphic non-prehensile maxilliped for the latter three genera.

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