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New insights into polyphyly of the harpacticoid genus *Delavalia* (Crustacea, Copepoda) through morphological and molecular study of an unprecedented diversity of sympatric species in a small South Korean bay

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Abstract

Polyphyly of the genus *Delavalia* Brady, 1869 has been postulated previously based on intuitive methods, but no phylogenetic study was ever conducted. A chance discovery of seven sympatric species of this genus in the highly industrialized Gwangyang Bay in South Korea, in addition to one species each from the closely related genera *Stenhelia* Boeck, 1865 and *Onychostenhelia* Itô, 1979, prompted a renewed interest in the phylogenetic relationships within the subfamily Stenheliinae Brady, 1880. Additional surveys along the Korean coast failed to produce *Delavalia* species, but comparative material was sourced from Posyet Bay in the Russian Far East. Aims of this study were to reconstruct phylogenetic relationships of the newly collected stenheliini using molecular methods, test the hypothesized polyphyly of *Delavalia*, formally describe any resulting monophyletic units, perform a comparative study of traditional morphological and novel micro-morphological characters, and describe all new *Delavalia* species. A fragment of the mtCOI gene was successfully PCR-amplified from 23 stenheliini specimens and an additional 300 specimens were studied for morphological characters. All phylogenetic analyses supported the presence of at least eight genetically divergent lineages, most with very high bootstrap values, and the polyphyletic nature of *Delavalia* is demonstrated. Three new genera, each supported by molecular data and a number of morphological synapomorphies, were erected to accommodate the newly discovered species and some previously described members of *Delavalia*: *Wellstenhelia* **gen. nov.**, *Itostenhelia* **gen. nov.**, and *Willenstenhelia* **gen. nov.** The Chinese *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.** is recorded for the first time in Korea, and six new species are described from Gwangyang Bay: *Wellstenhelia calliope* **sp. nov.**, *Wellstenhelia clio* **sp. nov.**, *Wellstenhelia erato* **sp. nov.**, *Wellstenhelia euterpe* **sp. nov.**, *Itostenhelia polyhymnia* **sp. nov.**, and *Willenstenhelia thalia* **sp. nov.** Additionally, *Itostenhelia golikovi* (Chislenco, 1978) **comb. nov.** is redescribed from newly collected material from the type locality in Russia and its male described for the first time, while *Wellstenhelia melpomene* **sp. nov.**, *Willenstenhelia urania* **sp. nov.**, and *Willenstenhelia terpsichore* **sp. nov.** are established as new names for previously reported populations of two presumably widely distributed *Delavalia* species.

Key words: Harpacticoida, Miraciidae, marine, systematics, phylogeny, barcoding, new species

Introduction

The subfamily Stenheliinae Brady, 1880 is currently recognised as one of three well-defined suprageneric groups within the second largest harpacticoid family Miraciidae Dana, 1846, beside the nominotypical subfamily and Diosaccinae Sars, 1906 (see Willen 2000; Boxshall & Halsey 2004; Wells 2007; Huys & Mu 2008). Stenheliins are common inhabitants of the marine benthos, and can be found from the deep sea (Willen 2003) to shallow brackish waters (Dussart & Defaye 2001). Although there is some disagreement about the exact number of morphological synapomorphies defining this subfamily (Willen 2000, 2002; Huys & Mu 2008), these six are undisputed for adults: laterally displaced genital apertures in females; triangular and usually bifid rostrum, with dorsal pair of sensilla inserted in deep anterior recesses; elongated basis and endopod of mandibula (often also with one extremely long and strong seta); maxilliped with only 3 syncoxal setae, closely positioned to one another, and setation of the ancestral second endopodal segment lost; female fifth leg with laterally directed exopod; and some form of sexual dimorphism in the second swimming leg (although probably secondarily lost in several species). Some additional synapomorphies are postulated for their naupliar morphology (Dahms et al. 2005) but they need to be verified in a broader taxon sampling (Huys & Mu 2008). However, we are yet to see either a morphology based or molecular phylogenetic analysis of this subfamily or any of its genera, and all previous discussions about their relationships were purely intuitive. Eighty-four valid stenheliin species (Wells 2007; Walter & Boxshall 2013) are currently classified into nine genera: *Anisostenhelia* Mu & Huys, 2002 (monospecific); *Beatricella* T. Scott, 1905 (monospecific); *Cladorostrata* Tai & Song, 1979 (two species); *Delavalia* Brady, 1869 (59 species and subspecies); *Melima* Por, 1964 (six species); *Muohuysia* Ozdikmen, 2009 (monospecific); *Onychostenhelia* Itô, 1979 (two species); *Pseudostenhelia* Wells, 1967 (four species); and *Stenhelia* Boeck, 1865 (eight species). The most speciose and morphologically most diverse genus *Delavalia* is also taxonomically most problematic, and expectedly postulated to be either paraphyletic (Willen 2002) or polyphyletic (Mu & Huys 2002). Several groups of species were recognized in this genus by Willen (2003) and Huys & Mu (2008), but without any phylogenetic or nomenclatural consideration. Coull (1976) provided the last updated key to 35 species and subspecies of *Delavalia* known at the time (modified from Lang 1965), Mu & Huys (2002) provided a key to species of *Stenhelia*, and Huys & Mu (2008) provided a key to genera of stenheliins.

Stenheliins are rare and not diverse in South Korea, despite this country being relatively well-surveyed for marine harpacticoids (Lee et al. 2012; Lee & Karanovic 2012). So far, only *Onychostenhelia bispinosa* Huys & Mu, 2008 was reported by Kim et al. (2011) (repeated in Lee et al. 2012), a species originally described from the Bohai Sea, China (Huys & Mu 2008). Therefore, it was a great surprise to discover ten sympatric species (one *Stenhelia*, one *Onychostenhelia*, and seven *Delavalia*) in Gwangyang Bay, on the southern coast of the Korean peninsula (Fig. 1). The surprise was even greater considering the fact that Gwangyang Bay is one of the most affected bays in Korea by industrial development, with a large man-made island in the middle of it. Further samplings on the south and east coast of Korea failed to produce any stenheliins, but we obtained for this study a sample from Posyet Bay near Vladivostok, Russia, which contained two species (one *Stenhelia* and one *Delavalia*). Preliminary morphological examination revealed that six out of eight *Delavalia* species are new to science, while one Korean species was identified as *Delavalia qingdaoensis* Ma & Li, 2011. The latter species was originally described from Jiaozhou Bay near Qingdao, China (Ma & Li 2011) and this represents its second record ever and the first one in Korea. The Russian *Delavalia* was identified as *Delavalia golikovi* Chislenko, 1978. While some of the eight studied *Delavalia* species proved to be morphologically quite similar to each other, others showed significant differences in traditionally used morphological characters, prompting the old question of monophyly of this group.

Aims of this study were to: examine morphologically all eight *Delavalia* species from Korea and Russia, using both traditional characters and novel microstructures of ornamentation of body somites; formally describe six new species; redescribe in detail the Korean population of *Delavalia qingdaoensis*; redescribe in detail the Russian *Delavalia golikovi*; derive a molecular phylogeny of Korean and east Russian stenheliins based on the mtCOI gene; test monophyly of the genus *Delavalia*; and define any possible monophyletic units.

Employing molecular techniques in addition to traditional morphological ones was one of the priorities of this study to aid in species delineation and reconstruction of their phylogenetic relationships. Recently, DNA-based species identification methods, referred to as “DNA barcoding”, have been widely employed to estimate levels of species diversity, with the 5’ end of the mitochondrial cytochrome C oxidase subunit I gene (mtCOI) proposed as

the “barcode” for all animal species (Hebert et al. 2003). The advantage of the mtCOI gene is that it often shows low levels of genetic variation within species, but high levels of divergence between species; for the most common divergence values in a variety of crustacean taxa see Lefébure et al. (2006). In recent years several studies on copepods showed that combining molecular and morphological methods can help answer questions related to cryptic speciation (Bláha et al. 2010; Sakaguchi & Ueda 2010; Karanovic & Krajicek 2012a, Hamrova et al. 2012), invasions of new habitats and colonisation pathways (Lee et al. 2003, 2007; Winkler et al. 2008; Karanovic & Cooper 2011a, 2012), anthropogenic translocation (Karanovic & Krajicek 2012a), short range endemism and allopatry (Karanovic & Cooper 2011a), and definition of supraspecific taxa in conservative genera or families (Huys et al. 2006, 2007, 2009, 2012; Wyngaard et al. 2010; Karanovic & Cooper 2011b, Karanovic & Krajicek 2012b). However, some studies showed that currently prevailing morphological methods of identifying copepod species are inadequate, and suggested the use of alternative microstructures, such as pores and sensilla pattern on somites (Alekseev et al 2006; Karanovic & Krajicek 2012a; Karanovic & Cho 2012; Karanovic & Lee 2012; Karanovic et al 2012, 2013), an approach also tested in this study of diverse but sympatric stenheliins.

Material and methods

Seventeen stations were sampled for this study in Gwangyang Bay, on the South Coast of South Korea (Fig. 1), on four occasions: 18 February 2012, 30 July 2012, 14 October 2012, and 18 November 2012. Depth ranged from four to 11 metres and environmental conditions changed greatly with seasons. A handheld multiparameter water quality meter YSI556 (YSI Environmental, Yellow Springs, USA) was used for all measurements, except for chlorophyll a, which was measured by manual filtering with different size filters, and temperature, which was measured with a mercury fill glass thermometer. Coordinates were taken with a Garmin GPS, model Oregon 300. Granular analysis of the sediment was conducted manually, following the methods and classification of Folk (1974). Sediment samples were primarily collected with a van Veen grab sampler (surface area: 0.1 m²) from the Hansan research vessel. Subsamples were then collected by acrylic corers (surface area: 10 cm²) for quantitative analysis, and surface sediments were collected by a small shovel for qualitative analysis. Each sediment sample was fixed in 99.9% ethanol. Animals in the sediments were extracted by Ludox method (Burgess 2001) and preserved in 99.9% ethanol for morphological or molecular studies. Specimens from Posyet Bay (Minonosok inlet) in Russia were collected with hand-nets (100 µm mesh size) using Scuba-diving from a sandy bottom and between four and seven metres of depth, and also fixed in 99.9% ethanol. Locality data and number of specimens are given in the Material examined section for each species below. All material is deposited at the National Institute of Biological Resources (NIBR), Incheon, South Korea.

Specimens were dissected and mounted on microscope slides in Faure's medium, which was prepared following the procedure discussed by Stock and von Vaupel Klein (1996), and dissected appendages were then covered by a coverslip. For the urosome or the entire animal, two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. By manipulating the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making possible the observation of morphological details. During the examination the water slowly evaporates and the appendages eventually remain in a completely dry Faure's medium, ready for long-term storage. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, equipped with N-PLAN (5x, 10x, 20x, 40x and 63x dry) or PL FLUOTAR (100x oil) objectives. Specimens that were not drawn were examined in propylene glycol and, after examination, were again preserved in 99.9% ethanol. Specimens for scanning electron microscopy (SEM) were dehydrated in progressive ethanol concentrations, transferred into pure isoamyl-acetate, critical-point dried, mounted on stubs, coated in gold, and observed under a Hitachi S-4700 microscope on the in-lens detector, with an accelerating voltage of 10 kV and working distances between 12.3 and 13.4 mm; micrographs were taken with a digital camera.

Morphological terminology follows Huys and Boxshall (1991), except for the numbering of the setae of the caudal rami and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), as an attempt to standardise the terminology for homologous appendages in different crustacean groups. Sensilla and pores on all somites (body segments) were numbered consecutively from the anterior to posterior part of the body and from the dorsal to ventral side, to aid in the recognition of serially

homologous structures and future comparisons with other species; they are not intended as a novel terminology. Only the first presented species is described in full, while all subsequent descriptions are shortened by making them comparative. Arabic numerals are used for designating pores and sensilla on somites in the first described species, as well as for all homologous structures in other species. A variety of other symbols were used to designate unique pores and sensilla in subsequent species descriptions (currency symbols, geometric shapes, Roman numerals, typography symbols and Greek letters).

Specimens for molecular analysis were examined without dissection under a compound microscope (objective 63x dry) in propylene glycol, using a cavity well slide with a central depression. After examination they were returned to 99.9% ethanol. Before amplification whole specimens were transferred into distilled water for two hours for washing (to remove ethanol), and then minced with a small glass stick. DNA was extracted from whole specimens, except in one case when only one antennula was available, using the LaboPass™ extraction kit (COSMO Co. Ltd., Korea) and following the manufacturer's protocols for fresh tissue, except that samples were incubated in the Proteinase K solution overnight, step five was skipped, and 60 instead of 200 µl of Buffer AE was added in the final step, to increase the density of DNA. Mitochondrial cytochrome oxidase subunit I (mtCOI) gene was amplified through polymerase chain reaction (PCR) using PCR premix (BiONEER Co.) in TaKaRa PCR thermal cycler (Takara Bio Inc., Otsu, Shiga, Japan). The amplification primers used were the 'universal' primers LCO1490 and HCO2198 (Folmer et al. 1994). The amplification protocol was: initial denaturation 94°C for 300s, 40 cycles of denaturation 94°C for 30s, annealing at 42°C for 120s, extension at 72°C for 60s; final extension at 72°C for 600s, and final product was stored at 4°C. PCR results were checked by electrophoresis of the amplification products on 1% agarose gel with ethidium bromide. PCR products were purified with a LaboPass™ PCR purification kit and sequenced in both directions using a 3730xl DNA analyzer (Macrogen, Korea). For this study, DNA was extracted and the COI fragment successfully PCR amplified from 23 *Stenheliin* specimens (Table 1).

Obtained sequences were checked manually and aligned by ClustalW algorithm (Thompson et al. 1994) in MEGA version 5 (Tamura et al. 2011). The alignment was checked again and all sites were unambiguously aligned. The best evolutionary model of nucleotide substitution for our dataset was established by Akaike Information Criterion, performed with jModelTest (Guindon & Gascuel 2003; Posada 2008). For the maximum likelihood (ML) analysis the Hasegawa-Kishino-Yano model (Hasegawa et al., 1985) with gamma distributed rate heterogeneity (HKY + G) was selected. Neighbour joining (NJ) analysis used the Tamura-Nei model (Tamura & Nei 1993) with uniform rates (TN). Maximum parsimony (MP) analysis was conducted using a heuristic search option and default options (TBR branch swapping, ACCTRAN character state optimisation), with the exception of using random stepwise addition repeated 100 times. All phylogenetic and molecular evolutionary analyses were conducted using MEGA version 5 (Tamura et al. 2011). Five hundred bootstrap replicates were performed to obtain a relative measure of node support for the resulting trees. Average pairwise NJ distances for each dataset were also computed in MEGA version 5 using the Tamura-Nei model. All trees were rooted with *Schizopera leptafurca* Karanovic & Cooper, 2012 from Western Australia, its mtCOI sequences also available from GenBank prior to this study [JQ390578.1], which belongs to the subfamily Diosaccinae Sars, 1906 of the family Miraciidae Dana, 1846 (see above).

Systematics

Subphylum Crustacea Brünich, 1772

Class Maxillopoda Dahl, 1956

Suclass Copepoda H. Milne Edwards, 1840

Order Harpacticoida Dana, 1846

Family Miraciidae Dana, 1846

Subfamily Stenheliinae Brady, 1880

Genus *Wellstenhelia* gen. nov.

Type species. *Wellstenhelia calliope* sp. nov.

Other species. *Wellstenhelia clio* sp. nov.; *Wellstenhelia erato* sp. nov.; *Wellstenhelia euterpe* sp. nov.; *Wellstenhelia malpomene* sp. nov.; *Delavalia quingdaoensis* Ma & Li, 2011; *Stenhelia (Delavalia) hanstromi* Lang, 1948; *Stenhelia (Delavalia) bocqueti* Soyer, 1971.

Etymology. The new genus name is dedicated to Prof. John Wells, Emeritus at the Victoria University of Wellington, New Zealand, for his contribution to the taxonomy of harpacticoids in general, and stenheliin miraciids in particular. His last name is prefixed to the existing genus name *Stenhelia*.

Diagnosis. Habitus robust, spindle shaped in dorsal view, widest at posterior end of cephalothorax and tapering towards posterior end of body; podoplean boundary between prosome and urosome conspicuous. Integument of all somites relatively weakly sclerotized, generally smooth, without cuticular windows but covered with sparse pattern of extremely minute and deep pits, only visible on highest magnifications on scanning electron microscope. Hyaline fringe of somites broad and smooth. Rostrum with bifid tip, pair of dorsal sensilla near tip, and a single central dorsal pore in proximal half; no spinules. Genital double-somite in female completely fused along ventral surface but with a deep suture indicating original segmentation between genital somite and third urosomite dorso-laterally and dividing double-somite into equally long halves; anterior part inflated and with several rough folds and sutures laterally, around laterally placed genital apertures. Preanal somite without surface ornamentation. Anal somite clefted medially at posterior half, with pair of large dorsal sensilla on sides of short, membraneous anal operculum, posterior row of strong spinules, and strong ventral spinules along medial cleft. Caudal rami more or less cylindrical, two to four times as long as wide, with several strong and long inner spinules and with seven setae (three lateral, one dorsal and three apical), all in posterior sixth of ramus length. Female antennula eight-segmented, with distal posterior corner of first segment produced into short process, and eighth segment with four lateral setae and apical acrothek. Male antennula strongly geniculate and nine-segmented, with additional large aesthetasc on third segment. Antenna composed of short coxa, slender and curved allobasis, one-segmented endopod, and three-segmented exopod; endopod with two lateral spines flanking two slender setae. Mandibula with long and distally slender central seta on cutting edge, with six slender setae on small one-segmented endopod, and with three lateral and six apical setae on elongated and curved exopod; four apical exopodal setae strong and spiniform, one of them extremely long. Maxillula composed of praecoxa, coxa, basis, one-segmented endopod, and one-segmented exopod; endopod and exopod confluent basally, with two and four setae respectively. Maxilla composed of large syncoxa, small basis and even smaller one-segmented endopod; three coxal endites, armature formula (from dorsal side) 4.3.3; basis with two lateral slender setae and two apical geniculate spines; endopod with five slender setae. Maxilliped not prehensile, four-segmented, with armature formula 0.3.2.2. All swimming legs of similar size and long in comparison to body length, without spiniform processes on intercoxal sclerites, but with spiniform processes on inner distal corners of basis of second to fourth legs, exopods three-segmented, endopod of first leg two-segmented, endopods of second to fourth legs three-segmented, except endopod of second leg in male of some species with second and third segments partly or completely fused; armature formula of exopods/endopods in female as follows: first leg, 0.1.022/1.211; second leg, 1.1.223/1.1.1(2)21; third leg, 1.1.323/1.1.321; fourth leg, 1.1.323/1.1.221; inner seta on first endopodal segments of second and third legs spiniform, short and curved; inner seta on first endopodal segment of fourth leg strong and long; sexual dimorphism expressed in relative strength of some setae of second to fourth swimming legs. Female fifth legs joined by small triangular intercoxal sclerite or fused medially, without posterior spinules on baseoendopod at base of exopod, but usually with small spiniform process; endopodal lobe with four or three strong setae; exopod more or less trapezoidal in shape, with narrow base, only slightly longer than greatest width, with short rows of strong inner and outer spinules, bearing six setae; second and third innermost exopodal setae short, slender, and smooth, other setae spiniform, strong and bipinnate. Baseoendopods of male fifth leg fused medially, smooth; exopod with three setae, innermost one strongest. Female sixth leg a minute flap covering genital aperture, almost completely fused to somite, with single short seta and two minute spines.

***Wellstenhelia calliope* sp. nov.**

(Figs. 2–11)

Type locality. South Korea, South Sea, Gwangyang Bay, sampling station 5, muddy sediments, 34.852500°N 127.684722°E (Fig. 1).

Specimens examined. Female holotype dissected on one slide (collection number NIBRIV0000232672), holotype's right antennula destroyed for DNA sequence (amplification successful, Code 0122), male allotype dissected on one slide (collection number NIBRIV0000232673), two males paratypes and one female paratype together on one SEM stub (collection number NIBRIV0000232674), two male paratypes and one copepodid paratype together in ethanol (collection number NIBRIV0000232675); one male destroyed for DNA sequence (amplification unsuccessful), type locality, 30 July 2012, leg. K. Kim.

Etymology. The species is named after Calliope (Ancient Greek: Καλλιόπη), one of nine Muses from Greek mythology, who was a patron of epic poetry and song. The species name is a noun in apposition (in the nominative case), despite the Recommendation 31A of the ICZN (1999) about avoidance of personal names as nouns in appositions, because there is no case for it being confusing or misleading. Nine Muses refer to the nine new species described in this paper.

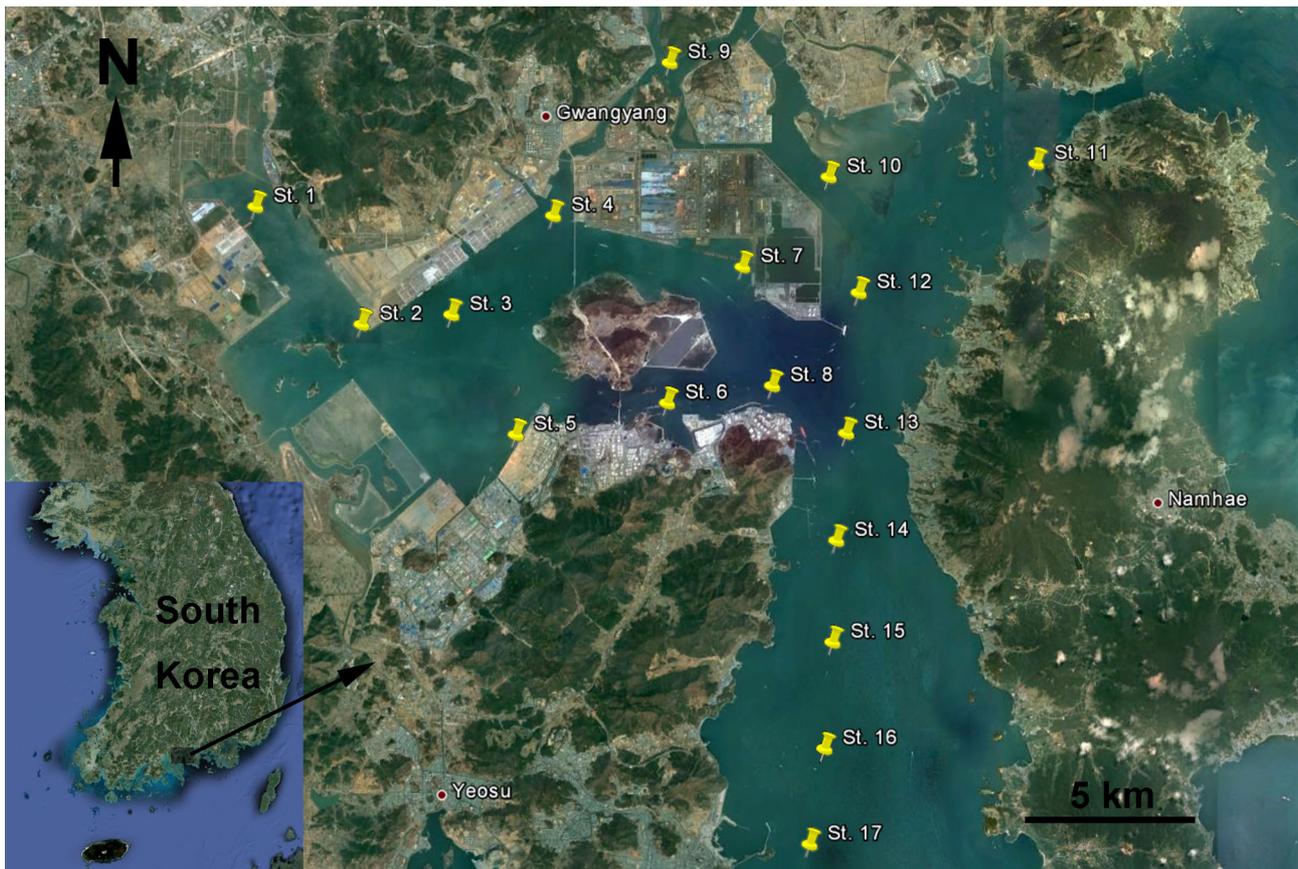


FIGURE 1. Map of 17 sampling locations in Gwangyang Bay. Inset showing location of the bay in South Korea. All maps from Google Earth.

Description. Female (based on holotype and one paratype). Total body length, measured from tip of rostrum to distal margin of caudal rami 742 and 755 μm respectively. Colour of preserved specimens yellowish; live specimens not observed. Nauplius eye not visible. Prosome comprising cephalothorax with completely fused first pedigerous somite, and three free pedigerous somites; urosome comprising first urosomite (= fifth pedigerous somite), genital double-somite (fused genital and third urosomites) and three free urosomites (last one being anal somite). Short sclerotized joint between prosome and urosome only discernible on ventral side. Habitus (Figs. 2A, B, 10A) robust, spindle shaped in dorsal view, widest at posterior end of cephalothorax and tapering posteriorly, boundary between prosome and urosome conspicuous; prosome/urosome length ratio 1.05, but prosome much wider and more voluminous. Body length/width ratio about 3; cephalothorax 1.7 times as wide as genital double-somite. Free pedigerous somites without lateral or dorsal expansions, pleurons only partly covering coxae of swimming legs in lateral view. Integument of all somites relatively weakly sclerotized, generally very smooth, without cuticular windows but covered with a sparse pattern of extremely minute and deep pits, only visible at highest magnifications on scanning electron microscope (such as in Fig. 11B). Hyaline fringe of all somites broad

and smooth, except for fourth pedigerous somite with narrow fringe dorsally, and for anal somite without hyaline fringe. Surface ornamentation of somites and caudal rami consisting of 78 paired and five unpaired pores and sensilla (numbered with Arabic numerals consecutively from anterior to posterior end of body, and from dorsal to ventral side in Figs. 2, 3, 4), and several rows of spinules on urosomites only.

Rostrum (Figs. 2C, 10E) large, trapezoidal, clearly demarcated at base, reaching midlength of second antennular segment, with bilobate tip, about 1.1 times as long as wide; with two dorsal sensilla near tip (no. 1) and single central dorsal pore at base (no. 2); base of rostrum about 3.4 times as wide as its anterior margin; sensilla inserted into deep recesses.

Cephalothorax (Figs. 2A, B, 3A, 10A) tapering anteriorly in dorsal view, about 0.9 times as long as wide; comprising 30% of total body length. Surface of cephalothoracic shield with two unpaired dorsal pores (nos. 14, 27), two unpaired dorsal sensilla (nos. 34, 40), 10 pairs of pores (nos. 6, 9, 10, 16, 19, 21, 28, 29, 33, 37), and 28 pairs of long sensilla (nos. 3–5, 7, 8, 11–13, 15, 17, 18, 20, 22–26, 30–32, 35, 36, 38, 39, 41, 42); sensilla and pores 32–42 belonging to first pedigerous somite incorporated into cephalothorax.

Pleuron of second pedigerous somite (first free) (Figs. 2A, B, 3C, 10B) with one pair of anterior dorsal pores (no. 43) and seven pairs of long sensilla (nos. 44–50); lateral pairs of sensilla nos. 44, 50, and 49 serially homologous to pairs nos. 32, 39, and 42 on first pedigerous somite respectively; other homologies difficult to define.

Third pedigerous somite (Figs. 2A, B, 3B, 10B) slightly smaller than second pedigerous somite, pleuron with one pair of anterior dorsal pores (no. 51) but with only five pairs of sensilla (nos. 52–56); anterior pores more widely spaced than on second pedigerous somite; recognising serially homologous pairs easier with lateral (52=44, 56=50, 55=48) than with dorsal sensilla (possibly 53=45 and 54=46).

Fourth pedigerous somite (Figs. 2A, B, D, 10B, C) much smaller and shorter than previous two somites, especially in dorsal view, pleuron with antero-lateral pair of pores (no. 57) and five pairs of sensilla (nos. 58–62); pores not serially homologous to previous two somites, but all sensilla share homologues on third pedigerous somite (58=53, 59=54, 60=55, 61=56, and 62=52).

First urosomite (Figs. 2A, B, 10C) about as long as fourth pedigerous somite, with one pair of dorsal anterior pores (no. 63), one pair of lateral pores (no. 67), and three pairs of sensilla along distal margin (nos. 64–66); hyaline fringe much wider than in fourth pedigerous somite.

Genital double-somite (Figs. 2A, B, 4A, 10C) 1.4 times as wide as long (ventral view); completely fused ventrally but with deep suture indicating original segmentation between genital and third urosomites dorso-laterally, thus dividing double-somite into equally long halves; anterior half of genital double-somite 1.2 times as wide as posterior, inflated laterally; anterior part with one pair of dorso-lateral pores (no. 68), two pairs of long dorsal sensilla (nos. 69 & 70), and two short rows of 6–8 strong spinules above sensilla no. 70; serially homologous pores and sensilla of anterior part of double-somite and those of first urosomite relatively easily established (i.e. 68=63, 69=64, and 70=65); posterior part with three pairs of posterior sensilla (nos. 71–73) and long row of strong spinules, interrupted dorsally between sensilla pair no. 71 and slightly ventro-laterally halfway between sensilla nos. 72 & 73; establishing serially homologous sensilla of posterior and anterior part of double-somite not easy (probably only 71=70); hyaline fringe wider than in first urosomite. Female genital complex (Fig. 4A) weakly sclerotized and hardly distinguishable from internal sutures and soft tissue, copulatory pores not exposed on surface; paired genital apertures situated ventro-laterally, close to anterior margin and covered by reduced sixth legs.

Third urosomite (Figs. 2A, B, 4A) with one pair of anterior ventro-lateral pores (no. 74), three pairs of posterior sensilla (nos. 75–77), and posterior row of spinules interrupted dorsally between dorsal pair of sensilla (no. 75) and laterally on both sides of lateral sensilla (no. 76); lateral interruption of posterior row of spinules wider than in genital double-somite; all sensilla with homologous pairs on genital double-somite (i.e. 75=71, 76=72, 77=73) but ventral pair (no. 77) much more widely spaced; hyaline fringe as wide as in genital double-somite. Fourth urosomite (preanal) (Figs. 2A, B, 4A) without ornamentation; hyaline fringe narrower than in third urosomite.

Anal somite (Figs. 2A, B, 4A, 10D) clefted medially in posterior half, with one pair of large dorsal sensilla (no. 78), two pairs of lateral pores (nos. 79 & 80), one pair of ventral pores (no. 81), posterior row of spinules at base of each caudal ramus, and two curved ventral rows of spinules between median cleft and ventral pores; anal operculum short, reduced to narrow and thin membrane dorsally at end of medial cleft, concave and situated

anterior to dorsal sensilla, representing less than 10% of somite's width, unornamented; anal sinus with several diagonal rows of hair-like spinules on both sides of median cleft, widely open, with weakly sclerotised walls, and without chitinous projections.

Caudal rami (Figs. 2A, B, E, F, 4A, 10D) long and slender, about twice as long as anal somite, widest at base, about 3.5 times as long as wide (ventral view), slightly divergent and nearly cylindrical, with space between them about one ramus width; armature consisting of seven setae (three lateral, one dorsal and three apical), all in posterior sixth of ramus length; ornamentation consisting of anterior ventro-median pore (no. 82), posterior ventral pore (no. 83), two or three short spinules at base of each lateral seta, three short spinules at base of innermost apical seta, and two parallel rows of long inner spinules. Dorsal seta smooth and slender, inserted close to inner margin, about half as long as caudal ramus, triarticulate at base (i.e. inserted on two pseudojoints). Lateral setae all smooth; ventralmost one longest and most slender, inserted very close to distal margin, about as long as dorsal seta; dorsalmost one strongest, about 0.7 times as long as ventralmost one, inserted more anteriorly than ventralmost one but more posterior than dorsal seta; central one half as long as dorsalmost one, also strong, inserted at about same level as dorsal seta. Inner apical seta smooth and very slender, 0.6 times as long as dorsal seta. Principal apical setae fused basally, both with breaking planes and unipinnate distally along outer margin; middle apical seta much stronger and longer, about 1.7 times as long as outer apical one and 3.5 times as long as caudal rami.

Antennula (Fig. 4B) eight-segmented, joined to cephalothorax with small triangular pseudosegment laterally, approximately 0.8 times as long as cephalothorax, with single short posterior row of spinules and single cuticular pore on first segment. Distal posterior corner of first segment produced into sharp process. Long aesthetasc on fourth segment slender, fused basally with adjacent large seta, and reaching tip of appendage; slender apical aesthetasc on eighth segment fused basally with two apical setae, forming apical acrothek. Setal formula: 1.11.8.6+ae.2.4.4.6+ae. Seta on first segment unipinnate, all others smooth. Dorsal setae on first and second segments with breaking planes. Length ratio of antennular segments, measured along caudal margin, 1 : 0.8 : 1 : 0.7 : 0.5 : 0.6 : 0.5 : 1.

Antenna (Fig. 4C) relatively short, composed of coxa, allobasis, one-segmented endopod and three-segmented exopod. Coxa short, with arched row of long posterior spinules. Allobasis longest and most robust segment of antenna, more than four times as long as coxa and about 1.1 times as long as endopod, widest at base and about three times as long as wide, with single unipinnate inner seta at about midlength and seven very long spinules along inner (convex) margin in proximal half. Endopod about as wide as distal part of allobasis, almost cylindrical, about five times as long as wide, with two surface frills subdistally, two lateral spines flanking two thin setae; apical armature consisting of seven setae, three strong, long, and geniculate, innermost one strong but short, and three short and slender; two slender apical setae fused basally; two lateral and two apical slender setae smooth; other armature pinnate; with row of long inner spinules. Exopod long and slender, almost cylindrical, about as long as allobasis but only half as wide; armature formula 1.1.4 and length ratio of segments 1 : 0.15 : 0.6; proximal segment with longitudinal row of strong inner spinules and transverse distal row of small anterior spinules, bearing a unipinnate seta at distomedial corner; second segment with a unipinnate setae at distomedial corner; distal segment with two arched transverse rows of small spinules anteriorly (one at midlength, the other close to distal margin), with one smooth inner seta, at about first third of its length, and three apical slender and smooth setae, which all fused basally.

Labrum large and complex tri-dimensional structure, trapezoidal in anterior view, rigidly sclerotized, with relatively wide and somewhat convex cutting edge, subapically with row of strong spinules and many rows of slender spinules apically and along posterior surface .

Paragnaths also forming complex tri-dimensional structure, trilobate, with two ellipsoid anterior lobes and one central posterior lobe, all fused at base, all lobes with numerous rows of slender anterior and apical spinules; posterior surface smooth.

Mandibula (Fig. 5A, B) with wide cutting edge on relatively short coxa, with two strong bicuspidate teeth ventrally, distally with long and slender central seta, eight bicuspidate teeth dorsally, and single dorsal unipinnate seta fused basally to tooth; teeth progressively decrease in size from ventral to dorsal side; dorsal seta only slightly longer but much stronger than central seta, and about twice as long as longest tooth; no ornamentation on coxa. Palp biramous, comprising basis, one-segmented exopod, and one-segmented endopod. Basis with somewhat inflated central part, about twice as long as wide, with three slender and smooth distal outer setae, with two arched rows of spinules in distal half. Exopod 0.75 times as long as basis and half as wide, narrowest medially, curved

back towards coxa and parallel with basis, with three lateral and six apical smooth setae; all lateral and two apical setae slender, four apical setae strong and geniculate, one of them (Fig. 5A) more than five times as long as exopod. Endopod only half as long as exopod, 2.7 times as long as wide, with one inner, three apical, and two outer slender and subapical setae; proximal outer seta bipinnate, other smooth.

Maxillula (Fig. 5C) composed of praecoxa, coxa, basis, one-segmented endopod, and one-segmented exopod; endopod and exopod fused basally. Praecoxa large; arthrite rectangular, with three posterior spinules near dorsal margin and one spinule at base of ventralmost apical spine, apically and subapically with eight strong curved spines, each with a dense tuft of distal spinules along convex margin. Coxa with anterior arched row of long spinules, endite shorter than praecoxal arthrite, apically (on inner margin) with one curved and stout, bipinnate seta, and two smooth and slender setae. Basis smaller than coxa with two endites reaching further medially than coxal endite, almost in line with praecoxal arthrite, with five spinules and three setae on dorsal endite, and four setae on ventral endite; only two setae on dorsal endite bipinnate, others smooth. Endopod minute, rectangular, with four slender and smooth apical setae. Exopod smaller than endopod, with two slender and smooth apical setae.

Maxilla (Fig. 5D) composed of large syncoxa, small basis and even smaller one-segmented endopod. Syncoxa with four rows of outer long spinules and with three endites; dorsal endite smallest, bilobate, with four setae, three of which strong and pinnate; central endite slender, with two pinnate setae, dorsal seta strong, with one spinule almost as strong as seta, giving it bifurcate appearance; ventral endite longest and strongest, with three strong, pinnate setae. Basis slightly larger than ventral endite of syncoxa, apically with two strong and geniculate, unipinnate spines, and two slender setae on ventral and posterior surfaces. Endopod only about 0.35 times as long as basis, 1.2 times as long as wide, with five slender and smooth apical setae, all equal in length.

Maxilliped (Fig. 5E) not prehensile, four-segmented, composed of coxa, basis, and two-segmented endopod. Coxa short, almost triangular, unarmed and unornamented. Basis largest and longest segment, about 2.3 times as long as wide and 2.5 times as long as coxa, with longitudinal row of slender inner spinules and row of shorter anterior spinules at base of three inner distal spiniform setae; all setae close to each other, strong and of similar length, two unipinnate with large pinnules, one bipinnate with smaller pinnules. First endopodal segment 0.6 times as long as basis but slightly wider, almost ovoid in shape, with two parallel longitudinal rows of large inner spinules, one of them continuing as transverse distal row on posterior surface, and another row of five long outer spinules; with two slender distomedial plumose setae, shorter anterior seta reaching beyond second endopodal segment, longer seta situated posteriorly. Second endopodal segment minute, nearly rectangular, apically with two subequal smooth and slender setae.

All swimming legs (Fig. 6) of similar size and long in comparison to body length, composed of small triangular and unarmed praecoxa, large rectangular and unarmed coxa, shorter and nearly pentagonal basis, slender three-segmented exopod, slender two- or three-segmented endopod; pair of legs joined by simple intercoxal sclerite.

First swimming leg (Fig. 6A) with smooth and short intercoxal sclerite, its distal margin nearly straight. Praecoxa somewhat triangular, longer than intercoxal sclerite but shorter than coxa, unornamented. Coxa 1.5 times as wide as long, with longitudinal row of long inner spinules, four shorter transverse rows of smaller anterior spinules proximally, distal row of slender spinules and outer row of small spinules at base of basis. Basis with one short but strong and finely bipinnate outer spine and one longer and stronger inner spine; the latter 1.6 times as long as the former, with strong pinnules on both sides, and one long distomedial pinnule; ornamentation of basis consists of three strong inner spinules, an anterodistal row of slender spinules at base of endopod, and several strong spinules at base of both spines. Exopod with all segments of about same length, each about 2.5 times as long as wide and with outer spinules and subdistally on anterior surface; first segment with four inner slender spinules; first two segments with single strong and finely bipinnate distolateral spine; second segment with slender distomedial seta; third segment with two strong and pinnate outer spines and two setae apically; apical setae not prehensile, with short outer pinnules and long and sparse inner pinnules; length ratio of elements on third segment from outer to inner margin 1 : 1.5 : 2.1 : 3.1. Endopod two-segmented, not prehensile, only slightly shorter than exopod; first endopodal segment 1.2 times as long as first exopodal segment and 2.3 times as long as wide, with strong inner and anterodistal spinules, with single bipinnate inner seta, the latter slender and about 0.6 times as long as segment; second segment slender, about 5.6 times as long as wide and 1.2 times as long as first segment, with continuous longitudinal row of strong outer spinules, with two slender inner seta, one strong and long apical spine, and another shorter spine distolaterally; apical spine about as long as inner distal seta, 1.9 times as long as outer distal spine, and 1.5 times as long as second segment but only about 0.7 times as long as longest exopodal seta.

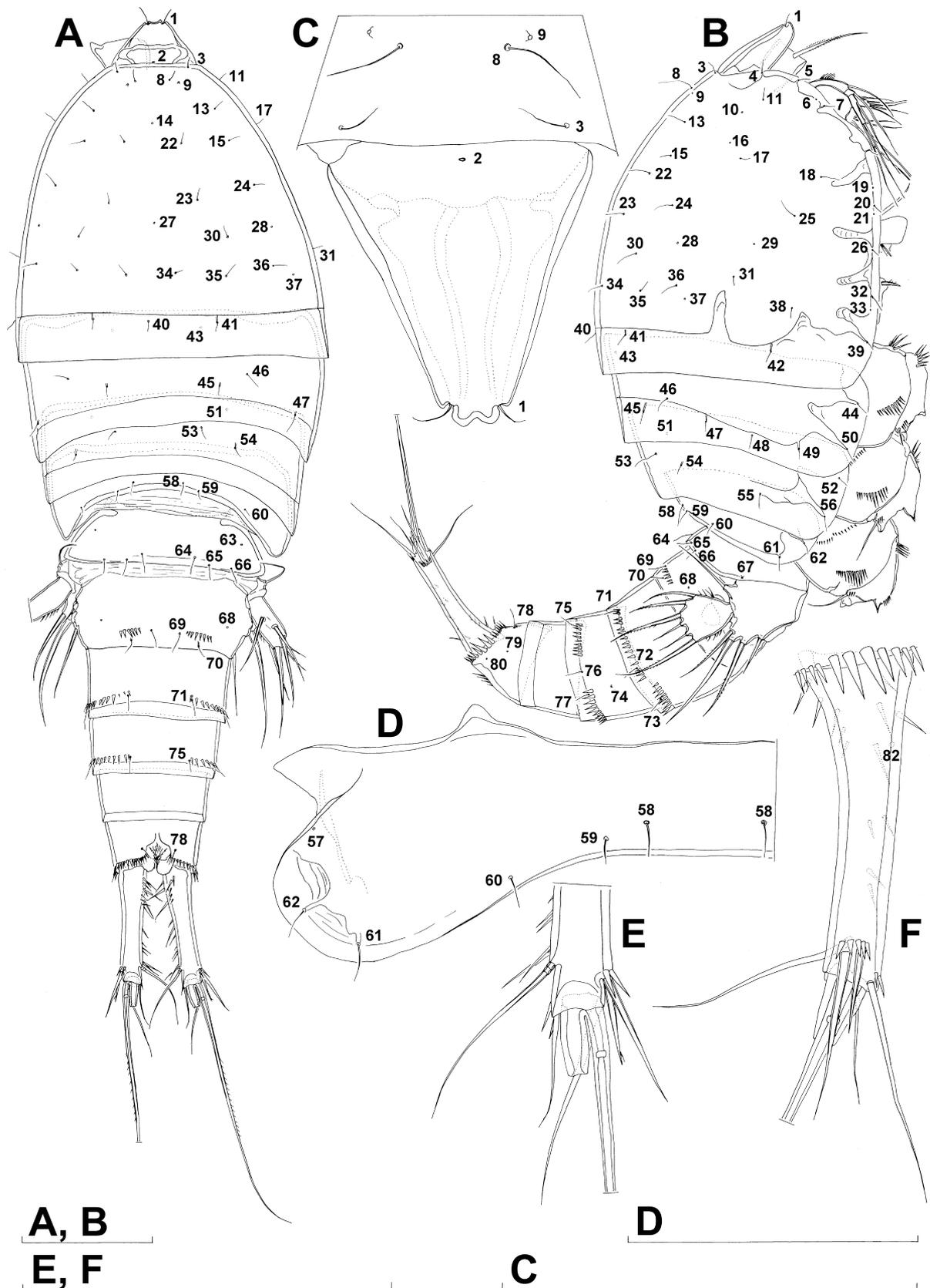


FIGURE 2. *Wellstenhelia calliope* sp. nov., line drawings, female holotype: A, habitus, dorsal view; B, habitus, lateral view; C, rostrum, dissected and flattened, dorsal view; D, pleuron of fourth pedigerous somite, dissected and flattened; E, posterior part of right caudal ramus, dorsal view; F, right caudal ramus, lateral view. Arabic numerals numbering sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side (excluding appendages). Scale bars 100 μ m.

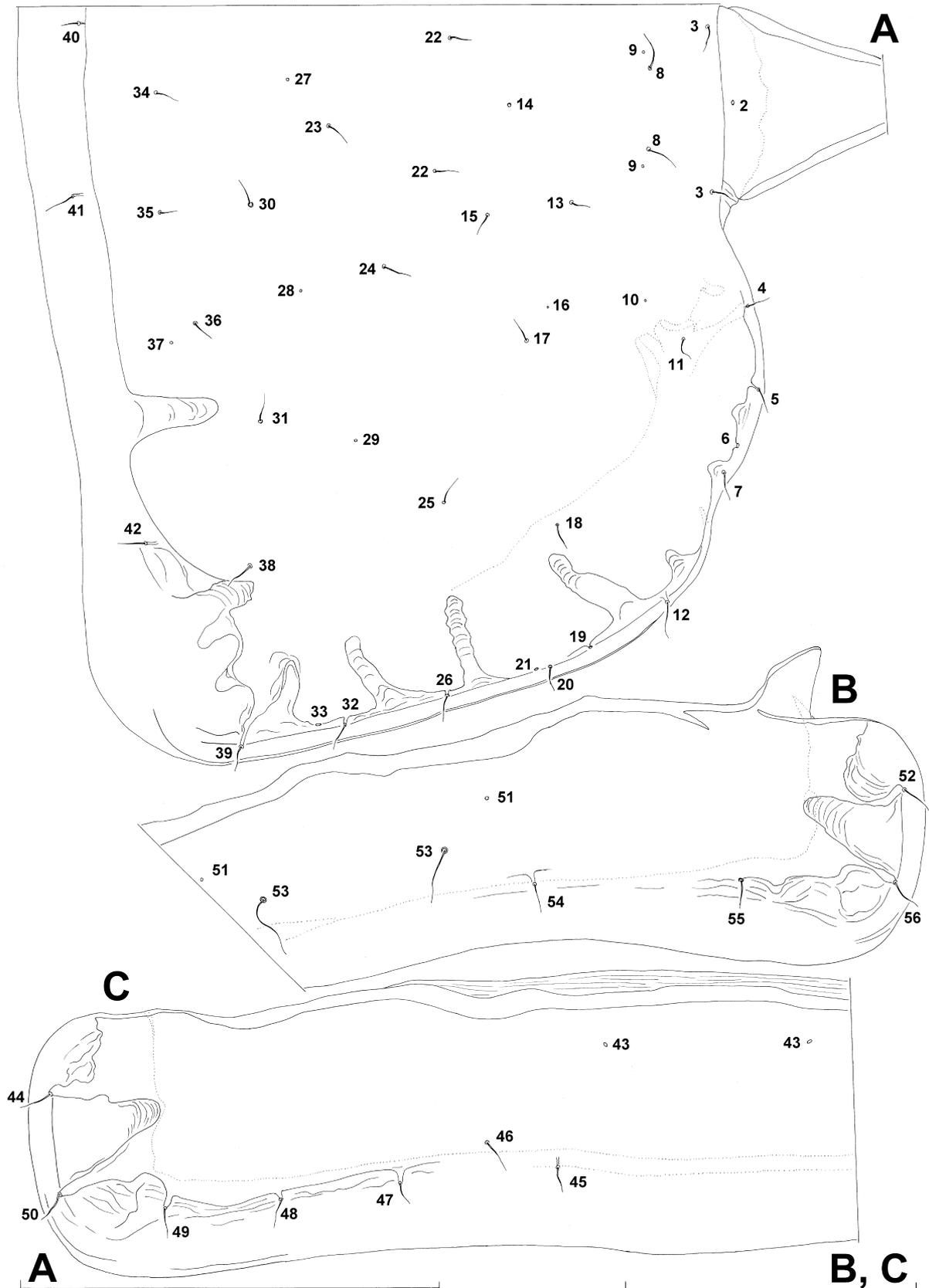


FIGURE 3. *Wellstenhelia calliope* sp. nov., line drawings, female holotype: A, cephalothoracic shield and posterior part of rostrum, dissected and flattened; B, pleuron of third pedigerous somite, dissected and flattened; C, pleuron of second pedigerous somite, dissected and flattened. Arabic numerals numbering sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side (excluding appendages). Scale bars 100 μ m.

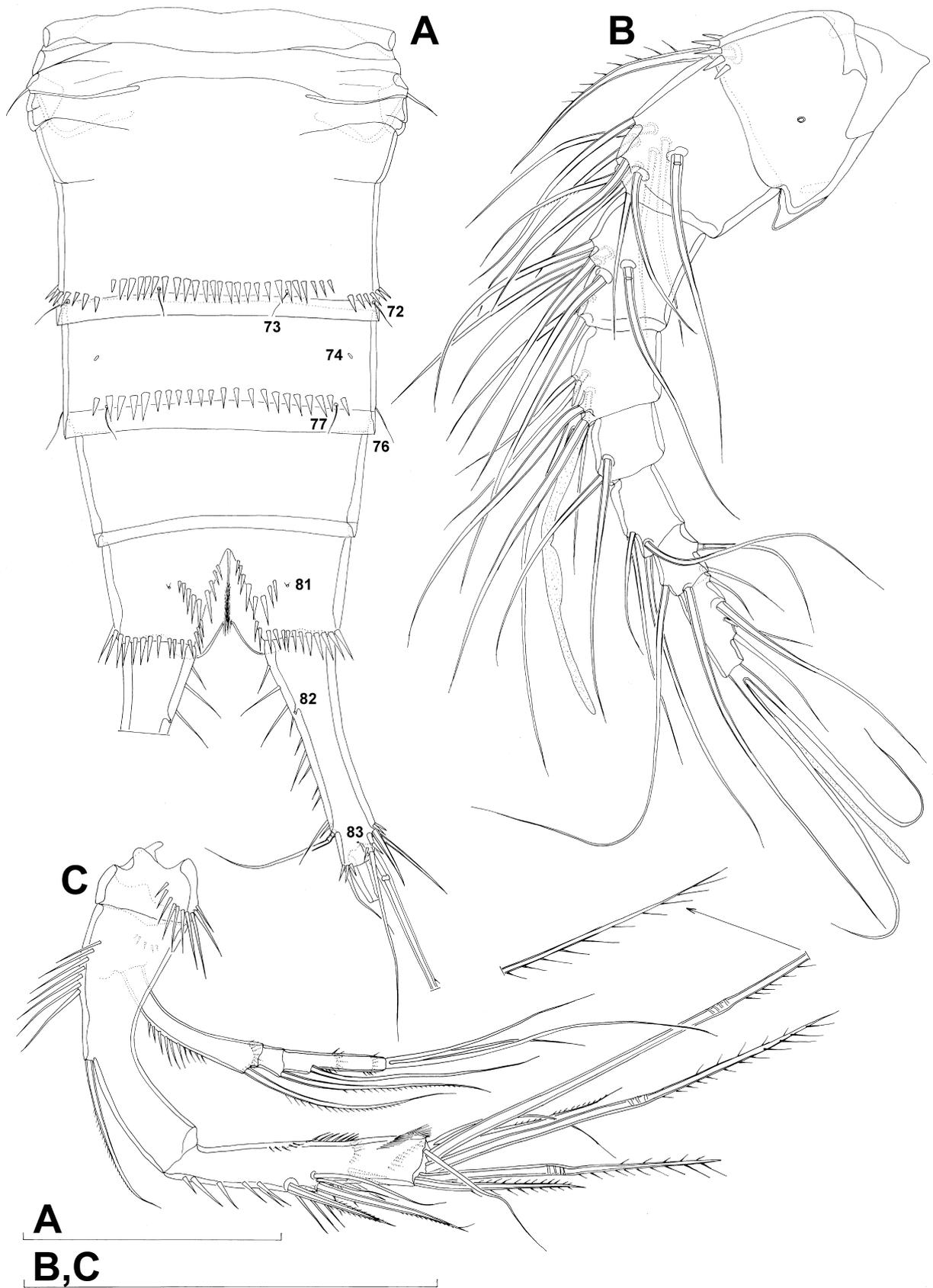


FIGURE 4. *Wellstenhelia calliope* sp. nov., line drawings, female holotype: A, abdomen, ventral view; B, antennula, dorsal view; C, antenna, posterior view (arrow points to separately drawn distal part of longest seta). Arabic numerals numbering sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side. Scale bars 100 μ m.

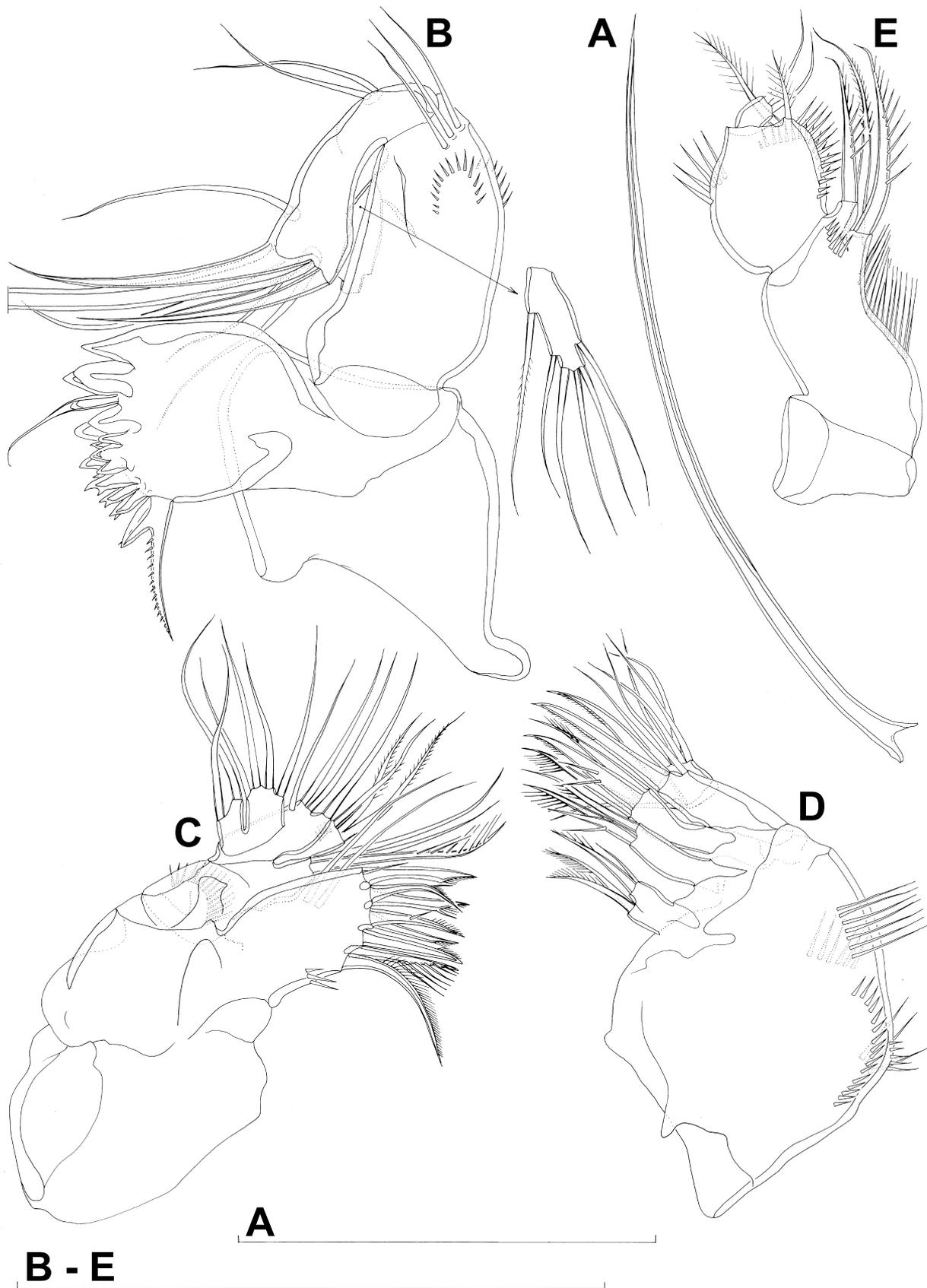


FIGURE 5. *Wellstenhelia calliope* sp. nov., line drawings, female holotype: A, strongest spine on mandibular palp, posterior view; B, mandibula, posterior view (arrow pointing separately drawn endopod); C, maxillula, posterior view; D, maxilla, anterior view; E, maxilliped, anterior view. Scale bars 100 μ m.

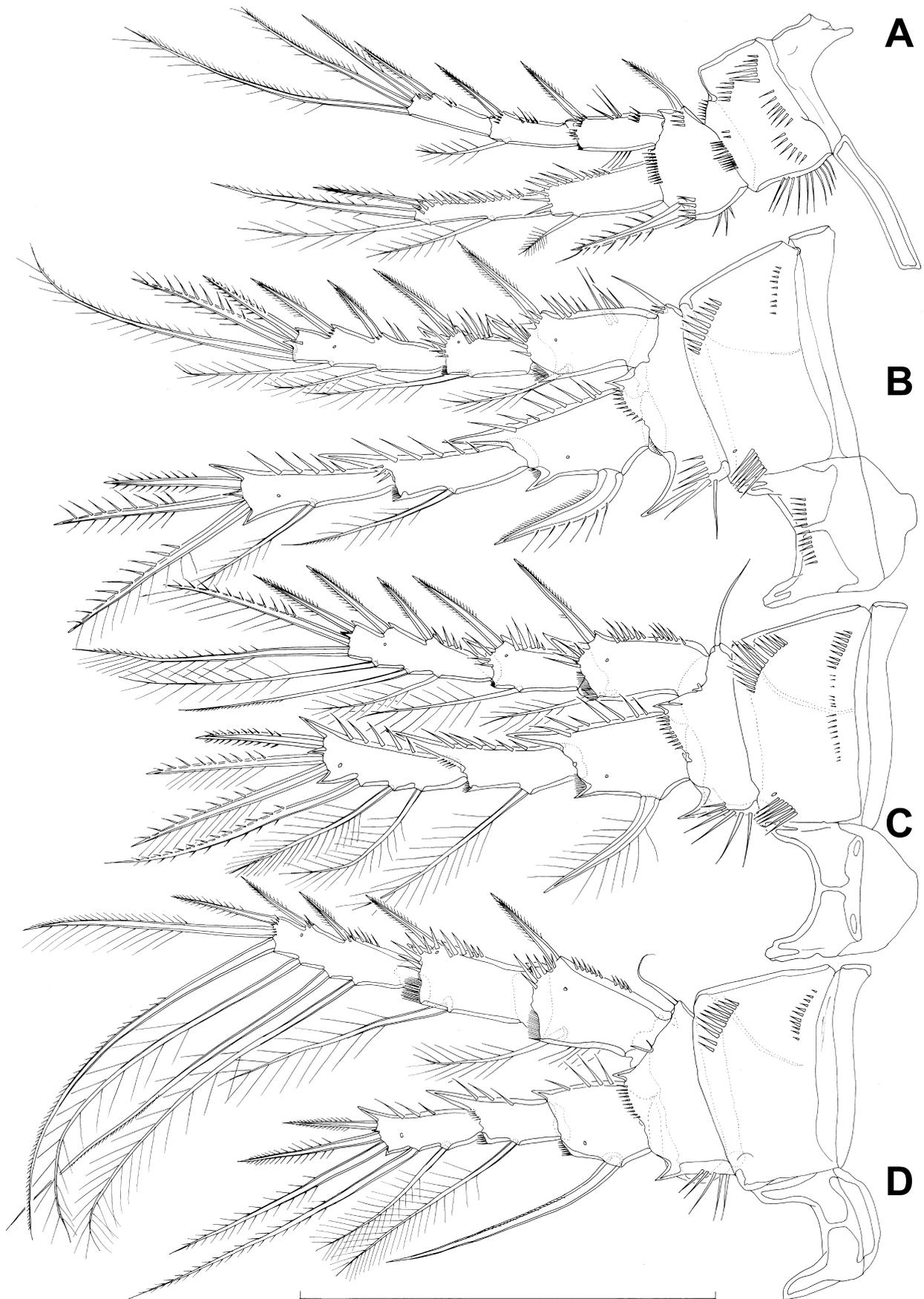


FIGURE 6. *Wellstenhelia calliope* sp. nov., line drawings, female holotype: A, first swimming leg, anterior view; B, second swimming leg, anterior view; C, third swimming leg, anterior view; D, fourth swimming leg, anterior view. Scale bar 100 μ m.

Second swimming leg (Fig. 6B), intercoxal sclerite with transverse distal row of small anterior spinules, distal margin deeply concave. Praecoxa short, unornamented. Coxa nearly 1.7 times as wide as long, anteriorly with pore and short row of long spinules near distomedial corner and two longer rows of spinules close to outer margin, proximal spinules smaller than distal ones. Basis with smooth, short and slender outer spine; inner distal corner produced into long and sharp process; anteriorly with distal row of small spinules and short row of long spinules close to inner margin; spine with two small spinules at base. First exopodal segment widest, third segment slender and about 3.6 times as long as wide, 1.5 times as long as second segment, and 1.4 times as long as first one; segments with single anterior pore, and outer and distal spinules (those on outer margin much stronger), and with inner distal frill on first two segments; first and second segments with single strong and finely bipinnate outer distal spine and slender bipinnate inner distal seta; third segment with three strong and finely bipinnate outer spines, two apical strong and bipinnate setae, and two slender and bipinnate inner setae; inner apical seta on third segment longest, about 1.7 times as long as outer apical one, twice as long as third segment, and 2.6 times as long as outer distal spine; outer distal corner of first and second segment produced into spiniform process. Endopod three-segmented, 1.1 times as long as exopod; all segments of about same length, but progressively narrower from proximal to distal end, each with outer distal corner produced into strong spiniform process and inner distal corner also spiniformly produced (though much less strongly than in exopod), each with row of strong outer spinules, first two segments additionally with small inner distal frill, and first and third segments with anterior cuticular pore; armature consisting of single bipinnate inner seta on first and second segments, and one inner and three apical elements on third segment (probably outermost spine and two strong setae); seta on first segment exceptionally strong and curved, other elements straight, inner seta on second segment slender and with distal inner row of minute pinnules in addition to long pinnules, inner seta on third segment also slender but just with long pinnules, apical setae with slender long inner pinnules and robust long outer pinnules; inner apical seta on third segment longest, 1.2 times as long as outer apical seta, 1.4 times as long as segment, and 1.6 times as long as outer apical spine.

Third swimming leg (Fig. 6C) similar to second swimming leg, except for smooth intercoxal sclerite, longer proximal row of spinules on coxa, slender outer seta and shorter inner distal process on basis, and three inner setae on third endopodal and exopodal segments each; middle inner seta on third exopodal segment with only minute distal inner pinnules, distal inner seta on third endopodal segment more robust than other inner setae and with short but strong pinnules on both margins, all other inner setae on exopod and endopod bipinnate with long and slender pinnules; inner seta on first endopodal segment slightly less strong than serially homologous one on second leg, but also curved.

Fourth swimming leg (Fig. 6D) relatively similar to third swimming leg, but with endopod only about 0.7 times as long as exopod, without pore or inner distal row of spinules on coxa, slightly shorter inner distal process on basis, much longer spiniform seta on first endopodal segment, only two inner setae on third endopodal segment, and longer and stronger inner setae on third exopodal segment.

Fifth leg (Fig. 7A) composed of wide baseoendopod (fused basis and endopod) and much smaller ovoid exopod, pair of legs joined by small triangular sclerite. Baseoendopod about 1.5 times as wide as long, more or less pentagonal, unornamented, with short spiniform process at base of exopod; outer basal seta slender and smooth, arising from short setophore, about 0.8 times as long as segment; endopodal lobe relatively narrow, trapezoidal, extending slightly beyond proximal third of exopod in length, with four stout, bipinnate setae, their length ratio, starting from inner side, 1 : 2.3 : 3.4 : 2. Exopod about 1.1 times as long as its maximum width, more or less trapezoidal, with narrow base, with two short rows of strong inner spinules, one row of strong outer spinules, and single anterior pore close to distal margin, with six setae; second and third seta from inner side short, slender, and smooth, other setae strong and bipinnate; length ratio of exopodal setae, starting from inner side, 1 : 0.4 : 0.4 : 0.8 : 0.6 : 0.6.

Sixth leg (Fig. 4A) minute flap covering ventro-lateral genital aperture, mostly fused to somite, unornamented, with single short and smooth seta near outer margin and two minute spines; inner minute spine fused basally to plate, forming small spiniform process. Sixth legs seemingly joined on ventral side by fold-like suture which hides copulatory pores.

Male (based on allotype and five paratypes). Body length from 605 to 684 μm (610 μm in allotype). Habitus (Figs. 8A, 11C), colour, rostrum (Figs. 8A, 10F), shape and most ornamentation on cephalothorax (Figs. 8A, 10F, 11D), shape and ornamentation of second pedigerous somite (Figs. 8B, 10F, 11E), third pedigerous somite (Figs.

8C, 10F, 11E), fourth pedigerous somite (Figs. 8D, 10F, 11E), most ornamentation on first urosomite (Fig. 9A, B, C, 11E), ornamentation of last three urosomites (Figs. 9A, B, C, 11F), caudal rami (Fig. 9A, B, C), antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 10F), and coxae, bases and exopods of second, third and fourth swimming legs as in female. Prosome/urosome ratio 1.05, greatest width at posterior end of cephalothorax, body length/width ratio about 3.1; cephalothorax twice as wide as genital somite in dorsal view. Genital somite and third urosomite not fused.

Cephalothorax (Figs. 8A, 10F, 11D) in addition to all sensilla and pores present in female with one additional pair of dorsal anterior sensilla (no. &) and one additional pair of dorsal posterior pores (no. @).

First urosomite (Figs. 9A, B, C, 11E) slightly narrower and longer than in female, with two additional rows of minute spinules above sensilla pair no. 65 and without lateral pore pair no. 67.

Genital somite (Figs. 9A, B, C, 11F) homologous to anterior part of genital double-somite in female, 1.3 times as wide as long in dorsal view, with all sensilla, pores, and spinules homologous to those in female present, with additional lateral pair of pores (no. #) and additional lateral row of large spinule between sensilla no. 70 and pore no. #; large and longitudinally positioned spermatophore visible inside on right side, four times as long as wide, twice as long as genital somite, its posterior end reaching slightly beyond distal margin of genital somite, its anterior part protruding into first urosomite and even slightly into fourth pedigerous somite.

Third urosomite (Figs. 9A, B, C, 11F) only half as long as genital somite, with three posterior pairs of sensilla as in female, but pair no. 72 situated more ventrally and pair no. 73 very close to each other; ventral row of spinules interrupted between sensilla pair no. 73; additional minute spinules between sensilla pair no. 71 present in allotype (Fig. 9A) but not in paratypes (11F).

Antennula (Figs. 8E, 11A) also as long as cephalothorax, but strongly geniculate and nine-segmented (basically female's sixth segment subdivided), with geniculation between third and fourth and sixth and seventh segments. Segments that participate in geniculation strengthened with cuticular plates along anterior surface, largest ones on seventh segment. Aesthetascs as in female, on fourth and last segments, but additional large aesthetasc present on third segment. First two and last two segments similar to female, except for additional row of minute spinules on first segment; third segment much shorter and distal part of it fused with fourth segment (as can be judged from armature position); fourth segment accordingly longer; fifth segment shorter, while sixth female segment virtually unrecognisable. Setal formula 1.11.6+ae.7+ae.1.2.1.4.6+ae. All setae smooth, except for short proximal seta on sixth segment.

Second swimming leg (Figs. 7B, 10F) with second and third endopodal segments fused (arrowed in Fig. 7B) but armature and ornamentation as in female.

Third swimming leg (Fig. 7C) with distal inner seta on third endopodal segment slender and plumose (arrowed in Fig. 7C), other armature and all ornamentation as in female.

Fourth swimming leg (Fig. 7D) with inner seta on first endopodal segment and distal inner seta on third endopodal segment slender and plumose (both arrowed in Fig. 7D), other armature and ornamentation as in female.

Fifth legs (Figs. 9A, B, C, 11B) much smaller than in female, without endopodal armature, and with baseoendopods fused medially into narrow plate. Exopod minute, ovoid, with single anterior proximal pore, and with two smooth setae and innermost bipinnate seta; length ratio of exopodal setae, starting from inner side, 1: 1.7 : 0.5.

Sixth legs (Fig. 9B, C) almost completely fused medially and to somite, forming simple flap, with concave hyaline fringe as only remnant of former subdivision; only functional genital aperture under right leg; each leg with three smooth setae, their length ratio from inner side, 1 : 2.1 : 1.7.

Variability. Most morphological features are conservative, including the sensilla and pores pattern of somites, and length ratio of different armature on appendages. The only significant form of morphological variability, except body length, was presence/absence of minute dorsal spinules on the third urosomite in males (Figs. 9A, 11F).

Morphological affinities. *Wellstenhelia calliope* sp. nov. differs from all congeners by the very narrow endopodal lobe on the female fifth leg (Fig. 7A), where the reduced space between two central setae can be considered as a clear autapomorphy. This species has long caudal rami (l/w index of about 3.5), which distinguishes it at once from the sympatric *Wellstenhelia clio* sp. nov., *Wellstenhelia erato* sp. nov., and *Wellstenhelia euterpe* sp. nov., as well as from the Mediterranean *Wellstenhelia bocqueti* (Soyer, 1971) comb. nov., and the Arctic *Wellstenhelia melpomene* sp. nov. The Swedish *Wellstenhelia hanstromi* (Lang, 1948) comb. nov.

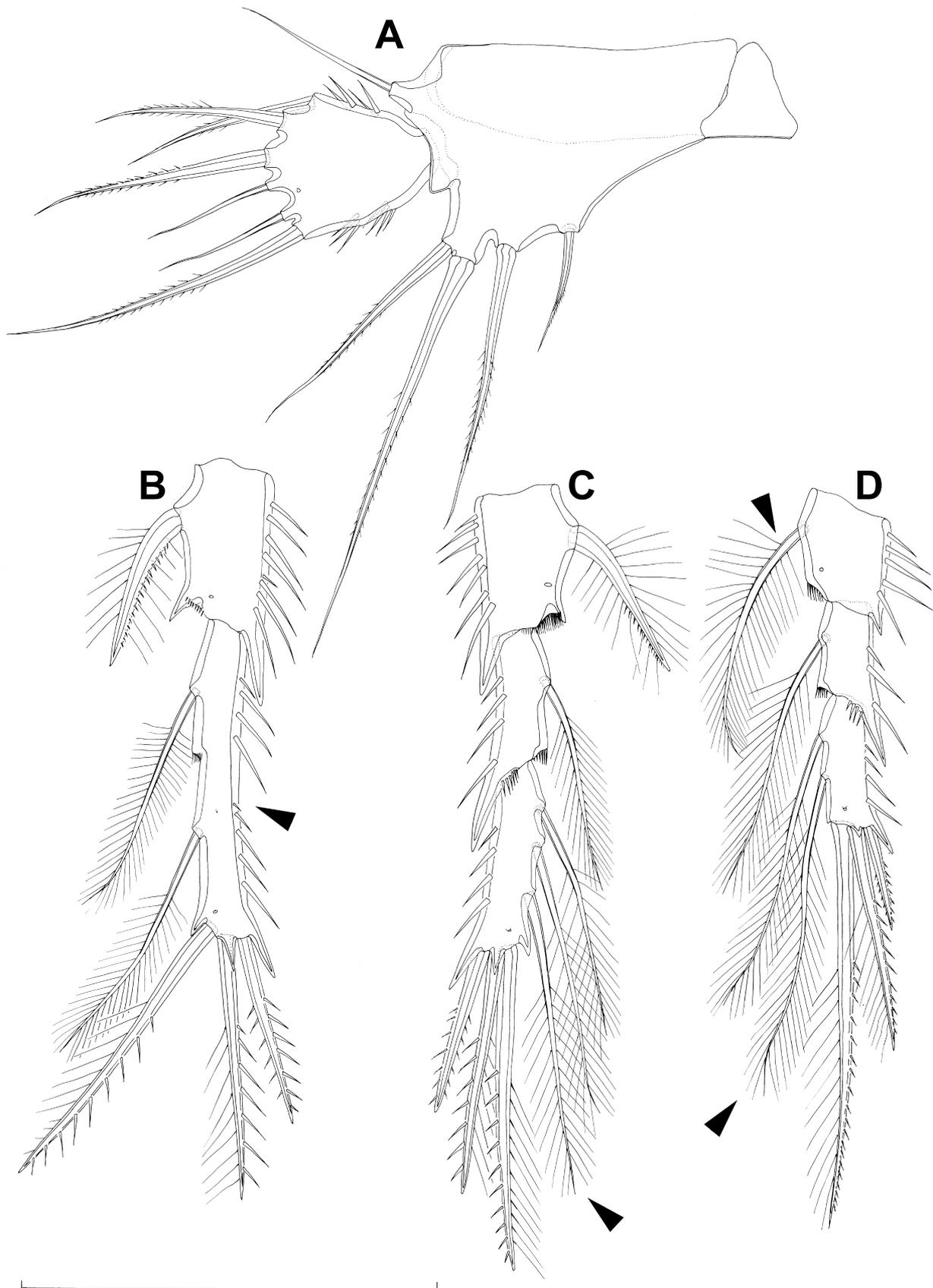


FIGURE 7. *Wellstenhelia calliope* sp. nov., line drawings, A, female holotype, B–D, male allotype: A, fifth leg, anterior view; B, endopod of second swimming leg, anterior view; C, endopod of third swimming leg, anterior view; D, endopod of fourth swimming leg, anterior view. Arrowheads point to sexually dimorphic features. Scale bar 100 μ m.

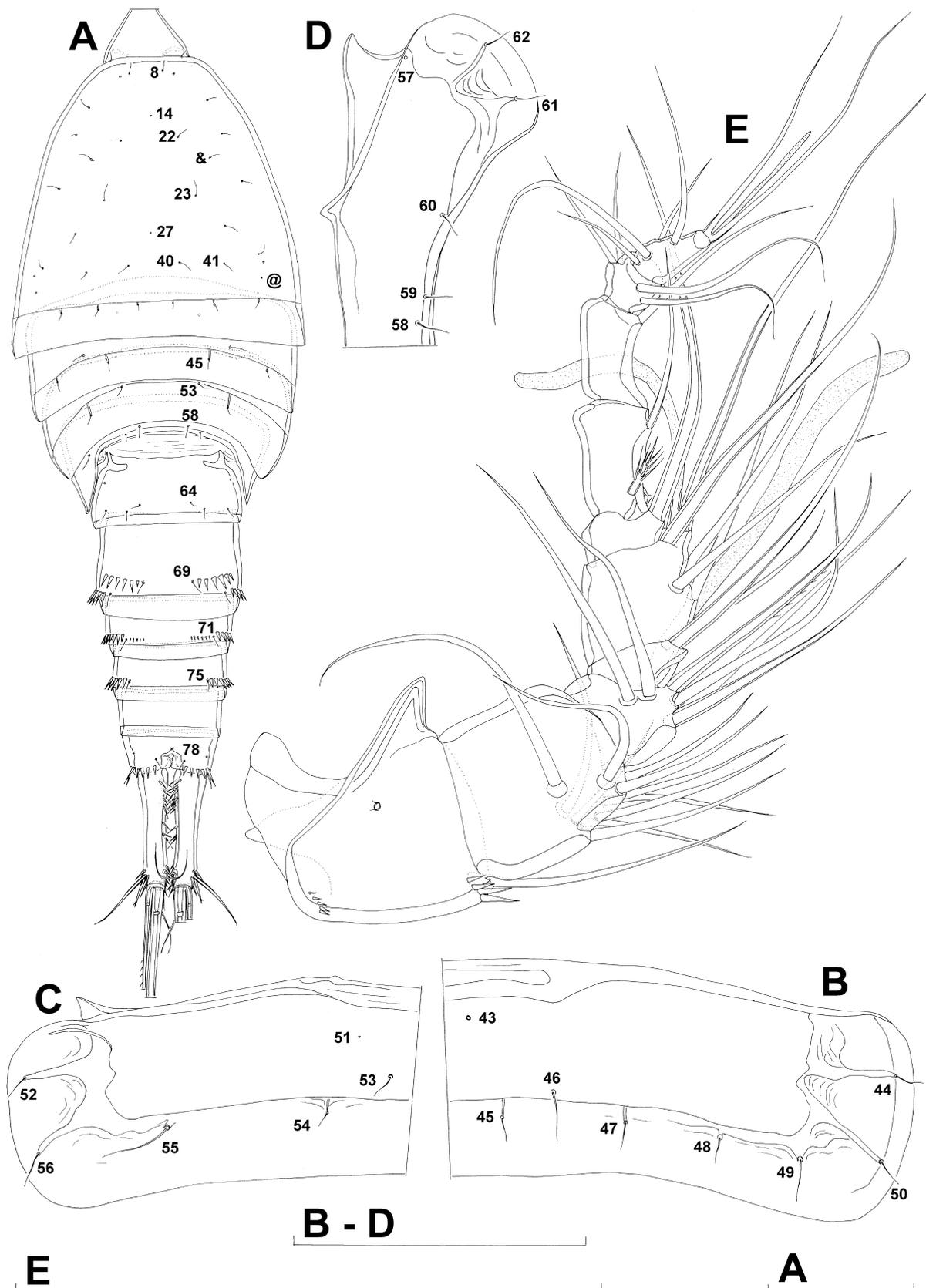


FIGURE 8. *Wellstenhelia calliope* sp. nov., line drawings, male allotype: A, habitus, dorsal view; B, pleuron of second pedigerous somite, dissected and flattened; C, pleuron of third pedigerous somite, dissected and flattened; D, pleuron of fourth pedigerous somite, dissected and flattened; E, antennule, dorsal view, slightly uncoiled and flattened. Arabic numerals indicate sensilla and pores homologous to those in female. Typography symbols (ampersand and at sign: & and @) indicate pores not present in female. Scale bars 100 μ m.

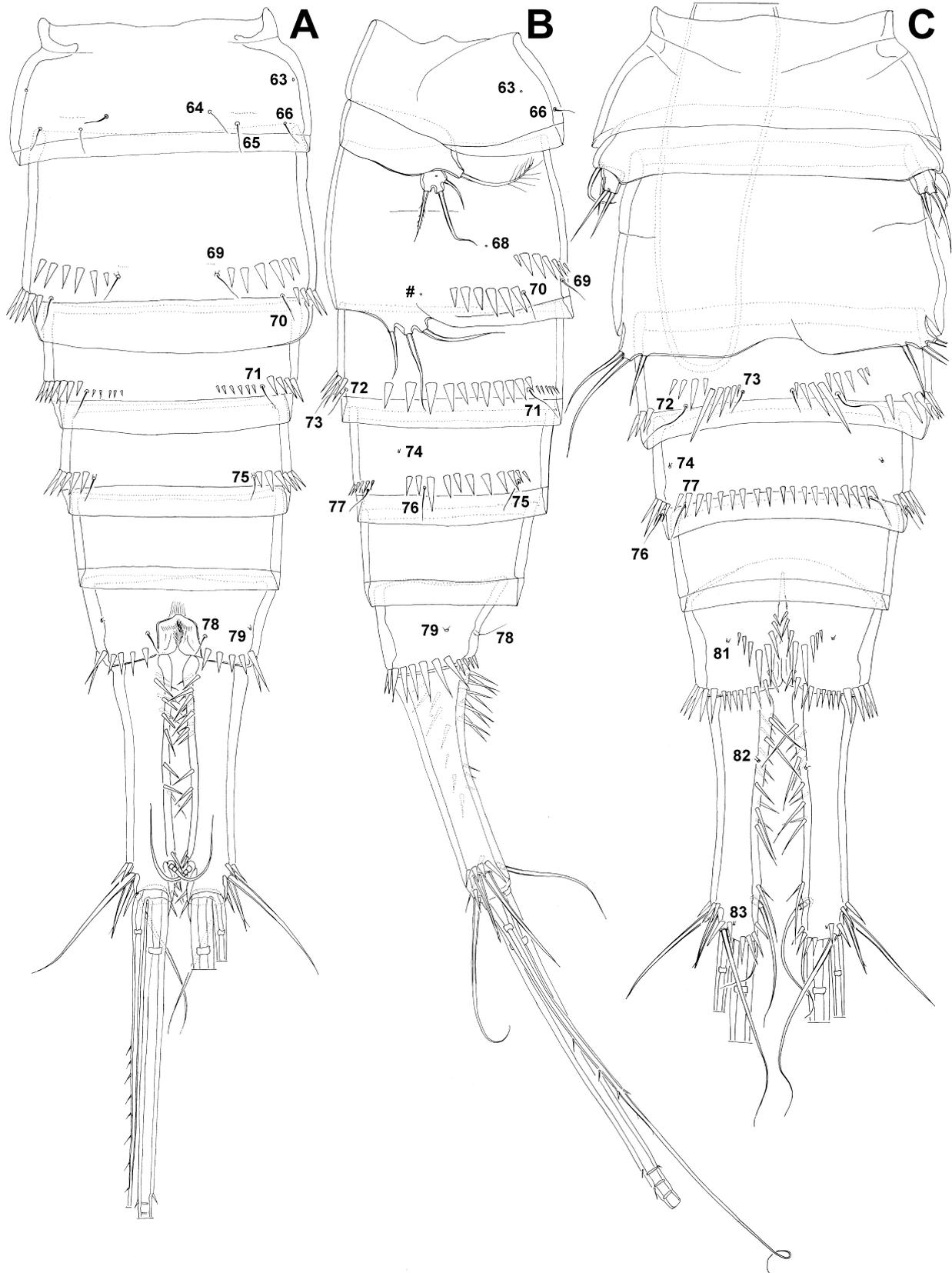


FIGURE 9. *Wellstenhelia calliope* sp. nov., line drawings, male allotype: A, urosome, dorsal view; B, urosome, lateral view; C, urosome with part of spermatophore visible inside, ventral view. Arabic numerals indicating sensilla and pores homologous to those in female. Typographic symbol (hash; #) indicating pore not present in female. Scale bars 100 μ m.

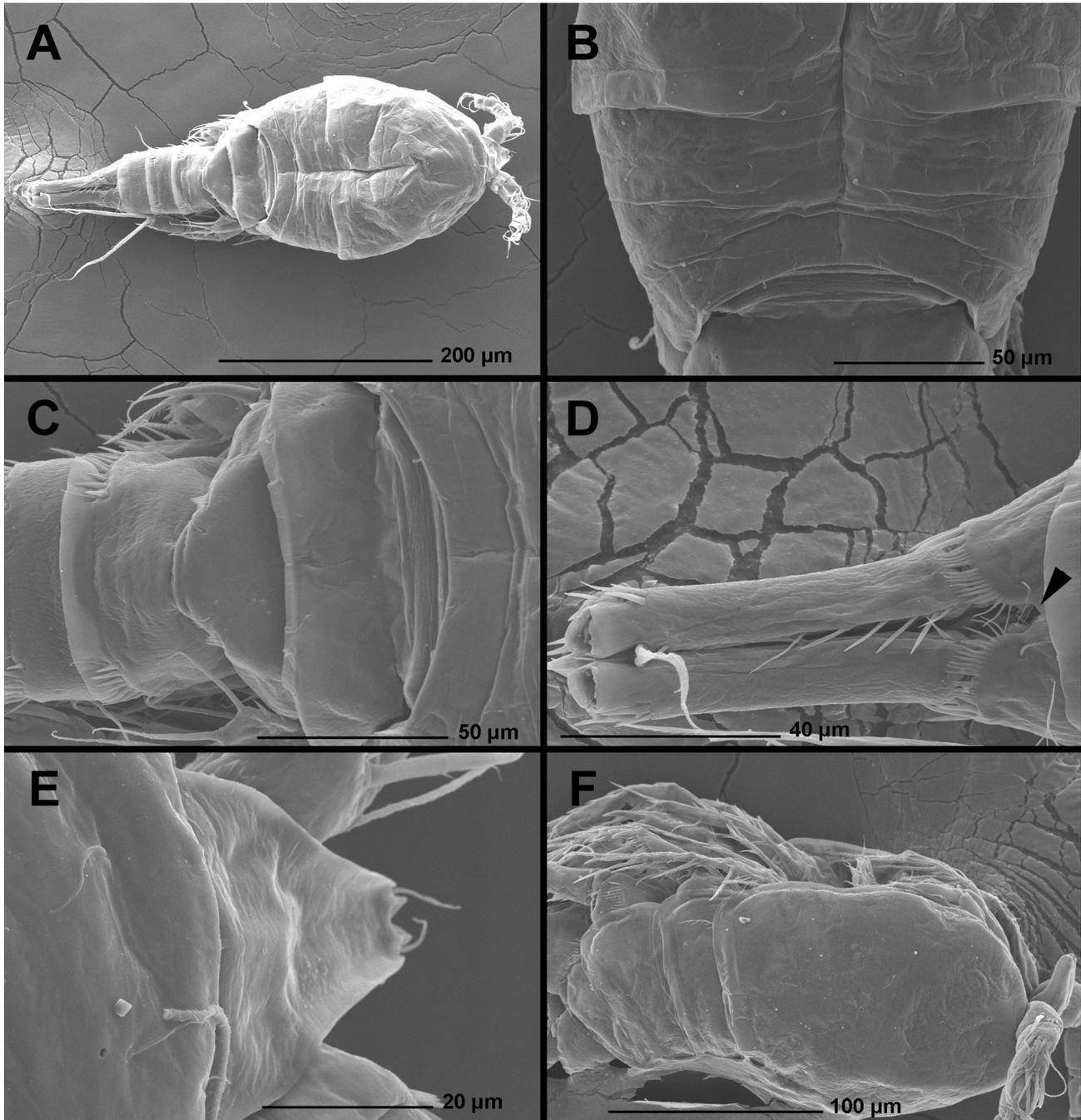


FIGURE 10. *Wellstenhelia calliope* sp. nov., scanning electron micrographs, A–E, female paratype, F, male paratype 1: A, habitus, dorsal view; B, second to fourth pedigerous somites, dorsal view; C, first urosomite and genital double-somite, dorsal view; D, anal somite and caudal rami, dorsal view; E, anterior part of cephalothorax and rostrum, dorsal view; F, prosome, lateral view. Arrowhead points to reduced anal operculum. Scale bars 20 μ m (E), 40 μ m (D), 50 μ m (B, C), 100 μ m (F), and 200 μ m (A).

also has somewhat shorter caudal rami than *Wellstenhelia calliope*, but differs additionally by its long innermost seta on the female fifth leg endopod, and short seta on the first endopodal segment of the fourth swimming leg (this character being a clear autapomorphy of *Wellstenhelia hanstromi*). Only the sympatric *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.** has caudal rami as elongated as *Wellstenhelia calliope*, but the former differs by its short second seta from inner side on the female fifth leg endopod (Fig. 25E), inflated inner principal caudal seta (Fig. 25C), longer spinules on the first leg coxa (Fig. 24F), narrower rostrum (Fig. 24C), reduced armature on the male second leg endopod (Fig. 26E), and transformed inner apical seta on the male fourth leg endopod (Fig. 26F), as well as many details in the ornamentation of somites, including absent pores and sensilla nos. 14, 19, 21, 33, 34,

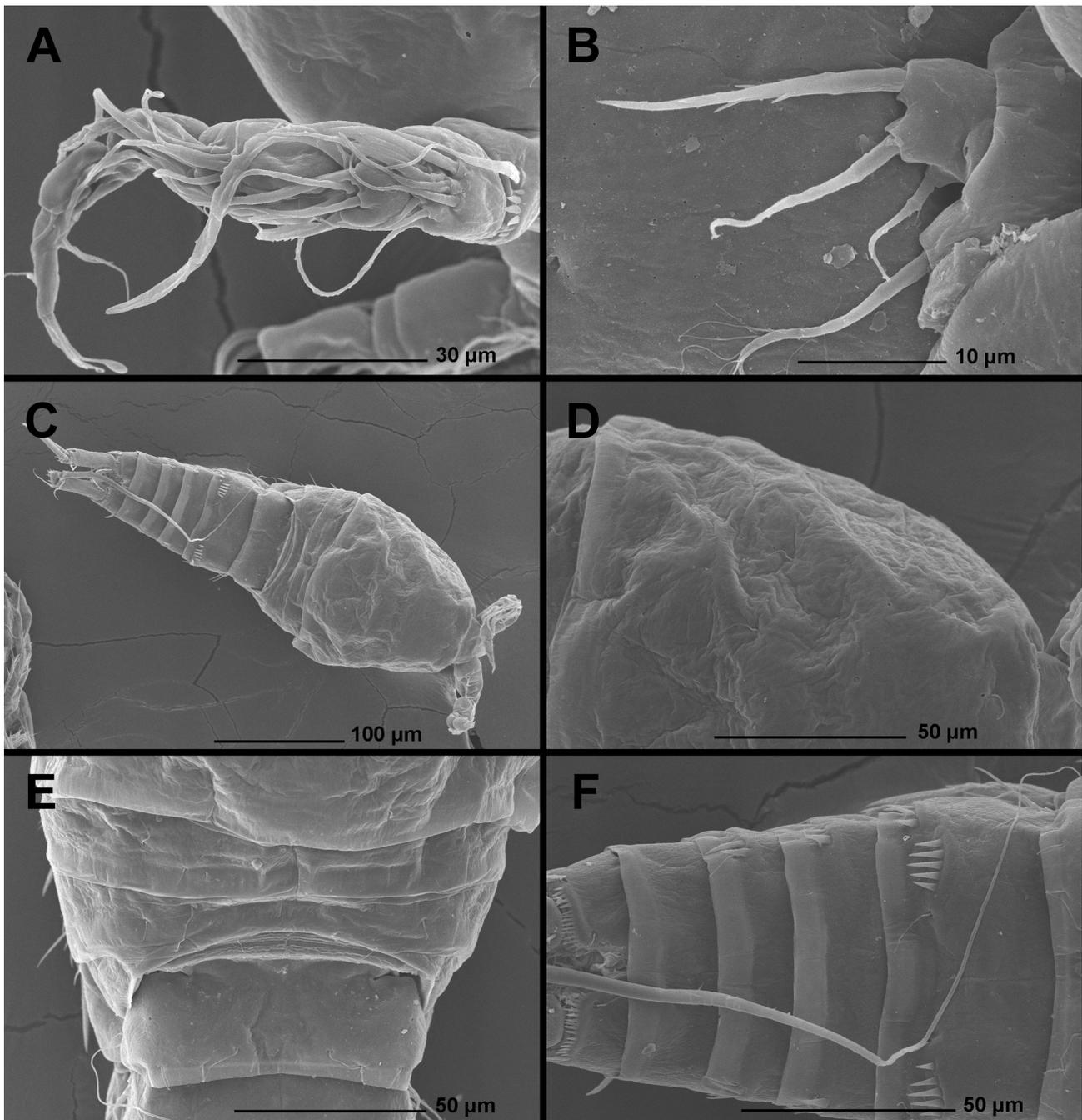


FIGURE 11. *Wellstenhelia calliope* sp. nov., scanning electron micrographs, A–B, male paratype 1, C–F, male paratype 2: A, antennula, ventro-lateral view; B, fifth leg and anterior part of genital somite, lateral view; C, habitus, dorsal view; D, left side of cephalothorax, dorsal view; E, pedigerous somites, dorsal view; F, abdomen, dorsal view. Scale bars 10 µm (B), 30 µm (A), 50 µm (D, E, F), and 100 µm (C).

35, 43, 48 (Fig. 24A, B, D), present sensilla nos. £, \$, wider space between sensilla no. 69, only four spinules in the dorsal row on the anterior part of the genital double-somite (Fig. 24B), much more slender and denser dorsal spinules along distal margin of the anal somite (Fig. 25B), etc. In fact, so many morphological differences between *Wellstenhelia calliope* and *Wellstenhelia qingdaoensis* suggest that their elongated caudal rami probably originated convergently (see also Ma & Li 2011). In *Wellstenhelia calliope* the innermost endopodal seta on the female fifth leg is much shorter than the next one (Fig. 7A), which distinguishes it at once from *Wellstenhelia clio* (with both setae long; Fig. 14C), *Wellstenhelia qingdaoensis* (both setae short; Fig. 25E), *Wellstenhelia euterpe* (innermost seta missing; Fig. 31G), *Wellstenhelia melpomene* (both setae long; Kornev & Chertoprud 2008), and *Wellstenhelia hanstromi* (both setae long; Lang 1948). Only *Wellstenhelia erato* and *Wellstenhelia bocqueti* have the innermost

setae significantly shorter than the next one (similar to that in *Wellstenhelia calliope*), but in *Wellstenhelia erato* this difference is much more pronounced (Fig. 19D), while in *Wellstenhelia bocqueti* there is a deep notch between these two setae (Soyer 1971). The proportion of different armature elements on the female fifth leg could be used alone to distinguish between different species of *Wellstenhelia* **gen. nov.**, except perhaps between *Wellstenhelia clio* and *Wellstenhelia hanstromi* (their affinities are discussed below).

***Wellstenhelia clio* sp. nov.**

(Figs. 12–17)

Type locality. South Korea, South Sea, Gwangyang Bay, sampling station 10, muddy sediments, 34.920944°N 127.785528°E (Fig. 1).

Specimens examined. Female holotype dissected on one slide (collection number NIBRIV0000232676), male allotype dissected on one slide (collection number NIBRIV0000232677), two male paratypes and three female paratypes together on one SEM stub (collection number NIBRIV0000232678), six male paratypes and eight female paratypes and six copepodid paratypes together in ethanol (collection number NIBRIV0000232679), five females destroyed for DNA sequence (amplification unsuccessful); type locality, 18 February 2012, leg. K. Kim.

Two male paratypes and three female paratypes and one copepodid paratype together in ethanol (collection number NIBRIV0000232680), one female destroyed for DNA sequence (amplification successful, Code 0187), type locality, 30 July 2012, leg. K. Kim.

One female destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 15, muddy sediments, 34.890139°N 127.795111°E (Fig. 1), 18 November 2012, leg. K. Kim. Three males and three females destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 12, muddy sediments, 34.951389°N 127.734361°E (Fig. 1), 18 November 2012, leg. K. Kim.

Etymology. The species is named after Clio (Ancient Greek: Κλειώ), one of nine Muses from Greek mythology, who was a patron of history. The species name is a noun in apposition (in the nominative case).

Description. Female (based on holotype and two paratypes). Body length from 540 to 617 µm (latter in holotype). Body segmentation, colour, nauplius eye, hyaline fringes, integument thickness and surface appearance as in *Wellstenhelia calliope* **sp. nov.**, including minute sparse pits visible only on highest magnifications on scanning electron microscope. Most somite ornamentation also similar to *Wellstenhelia calliope*, and presumed homologous pores and sensilla numbered with same Arabic numerals (see Figs. 12A, B, C, 13A, B, C, 14A) to allow easier comparison. Habitus (Figs. 12A, B, 16A) more robust, with prosome/urosoma length ratio 1.2, body length/width ratio about 2.9, and cephalothorax nearly twice as wide as genital double-somite.

Rostrum (Figs. 12C, 16B) slightly narrower in dorsal view than in *Wellstenhelia calliope* (arrowed in Fig. 12C), but without any other difference in shape or ornamentation.

Cephalothorax (Figs. 12A, B, C, 13B, 16C) about 0.8 times as long as wide; represents 28% of total body length. Surface of cephalothoracic shield ornamented as in *Wellstenhelia calliope*; except two additional sensilla (nos. \$, £) and one additional pore (no. ¥) present, two lateral pores (nos. 19, 33) missing, sensilla no. 40 paired, and somewhat different relative position of pores nos. 9, 10, 28 (arrowed in Figs. 12A, C).

Pleuron of second pedigerous somite (Figs. 12A, B, 16D) ornamented as in *Wellstenhelia calliope*, except lateral pair of sensilla no. 48 missing (arrowed in Fig. 12A).

Pleurons of third pedigerous somite (Figs. 12A, B, 13C, 16D), fourth pedigerous somite (Figs. 12A, B, 14A, 16D), and first urosomite (Fig. 12A, B, 16E) as in *Wellstenhelia calliope*.

Genital double-somite (Figs. 12A, B, 13A, 16E) as in *Wellstenhelia calliope*, except anterior part even more inflated laterally, forming blunt chitinous processes, ventral pair of sensilla (no. 73) much more widely spaced, and two additional rows of minute spinules in anterior half (arrowed in Fig. 12B).

Last three urosomites (Figs. 12A, B, 13A, 16F) as in *Wellstenhelia calliope*, except for short lateral rows of spinules on preanal somite, more widely spaced sensilla nos. 74 & 78, and more ventrally located pores 79 & 80.

Caudal rami (Figs. 12A, B, 13A, 16F) short and stout, much shorter than in *Wellstenhelia calliope* (arrowed in Fig. 12A), about 1.3 times as long as anal somite, cylindrical, 2.1 times as long as wide (ventral view), slightly divergent, and with space between them about one ramus width; ornamentation and armature as in *Wellstenhelia calliope*, except central part of inner margin without spinules and middle lateral seta much shorter (both arrowed in Fig. 13A).

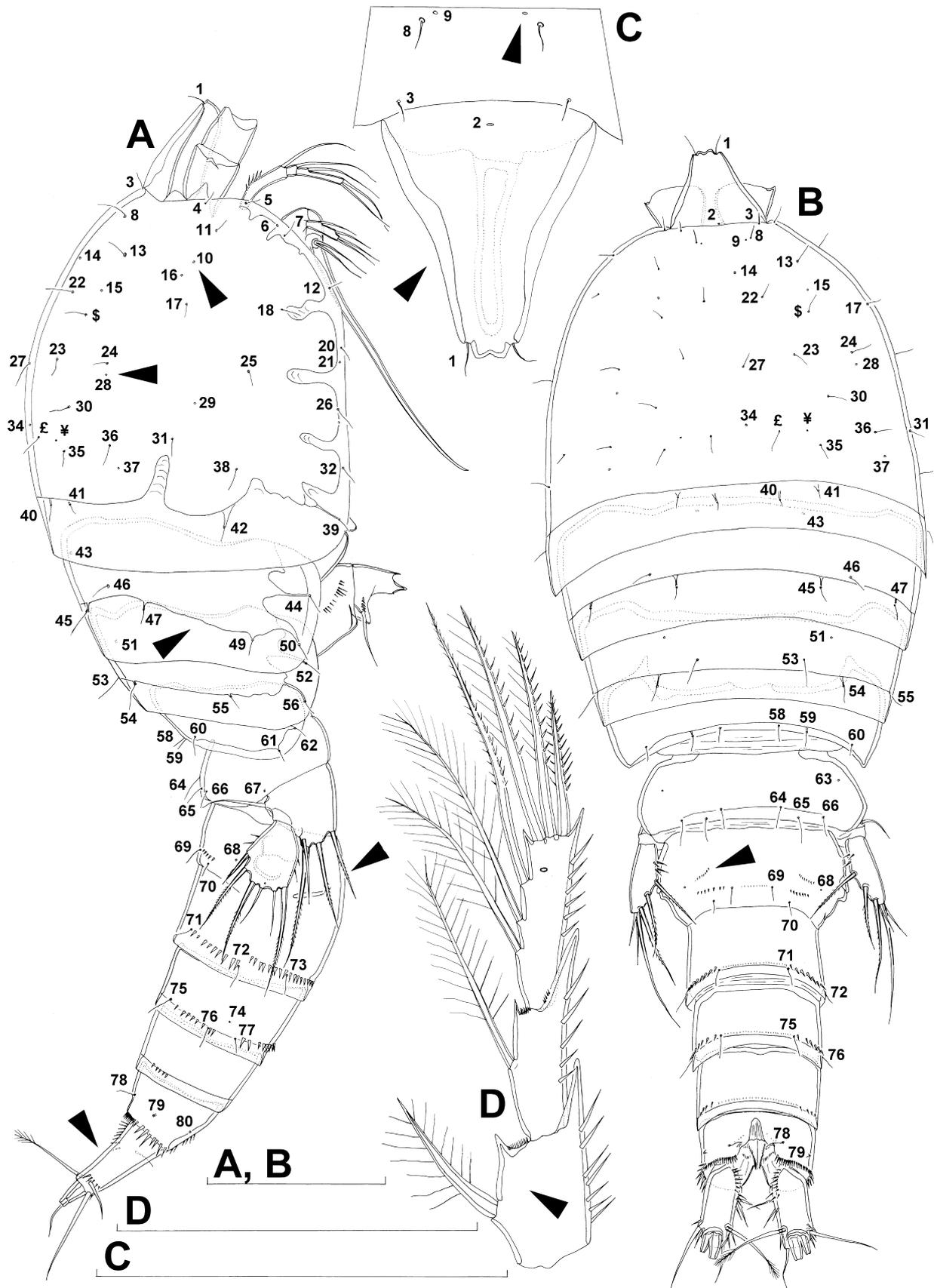


FIGURE 12. *Wellstenhelia clio* sp. nov., line drawings, female holotype: A, habitus, lateral view; B, habitus, dorsal view; C, rostrum, dissected and flattened, dorsal view; D, endopod of third swimming leg. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Currency symbols (\$, £, ¥) indicate unique sensilla and pores. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

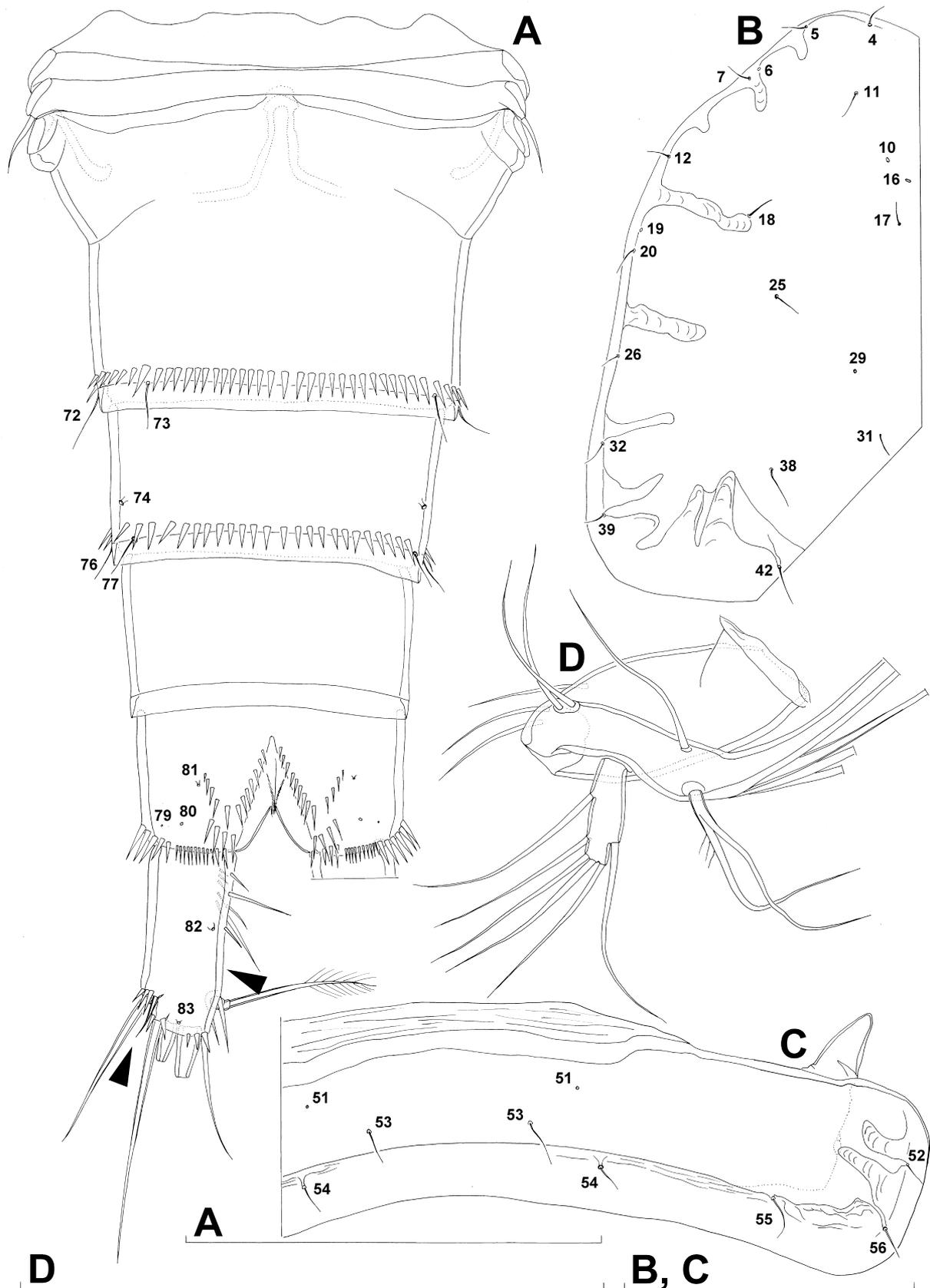


FIGURE 13. *Wellstenhelia clio* sp. nov., line drawings, female holotype: A, abdomen, ventral view; B, left side of cephalothoracic shield, dissected and flattened; C pleuron of third pedigerous somite, dissected and flattened; D, mandibular palp, anterior view. Arabic numerals indicating sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads pointing most prominent specific features. Scale bars 100 µm.

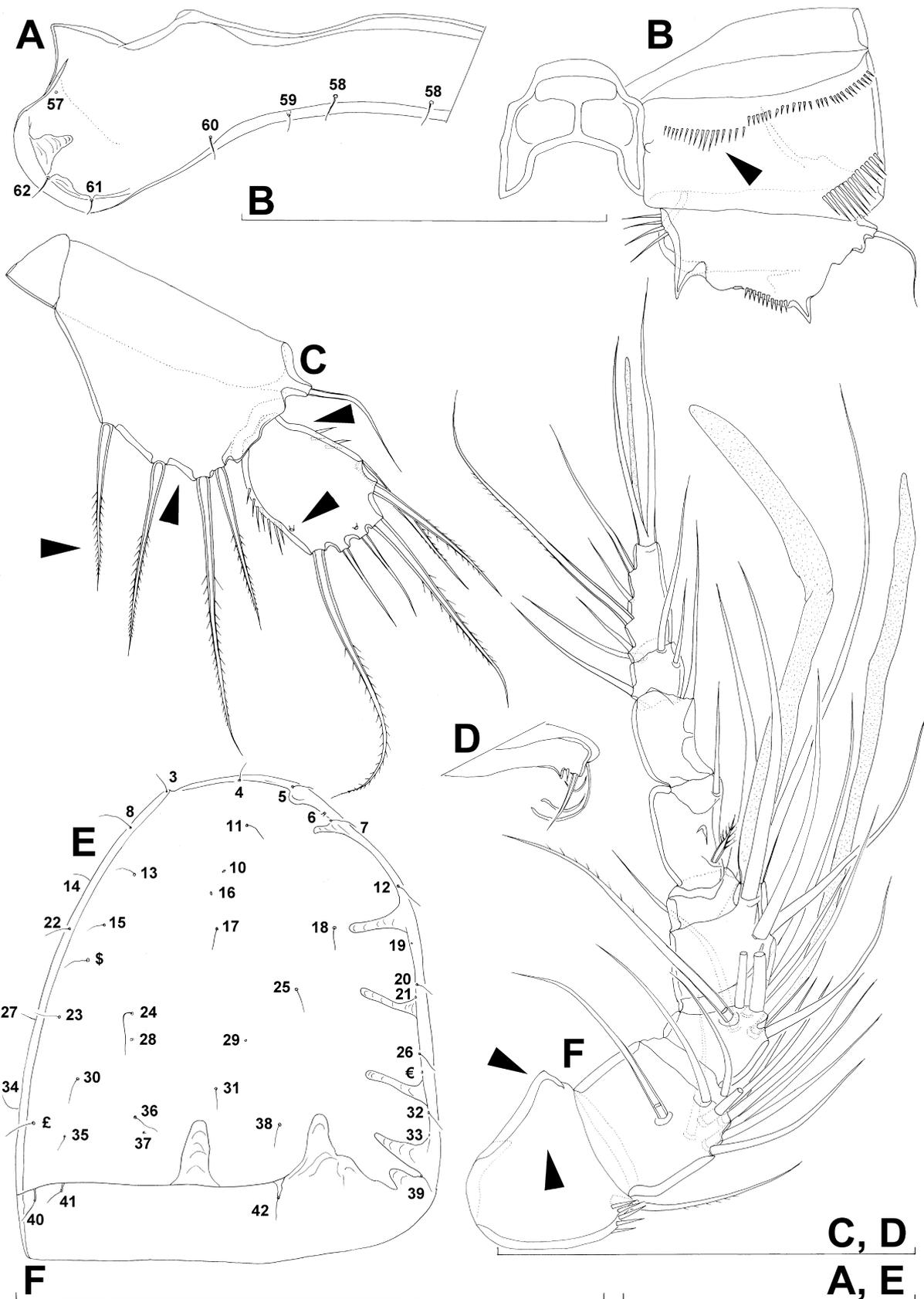


FIGURE 14. *Wellstenhelia clio* sp. nov., line drawings, A–D, female holotype, E–F, male allotype: A, pleuron of fourth pedigerous somite, dissected and flattened; B, fourth swimming leg without rami, anterior view; C, fifth leg, dissected and flattened, anterior view; D, sixth leg on genital somite, ventro-lateral view; E, cephalothoracic shield, lateral view; F, antennula, dorsal view. Arabic numerals indicating sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Currency symbols (\$, £, €) indicating unique sensilla and pores. Arrowheads pointing most prominent specific features. Scale bars 100 μ m.

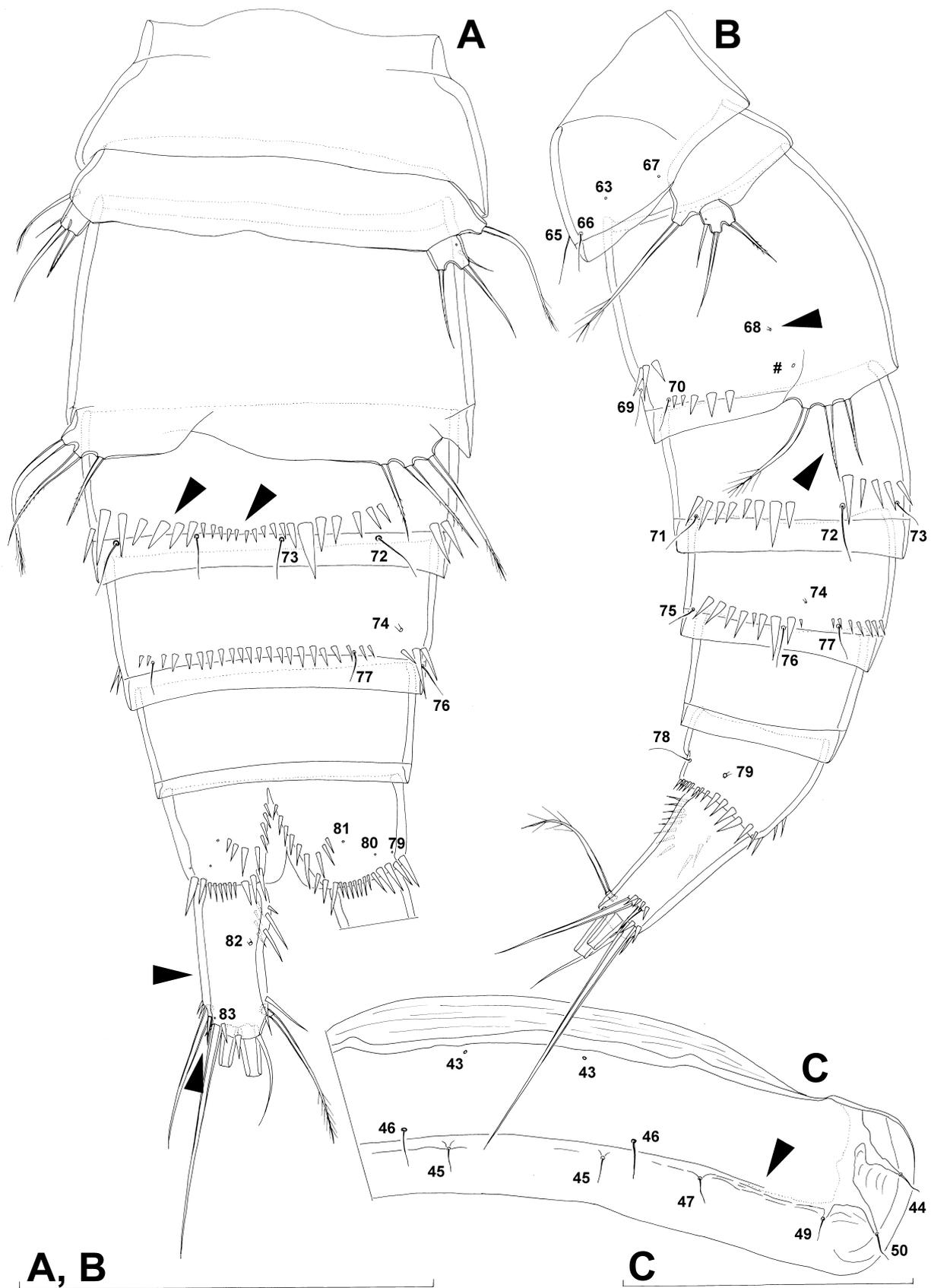


FIGURE 15. *Wellstenhelia clio* sp. nov., line drawings, male allotype: A, urosome, ventral view; B, urosome, lateral view; C, pleuron of second pedigerous somite, dissected and flattened. Arabic numerals and hash mark (#) indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

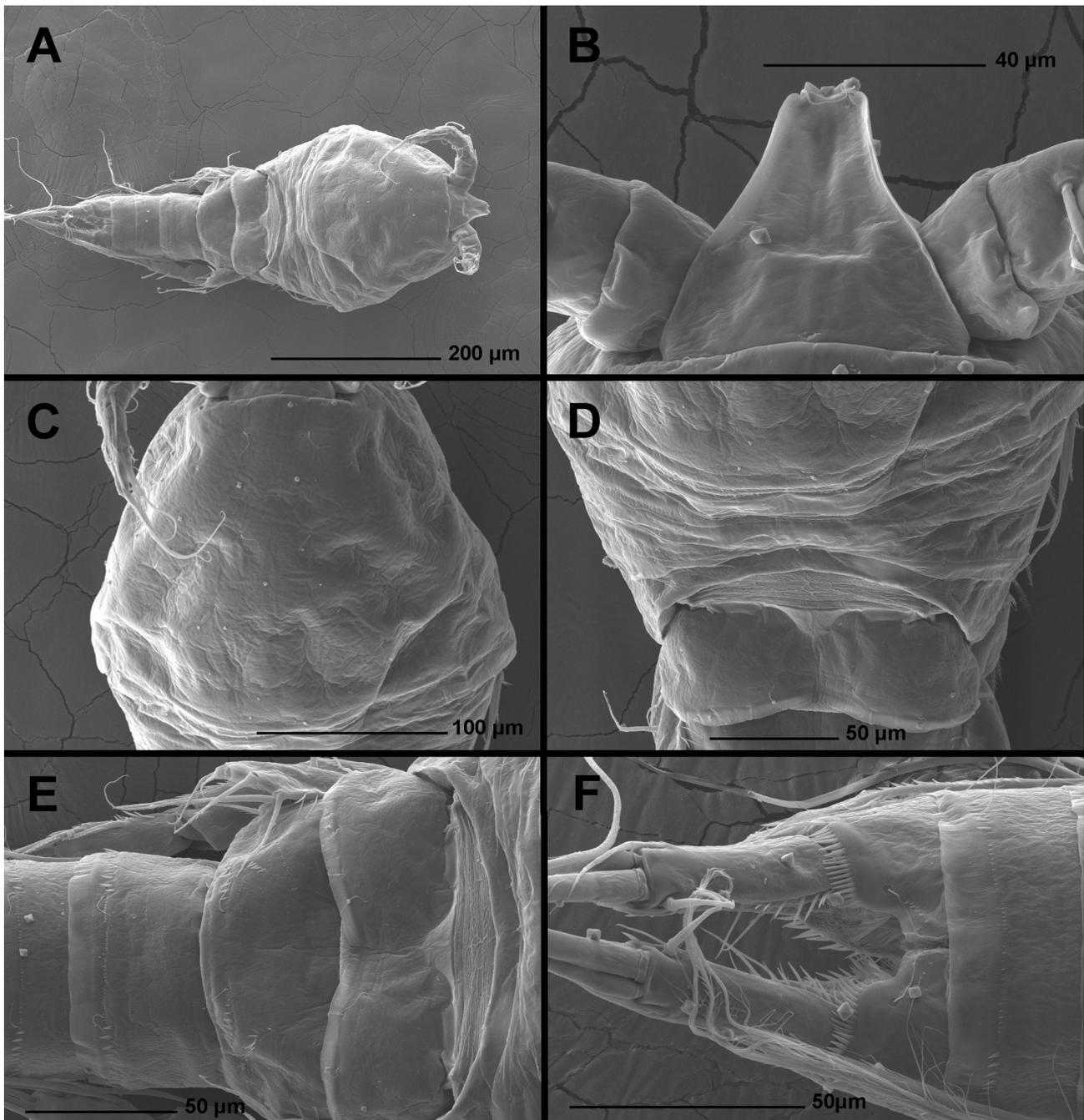


FIGURE 16. *Wellstenhelia clio* sp. nov., scanning electron micrographs, female paratype: A, habitus, dorsal view; B, rostrum, dorsal view; C, cephalothorax, dorsal view; D, pedigerous somites, dorsal view; E, first urosomite and genital double-somite, dorsal view; F, anal somite and caudal rami, dorsal view. Scale bars 40 µm (B), 50 µm (D, E, F), 100 µm (C), and 200 µm (A).

Antennula (Fig. 16A), antenna, labrum, paragnaths, mandibula (Fig. 13D), maxillula, maxilla, and maxilliped as in *Wellstenhelia calliope*.

Swimming legs (Figs. 12D, 14B) segmentation, ornamentation, armature, and even proportions of various armature elements as in *Wellstenhelia calliope*, except proximal rows of spinules on coxae slightly longer (arrowed in Fig. 14B) and first endopodal segments without anterior pore (arrowed in Fig. 12D).

Fifth leg (Figs. 12A, 14C) segmentation, general shape, number of armature elements, and most ornamentation as in *Wellstenhelia calliope*, except innermost endopodal seta proportionately longer (arrowed in Figs. 12A, 14C), space between two central endopodal setae wider (arrowed in Fig. 14C), exopod wider at base (arrowed in Fig. 14C), and additional pore present on anterior surface of exopod (arrowed in Fig. 14C). Length ratio of endopodal

setae, starting from inner side, 1 : 1.2 : 1.7 : 1. Length ratio of exopodal setae, starting from inner side, 1 : 0.3 : 0.3 : 0.8 : 0.6 : 0.6.

Sixth leg (Fig. 14D) as in *Wellstenhelia calliope*.

Male (based on allotype and five paratypes). Body length from 519 to 564 μm (555 μm in allotype). Habitus (Fig. 17A), colour, rostrum (Fig. 17C), shape and almost all ornamentation of cephalothorax (Figs. 14E, 17A, C), shape and ornamentation of second pedigerous somite (Figs. 15C, 17A) (including missing sensilla pair no. 48; arrowed in Fig. 15C), third pedigerous somite (Fig. 17A), and fourth pedigerous somite (Fig. 17A), ornamentation of first urosomite (Figs. 15B, 17B), ornamentation of last three urosomites (Figs. 15A, B, 17A, B), caudal rami (Fig. 15A, B, 17A), antenna (Fig. 17D), labrum (Fig. 17D), paragnaths, mandibula, maxillula, maxilla (Fig. 17E), maxilliped (Fig. 17E), first swimming leg (Fig. 17F), and coxae, bases, and exopods of second, third, and fourth swimming legs as in female. Prosome/urosome ratio 1.1, greatest width at posterior end of cephalothorax, body length/width ratio about 3.5; cephalothorax twice as wide as genital somite in dorsal view. Genital somite and third urosomite not fused.

Cephalothorax (Figs. 14E, 17A, C) in addition to all sensilla and pores present in female, with one additional pair of lateral pores in posterior half (no. ϵ).

First urosomite (Figs. 15B, 17B) slightly narrower and longer than in female but also with three pairs of sensilla (nos. 64, 65, 66) and two pairs of pores (nos. 63, 67).

Genital somite (Figs. 15A, B, 17B) somewhat wider and with fewer spinules than in *Wellstenhelia calliope*, but with all ornamentation same, except pore no. 68 situated more ventrally (arrowed in Fig. 15B), i.e. much closer to pore no. #, and in one paratype two pores extremely close to each other (Fig. 17B).

Third urosomite (Figs. 15A, B, 17B) as in *Wellstenhelia calliope*, except ventral row of spinules not interrupted between sensilla pair no. 73 and not broken between sensilla nos. 72 & 73 (both arrowed in Fig. 15A).

Antennula (Figs. 14F, 17C) shape, segmentation, armature, and most ornamentation as in *Wellstenhelia calliope*, except spiniform process on first segment smaller (arrowed in Fig. 15F), dorsal pore missing (arrowed in Fig. 15F), and aesthetascs on third and fourth segments longer.

Fifth leg (Figs. 15A, B, 17B) shape, armature, and ornamentation as in *Wellstenhelia calliope*, except for shallow ventral notch on fused baseoendopods.

Sixth legs (Fig. 15A, B, 17B) as in *Wellstenhelia calliope*, except middle seta proportionately shorter (arrowed in Fig. 15B).

Variability. Most morphological features are extremely conservative, including the sensilla and pores pattern of somites, and length ratio of different armature on appendages. Except for body length, the only other variable feature was the position of lateral pore no. 68 on the male genital somite (arrowed in Fig. 15B).

Morphological affinities. *Wellstenhelia clio* **sp. nov.** has no obvious autapomorphy that would distinguish it at once from all other congeners. As mentioned above, its female fifth leg (Fig. 14C) is relatively similar to that in the Swedish *Wellstenhelia hanstromi* (Lang, 1948) **comb. nov.**, with two inner endopodal setae of about the same length and strength and as long as the outermost endopodal seta (see Lang 1948), although not as long as those in the Arctic *Wellstenhelia melpomene* **sp. nov.** (see Kornev & Chertoprud 2008). However, this may be a plesiomorphic character, as a similar fifth leg endopod can be found in several lineages of the genus *Delavalia* Brady, 1869. Unfortunately, both *Wellstenhelia hanstromi* and *Wellstenhelia melpomene* are known so far only from a very limited set of female morphological characters (Lang 1948; Kornev & Chertoprud 2008) and most features cannot be compared. Even so, there is no doubt that all three represent separate species, as *Wellstenhelia hanstromi* has much longer caudal rami and a shorter seta on the first endopodal segment of the fourth leg than the other two, and *Wellstenhelia melpomene* has a longer exopod and all setae on the fifth leg, while *Wellstenhelia clio* has a shorter endopod of the first leg. In the absence of other evidence we have to assume that *Wellstenhelia clio* is probably morphologically most similar to *Wellstenhelia melpomene*, as these two species also have very similar caudal rami.

Other congeners can be easily distinguished from *Wellstenhelia clio* by many characters. *Wellstenhelia calliope* **sp. nov.** and *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.** have much longer caudal rami and a shorter innermost seta on the female fifth leg endopod; *Wellstenhelia euterpe* **sp. nov.** has much shorter caudal rami and only three setae on the female fifth leg endopod; while *Wellstenhelia erato* **sp. nov.** and *Wellstenhelia bocqueti* (Soyer, 1971) **comb. nov.** have a much shorter innermost seta on the female fifth leg endopod. Each species can additionally be distinguished from *Wellstenhelia clio* by some other feature in the proportion of armature elements

or ornamentation of somites. Numerous differences between this species and *Wellstenhelia calliope* are indicated by arrowheads in Figs. 12A, B, C, D, 13A, 14B, C, F, 15A, B, C.

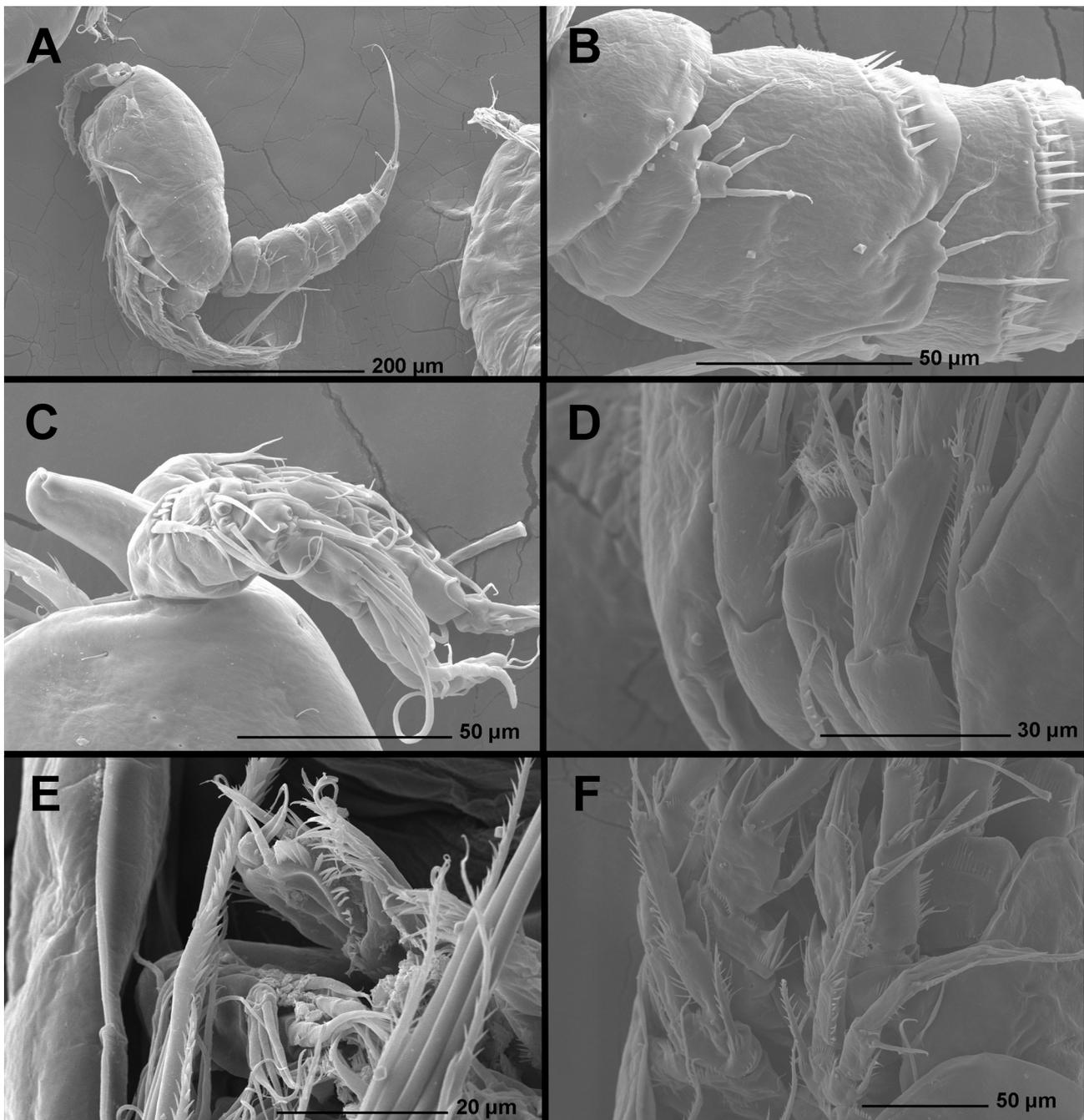


FIGURE 17. *Wellstenhelia clio* sp. nov., scanning electron micrographs, A–B, male paratype 1, C, male paratype 2, D–F, male paratype 3: A, habitus, lateral view; B, fifth pedigerous and anal somites, lateral view; C, antennula and rostrum, lateral view; cephalothorax, dorsal view; D, labrum and antennae, ventro-lateral view; E, maxilla and mailliped, ventral view; F, first and second swimming leg, ventro-anterior view. Scale bars 20 µm (E), 30 µm (D), 50 µm (B, C, F), and 200 µm (A).

***Wellstenhelia erato* sp. nov.**

(Figs. 18–23)

Type locality. South Korea, South Sea, Gwangyang Bay, sampling station 12, muddy sediments, 34.951389°N 127.734361°E (Fig. 1).

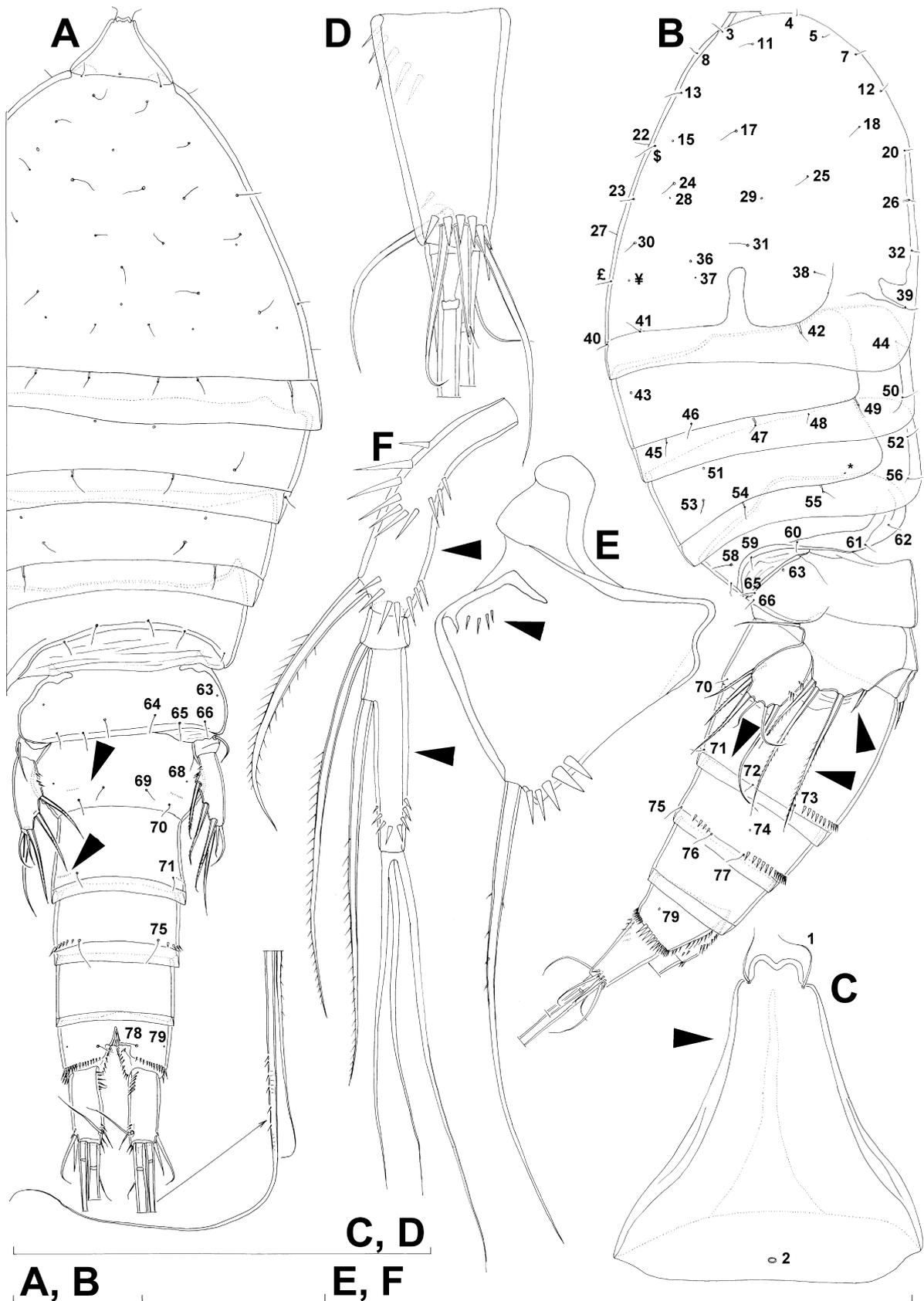


FIGURE 18. *Wellstenhelia erato* sp. nov., line drawings, female holotype: A, habitus, dorsal view; B, habitus, lateral view; C, rostrum, dissected and flattened, dorsal view; D, right caudal ramus, lateral view; E, first segment of antennula, dorsal view; F, exopod of antenna, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Currency symbols (\$, £, ¥) indicate sensilla and pores presumably homologous to those in *Wellstenhelia clio*. Asterisk indicates unique pore. Arrowheads point to most prominent specific features. Scale bars 100 µm.

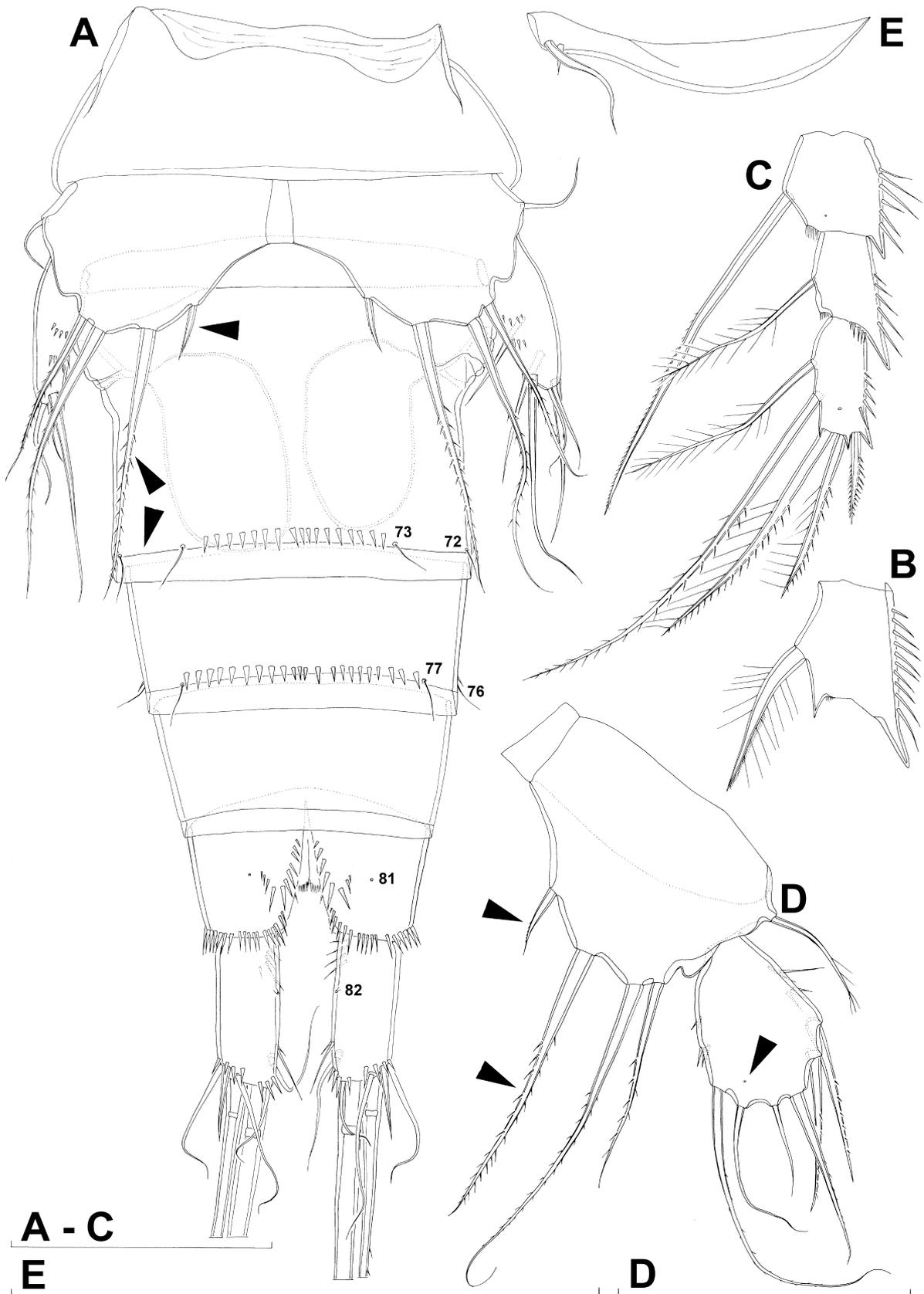


FIGURE 19. *Wellstenhelia erato* sp. nov., line drawings, female holotype: A, urosome, ventral view; B, first endopodal segment of second swimming leg, anterior view; C, endopod of fourth swimming leg, anterior view; D, fifth leg, dissected and flattened, anterior view; E, sixth leg on genital double-somite, lateral view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

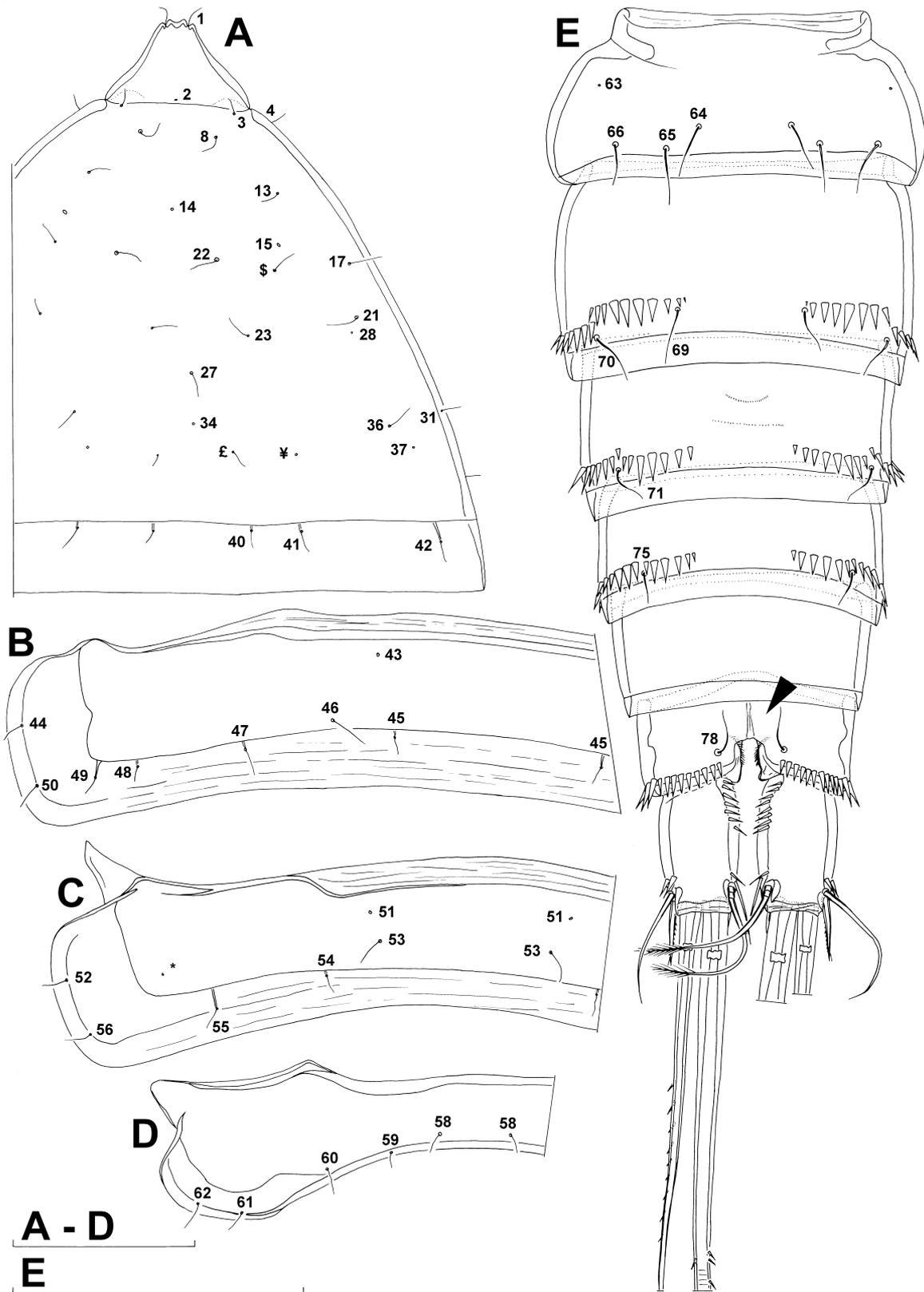


FIGURE 20. *Wellstenhelia erato* sp. nov., line drawings, A–D, female holotype, E, male allotype: A, cephalothorax, dorsal view; B, pleuron of second pedigerous somite, dissected and flattened; C, pleuron of third pedigerous somite, dissected and flattened; D, pleuron of fourth pedigerous somite, dissected and flattened; E, urosome, dorsal view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Currency symbols (\$, £, ¥) indicate sensilla and pores presumably homologous to those in *Wellstenhelia clio*. Asterisk indicates unique pore. Arrowheads point to most prominent specific features. Scale bars 100 µm.

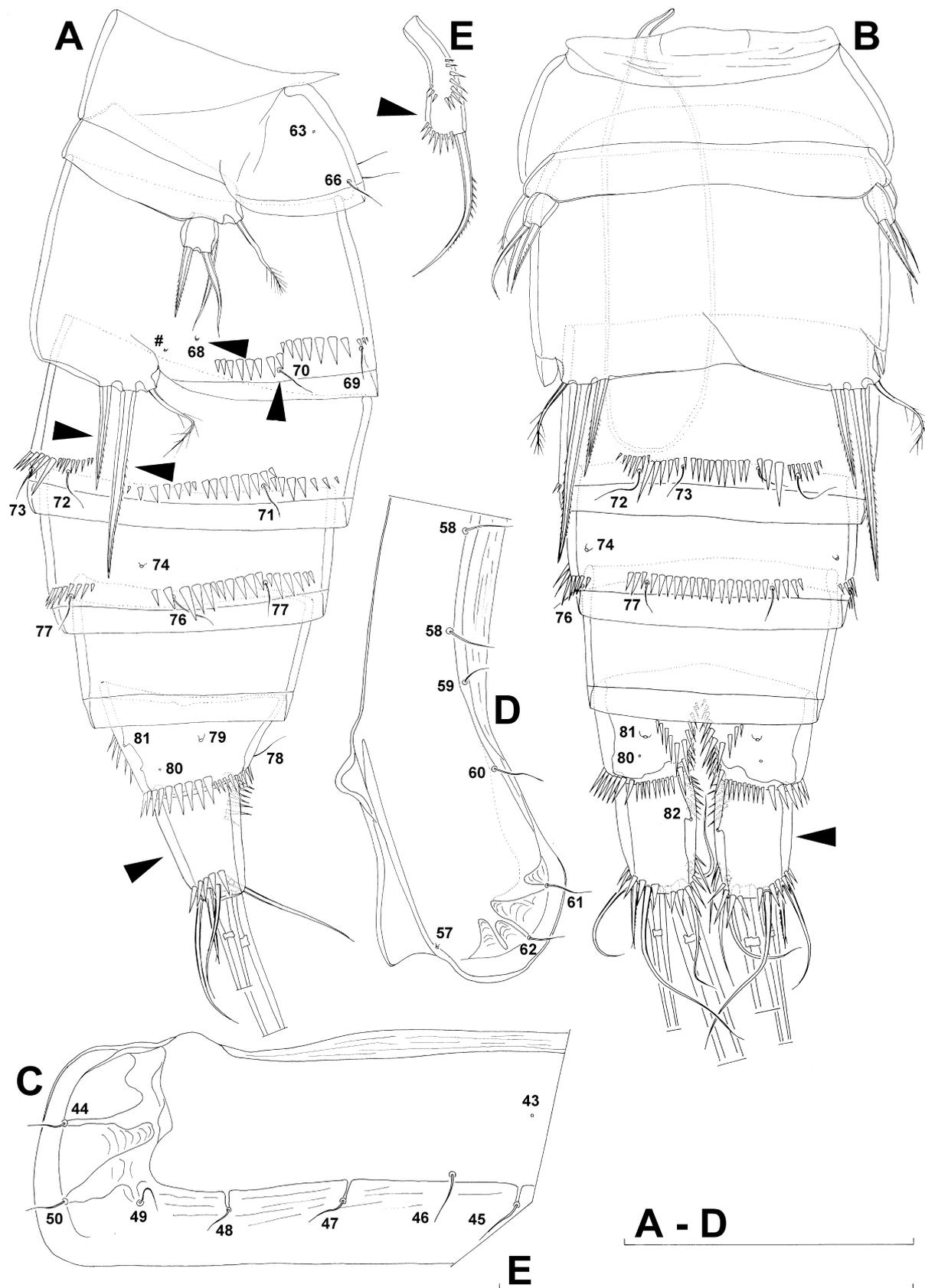


FIGURE 21. *Wellstenhelia erato* sp. nov., line drawings, male allotype: A, urosome, lateral view; B, urosome with spermatophore visible inside, ventral view; C, pleuron of second pedigerous somite, dissected and flattened; D, pleuron of fourth pedigerous somite, dissected and flattened; E, first exopodal segment of antenna, anterior view. Arabic numerals and hash mark (#) indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

Specimens examined. Female holotype dissected on one slide (collection number NIBRIV0000232681), male allotype dissected on one slide (collection number NIBRIV0000232682), female paratype on SEM stub (collection number NIBRIV0000232683), male paratype in ethanol (collection number NIBRIV0000232684), type locality, 14 October 2012, leg. K. Kim.

Two females destroyed for DNA sequence (amplification unsuccessful), type locality, 18 November 2012, leg. K. Kim.

Etymology. The species is named after Erato (Ancient Greek: Ἐρατώ), one of nine Muses from Greek mythology, who was a patron of erotic poetry and song. The species name is a noun in apposition (in the nominative case).

Description. Female (based on holotype and three paratypes). Body length from 820 to 885 μm (882 μm in holotype). Body segmentation, colour, nauplius eye, hyaline fringes, integument thickness and surface appearance as in *Wellstenhelia calliope* **sp. nov.**, including minute sparse pits visible only on highest magnifications on scanning electron microscope. Most somite ornamentation also similar to *Wellstenhelia calliope*, and presumed homologous pore and sensilla also numbered with same Arabic numerals (see Figs. 18A, B, C, 19A, 20A, B, C, D) to allow easier comparison. Habitus (Figs. 18A, B) more robust, with prosome/urosome length ratio close to 1.4, body length/width ratio about 2.8, and cephalothorax 2.3 times as wide as genital double-somite.

Rostrum (Fig. 18C) with wide base and narrow anterior part in dorsal view (arrowed in Fig. 18C) but without any other difference in shape or ornamentation to that in *Wellstenhelia calliope*.

Cephalothorax (Figs. 18A, B, 20A, 23A) about 0.9 times as long as wide; represents 31% of total body length. Surface of cephalothoracic shield with 36 paired or unpaired sensilla and pores, most of which probably homologous to those in *Wellstenhelia calliope* (indicated with Arabic numerals in illustrations) and *Wellstenhelia clio* (indicated with currency symbols in illustrations), but seven pores and sensilla missing (nos. 6, 9, 10, 16, 19, 33, 35); absolute and relative positions of some pores and sensilla differ.

Pleuron of second pedigerous somite (Figs. 20 B, 23B) as in *Wellstenhelia calliope*, except lateral sensilla no. 48 much closer to sensilla no. 49, and anterior pair of pores no. 43 more widely spaced.

Pleuron of third pedigerous somite (Figs. 20C, 23B) as in *Wellstenhelia calliope*, except one additional lateral pore present (no. *) and anterior pair of pores no. 51 less widely spaced.

Pleuron of fourth pedigerous somite (Figs. 20D, 23B) as in *Wellstenhelia calliope*, except anterior lateral pore no. 57 missing.

First urosomite (Figs. 18A, B, 23B, C) as in *Wellstenhelia calliope*, except lateral pore no. 67 missing.

Genital double-somite (Figs. 18A, B, 19A, 23C) as in *Wellstenhelia calliope*, except no large dorsal or lateral spinules (arrowed in Figs. 18A, B, 19A), ventral pair of sensilla no. 73 more widely spaced, and two large seminal receptacles clearly visible inside.

Last threeurosomites (Figs. 18A, B, 19A, 23E, F) as in *Wellstenhelia calliope*, except lateral pore no. 80 missing.

Caudal rami (Figs. 18A, B, D, 19A, 23F) short and stout, similar in shape to those in *Wellstenhelia clio*, about as long as anal somite, cylindrical, 2.3 times as long as wide (ventral view), parallel, and with space between them less than one ramus width; ornamentation and armature as in *Wellstenhelia calliope*, except central part of inner margin without spinules and ventral pore no. 83 missing.

Antennula (Fig. 18E) as in *Wellstenhelia calliope*, except first segment without dorsal pore, with less sharp process, and with additional row of minute spinules basally (arrowed in Fig. 18E).

Antenna (Fig. 18F) as in *Wellstenhelia calliope*, except first exopodal segment inflated in distal half and third exopodal segment without central row of spinules (both arrowed in Fig. 18F).

Labrum, paragnaths, mandibula, maxillula, maxilla, and maxilliped as in *Wellstenhelia calliope*.

Swimming legs (Fig. 19B, C) segmentation, ornamentation, armature, and proportions of various armature elements as in *Wellstenhelia calliope*, except first endopodal segment of second leg without anterior pore.

Fifth leg (Figs. 18B, 19A, D, 23D) segmentation, general shape, number of armature elements, and even most ornamentation as in *Wellstenhelia calliope*, except innermost endopodal seta proportionately shorter (arrowed in Figs. 18B, 19A, D), second endopodal seta from inner side proportionately longer (arrowed in Figs. 18B, 19A, D), and anterior pore of exopod closer to inner margin (arrowed in Fig. 19D). Length ratio of endopodal setae, starting from inner side, 1 : 4.2 : 5.2 : 3. Length ratio of exopodal setae, starting from inner side, 1 : 0.5 : 0.3 : 0.55 : 0.5 : 0.5.

Sixth leg (Fig. 19E) simple narrow cuticular plate, unornamented, with single smooth and short outer seta flanking single minute inner spine; latter about same size as some larger spinules on genital double-somite.

Male (based on allotype). Body length 760 µm. Habitus, colour, rostrum (Fig. 22A), shape and ornamentation of cephalothorax, second pedigerous somite (Figs. 21C), and third pedigerous somite, shape and most ornamentation of fourth pedigerous somite (Fig. 21D), ornamentation of first urosomite (Figs. 20E, 21A, B), ornamentation of last three urosomites (Figs. 20E, 21A, B), armature and ornamentation of caudal rami (Figs. 20E, 21A, B), antenna (Fig. 21E), labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg (Fig. 22B), and coxae, bases and exopods of third and fourth swimming legs as in female. Prosome/urosome ratio 1.45, greatest width at posterior end of cephalothorax, body length/width ratio about 3.1; cephalothorax 2.4 times as wide as genital somite in dorsal view. Genital somite and third urosomite not fused.

Pleuron of second pedigerous somite (Fig. 21C) with sensilla no. 48 not so close to sensilla no. 49 as in female but everything else same.

Pleuron of fourth pedigerous somite (Fig. 21D) with anterior lateral pore no. 57 present, all other ornamentation as in female.

First urosomite (Figs. 20E, 21A, B) narrower than in female but also with three pairs of dorsal sensilla (nos. 64, 65, 66) and one pair of lateral pores (no. 63).

Genital somite (Figs. 20E, 21A, B) somewhat wider than in *Wellstenhelia calliope*, but with all ornamentation same, except pore no. 68 situated more ventrally (arrowed in Fig. 21A), i.e. much closer to pore no. #, and lateral row of spinules less broken near sensilla no. 70 (arrowed in Fig. 21A); large spermatophore visible inside genital somite, longitudinally placed on right side, about as long as that in *Wellstenhelia calliope*.

Third urosomite (Figs. 20E, 21A, B) as in *Wellstenhelia clio*, i.e. ventral row of spinules uninterrupted between sensilla no. 73, except few more large spinules present dorsally from sensilla no. 71.

Anal somite (Figs. 20E, 21A, B) as in female, except lateral pore no. 80 present.

Caudal rami (Figs. 20E, 21A, B) shorter than in female (arrowed in Fig. 21A, B), with length/width ratio in ventral view of just below 1.5, but armature and ornamentation as in female, including missing ventral pore no. 83.

Antennula (Fig. 22A) shape, segmentation, ornamentation, and most armature as in *Wellstenhelia calliope*, except second segment proportionately shorter (arrowed in Fig. 22A), aesthetascs proportionately longer, and second, third and fourth segment with one, one, and two additional setae respectively (latter arrowed in Fig. 22A); setal formula thus 1.12.7+ae.9+ae.1.2.1.4.6+ae.

Third swimming leg endopod (Fig. 22C) without anterior pore and with distal inner seta on third segment slender.

Fourth swimming leg endopod (Fig. 22D) without anterior pore on first segment and with inner seta on first segment and distal seta on third segment slender and shorter than those in female.

Fifth leg (Fig. 21A, B) shape, armature, and ornamentation as in *Wellstenhelia calliope*, except exopod proportionately larger and with much strong inner armature element.

Sixth leg (Fig. 21A, B) shape, ornamentation, and number of armature elements as in *Wellstenhelia calliope*, except inner and middle elements strong spines (both arrowed in Fig. 21A) and middle one exceptionally long, reaching beyond midlength of fourth urosomite; length ratio of armature elements, starting from inner side, 1 : 1.8 : 1.

Variability. All morphological features are extremely conservative among the four female specimens examined, while only one male was available for morphological examination.

Morphological affinities. *Wellstenhelia erato* **sp. nov.** differs from all congeners by the minute innermost endopodal seta on the female fifth leg (Fig. 19D), which can be considered as a clear autapomorphy of this species. Other possible autapomorphies include an inflated first exopodal segment of the antenna (Fig. 18F) and very strong elements on the male sixth leg (Fig. 21A, B). However, the former character was not described for *Wellstenhelia hanstromi* (Lang, 1948) **comb. nov.** and *Wellstenhelia melpomene* **sp. nov.**, while males (or male characters) are still unknown for *Wellstenhelia hanstromi*, *Wellstenhelia melpomene*, *Wellstenhelia euterpe* **sp. nov.**, and *Wellstenhelia bocqueti* (Soyer, 1971) **comb. nov.** *Wellstenhelia calliope* **sp. nov.** and *Wellstenhelia bocqueti* also have the innermost endopodal seta on the female fifth leg relatively short, although not as short as in *Wellstenhelia erato*, but the former differs by its much longer caudal rami, while the latter has a deep notch on the female fifth leg endopod, as well as the principal caudal setae confluent at base.

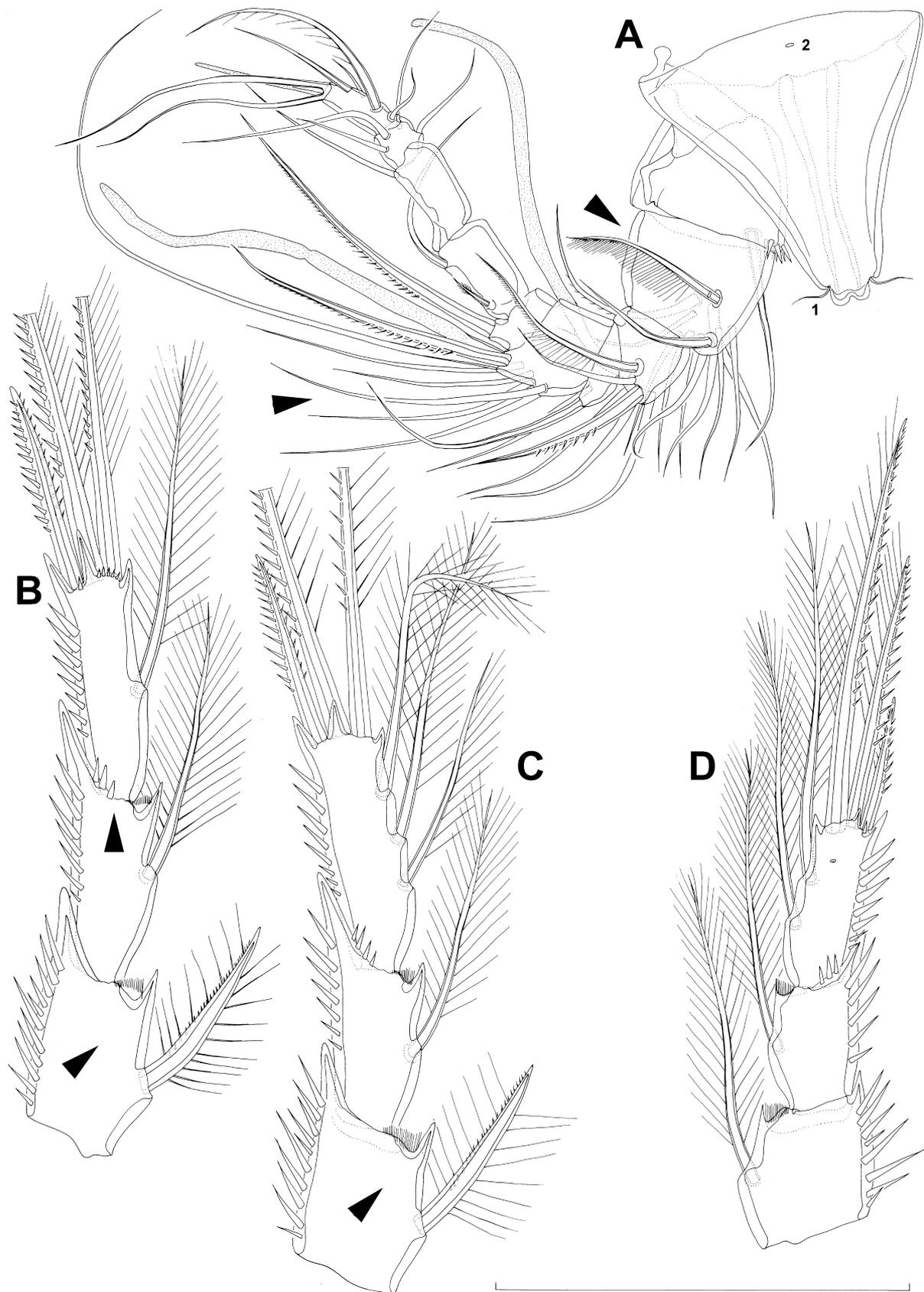


FIGURE 22. *Wellstenhelia erato* sp. nov., line drawings, male allotype: A, antennula slightly uncoiled and rostrum compressed, dorsal view; B, endopod of second swimming leg; C, endopod of third swimming leg; D, endopod of fourth swimming leg. Arabic numerals on rostrum indicate sensillum and pore homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bar 100 μ m.

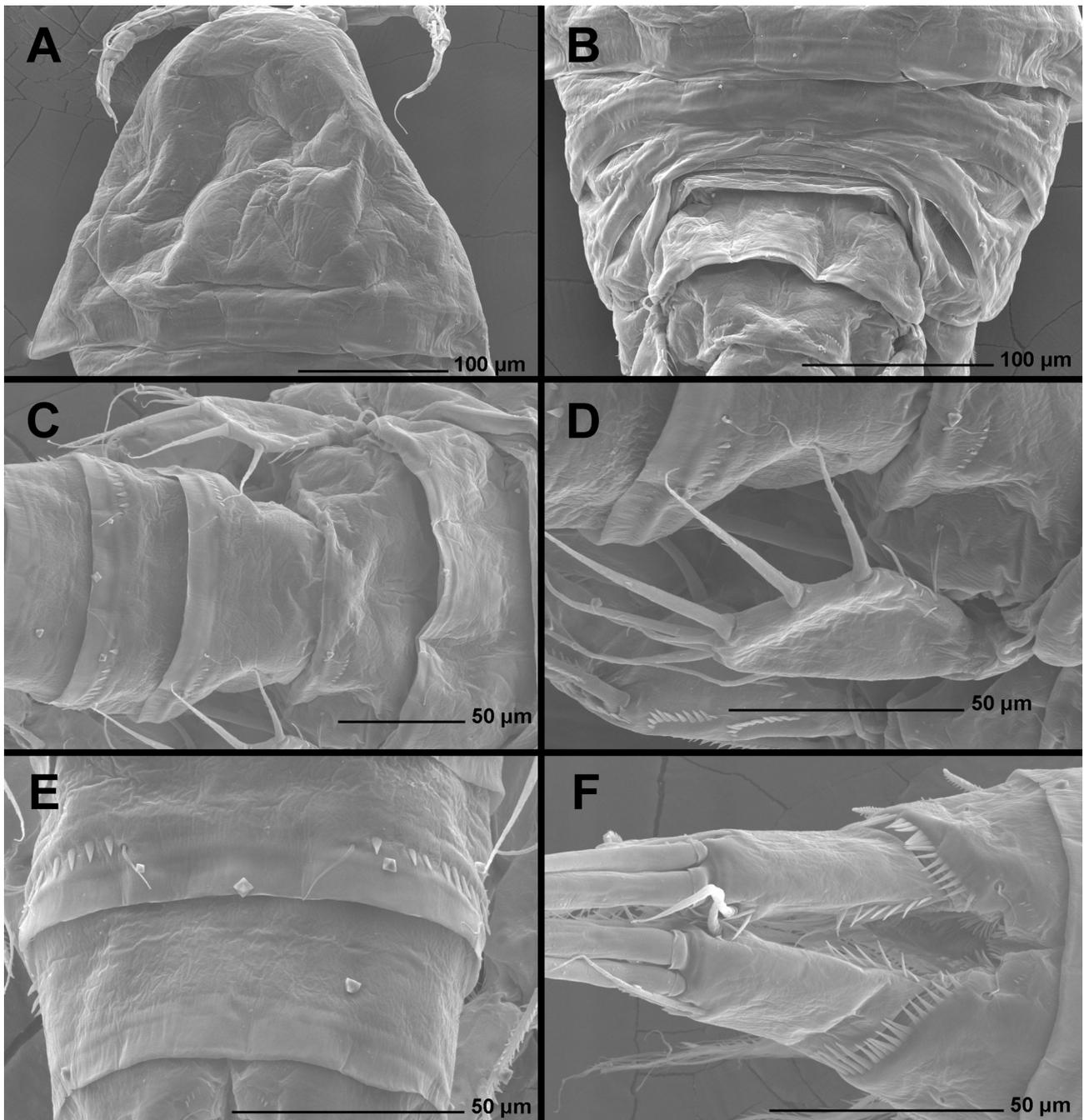


FIGURE 23. *Wellstenhelia erato* **sp. nov.**, scanning electron micrographs, female paratype: A, cephalothorax, dorsal view; B, pedigerous somites, dorsal view; C, anterior part of urosome, dorsal view; D, right fifth leg, dorsal view; E, fourth and fifth (preanal) urosomal somites, dorsal view; F, anal somite and caudal rami, dorsal view. Scale bars 50 µm (C, D, E, F) and 100 µm (A, B).

Other congeners can be easily distinguished from *Wellstenhelia erato* by many characters. *Wellstenhelia hanstromi* and *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.** have much longer caudal rami; *Wellstenhelia euterpe* **sp. nov.** has much shorter caudal rami and only three setae on the female fifth leg endopod; while *Wellstenhelia clio* **sp. nov.** and *Wellstenhelia malpomene* **sp. nov.** have a much longer innermost seta on the female fifth leg endopod. Each species can additionally be distinguished from *Wellstenhelia erato* by some other feature in the proportion of armature elements or ornamentation of somites. Numerous differences between this species and *Wellstenhelia calliope* and *Wellstenhelia clio* are indicated by arrowheads in Figs. 18A, B, C, E, F, 19A, D, 20E, 21A, B, E. These include absence of large dorsal spinules on the genital double-somite, absence of many sensilla and pores on prosomite, but also some novel features, such as lateral pore on the third pedigerous somite

(no. *). *Wellstenhelia erato* is also the largest of all Korean sympatric congeners, and probably the largest species of *Wellstenhelia* **gen. nov.**

***Wellstenhelia qingdaoensis* (Ma & Li, 2011) comb. nov.**

(Figs. 24–29)

Synonymy. *Delavalia qingdaoensis* sp. nov. – Ma & Li 2011, p. 1087, figs. 1–8.

Specimens examined. One female dissected on one slide (collection number NIBRIV0000232685), one male dissected on one slide (collection number NIBRIV0000232686), three females together on one SEM stub (collection number NIBRIV0000232687), 20 females and five copepodids in ethanol (collection number NIBRIV0000232688), 11 females destroyed for DNA sequence (one successful amplification, Code 0113), South Korea, South Sea, Gwangyang Bay, sampling station 15, muddy sediments, 34.890139°N 127.795111°E, 18 November 2012, leg. K. Kim (Fig. 1).

One female destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 12, muddy sediments, 34.951389°N 127.734361°E, 18 November 2012, leg. K. Kim (Fig. 1).

One female destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 14, muddy sediments, 34.924333°N 127.852333°E, 18 November 2012, leg. K. Kim (Fig. 1).

One female destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 17, muddy sediments, 34.824222°N 127.787750°E, 18 November 2012, leg. K. Kim (Fig. 1)

Redescription. Female (based on six examined specimens). Body length from 523 to 611 µm. Body segmentation, colour, nauplius eye, hyaline fringes, integument thickness and surface appearance as in *Wellstenhelia calliope* **sp. nov.**, including minute sparse pits visible only on highest magnifications on scanning electron microscope (for example, see Fig. 28D). Most somite ornamentation also similar to *Wellstenhelia calliope*, and presumed homologous pore and sensilla also numbered with same Arabic numerals (see Figs. 24A, B, C, D 25A, B) to allow easier comparison. Habitus (Figs. 24A, B, 27A, 28A) more robust, with prosome/urosome length ratio about one, body length/width ratio 3.1, and cephalothorax twice as wide as genital double-somite.

Rostrum (Figs. 24C, 27B) with slightly narrower tip than in *Wellstenhelia calliope* (arrowed in Fig. 24C), but without any other difference in shape or ornamentation.

Cephalothorax (Figs. 24A, B, 27A, 28B) about 0.9 times as long as wide; represents 26% of total body length. Surface of cephalothoracic shield with 36 paired or unpaired sensilla and pores, most of which probably homologous to those in *Wellstenhelia calliope* (indicated with Arabic numerals in illustrations) and *Wellstenhelia clio* (indicated with currency symbols in illustrations), but six pores and sensilla missing (nos. 14, 19, 21, 33, 34, 35); absolute and relative positions of some pores and sensilla different; posterior dorsal sensilla no. 40 paired.

Pleuron of second pedigerous somite (Figs. 24D, 28C, D) ornamented as in *Wellstenhelia calliope*, except lateral pair of sensilla no. 48 (arrowed in Fig. 24D) and anterior pair of pores no. 43 missing.

Pleurons of third pedigerous somite (Figs. 24A, B, 28C), fourth pedigerous somite (Figs. 24A, B, 28C), and first urosomite (Figs. 24A, B, 27C, 28C) as in *Wellstenhelia calliope*.

Genital double-somite (Figs. 24A, B, 25A, 27C) as in *Wellstenhelia calliope*, except anterior part even more inflated laterally, forming spiniform chitinous processes, central part even more constricted, only four large dorsal sensilla present in anterior part (arrowed in Fig. 24B), and ventral pair of sensilla no. 73 much more widely spaced (arrowed in Fig. 25A).

Last three urosomites (Figs. 24A, B, 25A, B, 27E, 28E) as in *Wellstenhelia calliope*, except anal somite slightly more elongated and with more slender and denser spinules along dorsal distal margin (arrowed in Fig. 25B).

Caudal rami (Figs. 24A, B, 25A, B, C, 27D, 29F) shape, armature and most ornamentation as in *Wellstenhelia calliope*, except central part of inner margin without spinules (arrowed in Fig. 25B, but see also Fig. 29F), posterior ventral pore no. 83 missing, principal apical setae strongly fused basally (arrowed in Fig. 25B), and middle apical seta inflated and in most specimens terminates bluntly (arrowed in Fig. 25C), i.e. shorter than outer apical seta; rami about twice as long as anal somite, nearly cylindrical, 4.3 times as long as wide (ventral view), slightly divergent, and with space between them about one ramus width.

Antennula (Figs. 24E, 27B), antenna (Fig. 29B), labrum, paragnaths, mandibula, maxillula, maxilla, and maxilliped as in *Wellstenhelia calliope*.

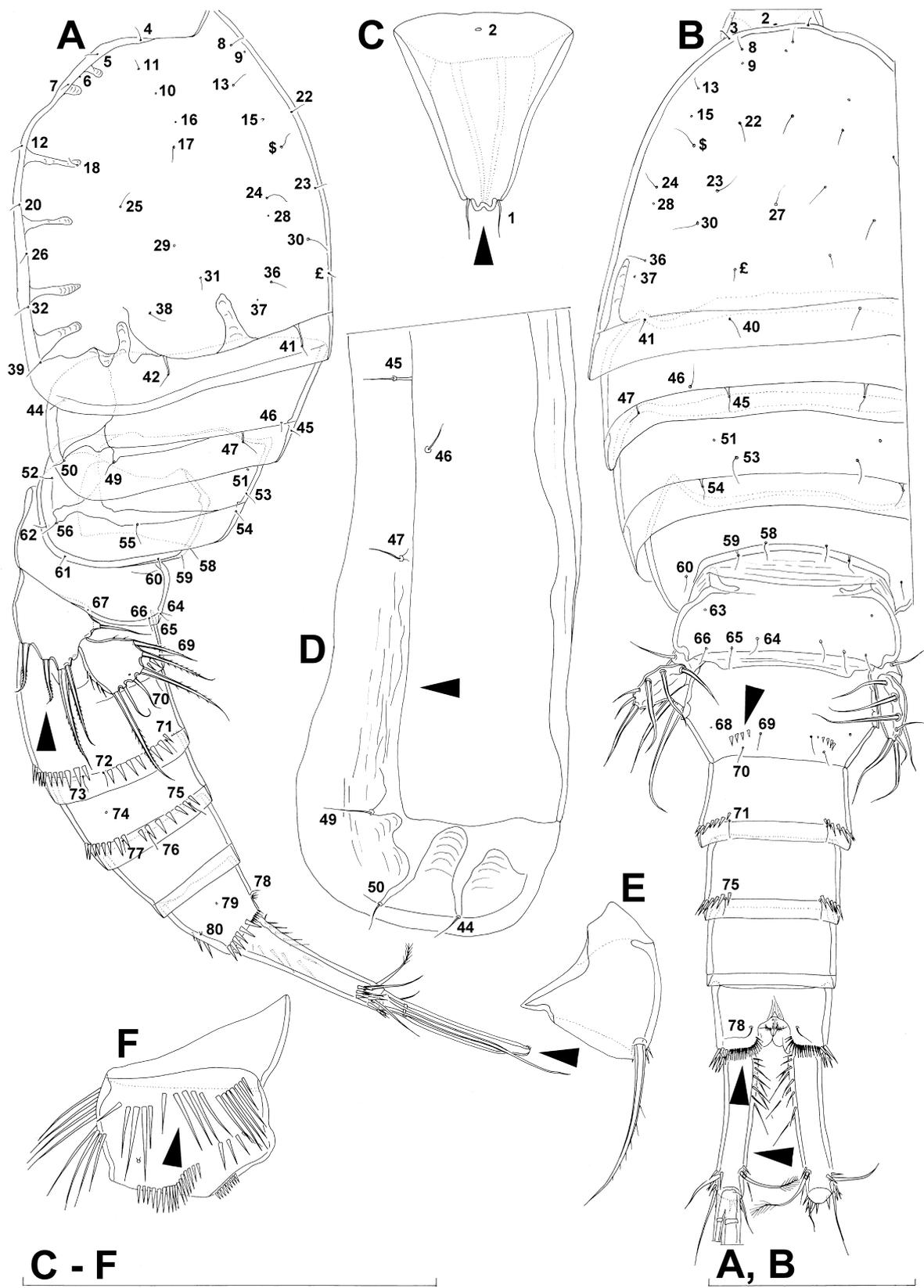


FIGURE 24. *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.**, line drawings, female holotype: A, habitus, lateral view; B, habitus, dorsal view; C, rostrum, dissected and flattened, dorsal view; D, pleuron of second pedigerous somite, dissected and flattened; E, first segment of antennula, ventral view; F, praecoxa and coxa of first swimming leg, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Currency symbols (\$, £) indicate sensilla and pores presumably homologous to those in *Wellstenhelia clio*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

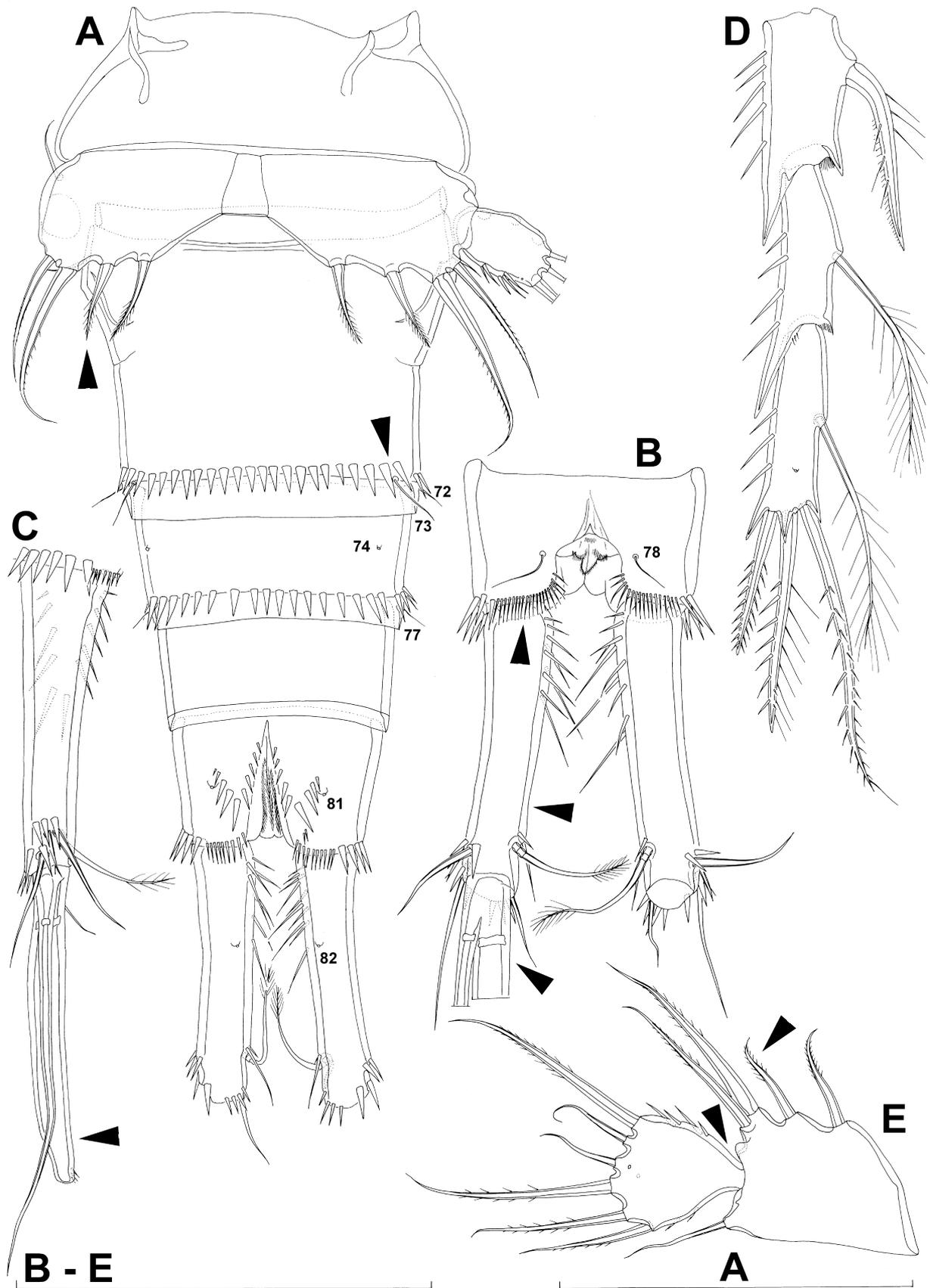


FIGURE 25. *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.**, line drawings, female holotype: A, urosome, ventral view; B, anal somite and caudal rami, dorsal view; C, left caudal ramus, lateral view; D, endopod of second swimming leg, anterior view; E, fifth leg flattened, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

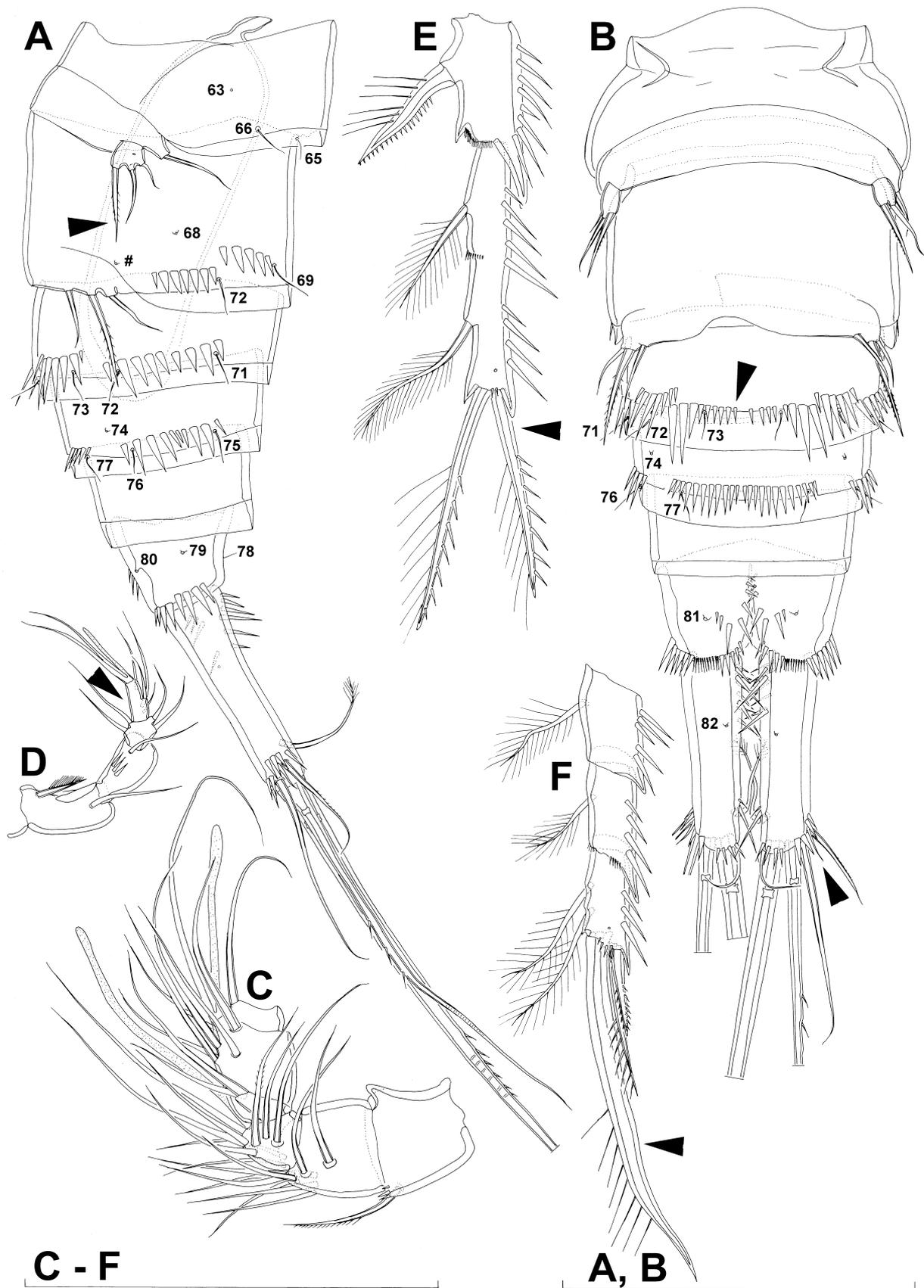


FIGURE 26. *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.**, line drawings, male allotype: A, urosome, lateral view; B, urosome, ventral view; C, proximal part of antennula, dorsal view; D, distal part of antennula, slightly uncoiled, dorso-anterior view. Arabic numerals and hash mark (#) indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

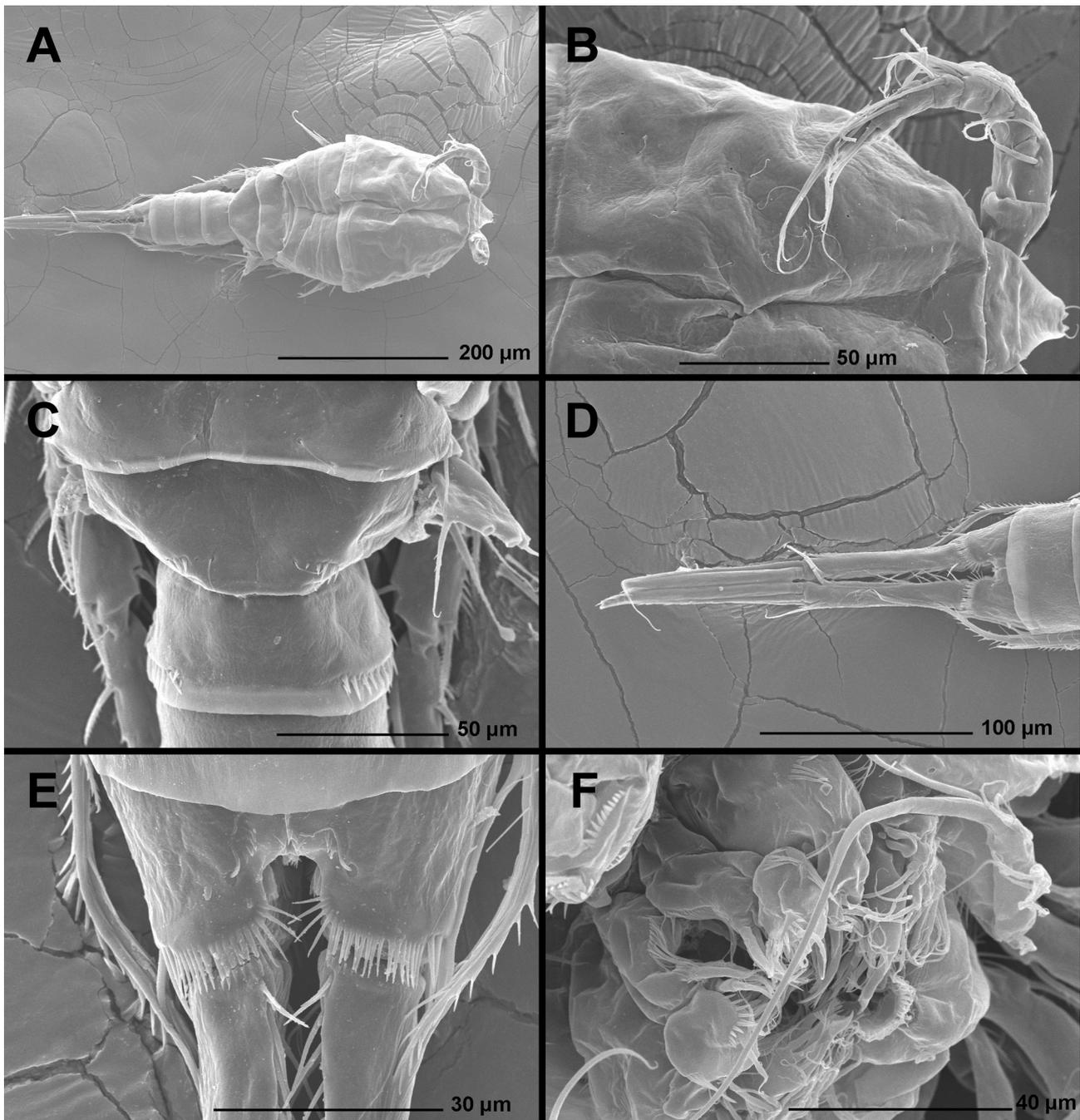


FIGURE 27. *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.**, scanning electron micrographs, A–E female paratype 1, F, male paratype 1: A, habitus, dorsal view; B, cephalothorax with central part collapsed and antennula, dorsal view; C, first urosomites and genital double-somite, dorsal view; D, anal somite and caudal rami, dorsal view; E, anal somite and anterior part of caudal rami, dorsal view; F, mouth appendages, ventral view. Scale bars 30 µm (E), 40 µm (F), 50 µm (B, C), 100 µm (D) and 200 µm (A).

Swimming legs (Figs. 24F, 25D, 29C, D) segmentation, ornamentation, armature, and even proportions of various armature elements as in *Wellstenhelia calliope*, except spinules in proximal row on coxae much longer (arrowed in Fig. 24F) and first endopodal segments without anterior pore.

Fifth leg (Figs. 24A, B, 25A, E, 29E) segmentation, general shape, number of armature elements, and most ornamentation as in *Wellstenhelia calliope*, except second endopodal seta from inner side proportionately much shorter (arrowed in Figs. 24A, 25A, E), basal part of exopod somewhat narrower (arrowed in Fig. 25E), and another pore visible on posterior side of exopod. Length ratio of endopodal setae, starting from inner side, 1 : 1 : 1.9 : 1.6. Length ratio of exopodal setae, starting from inner side, 1 : 0.4 : 0.4 : 1 : 0.7 : 0.6.

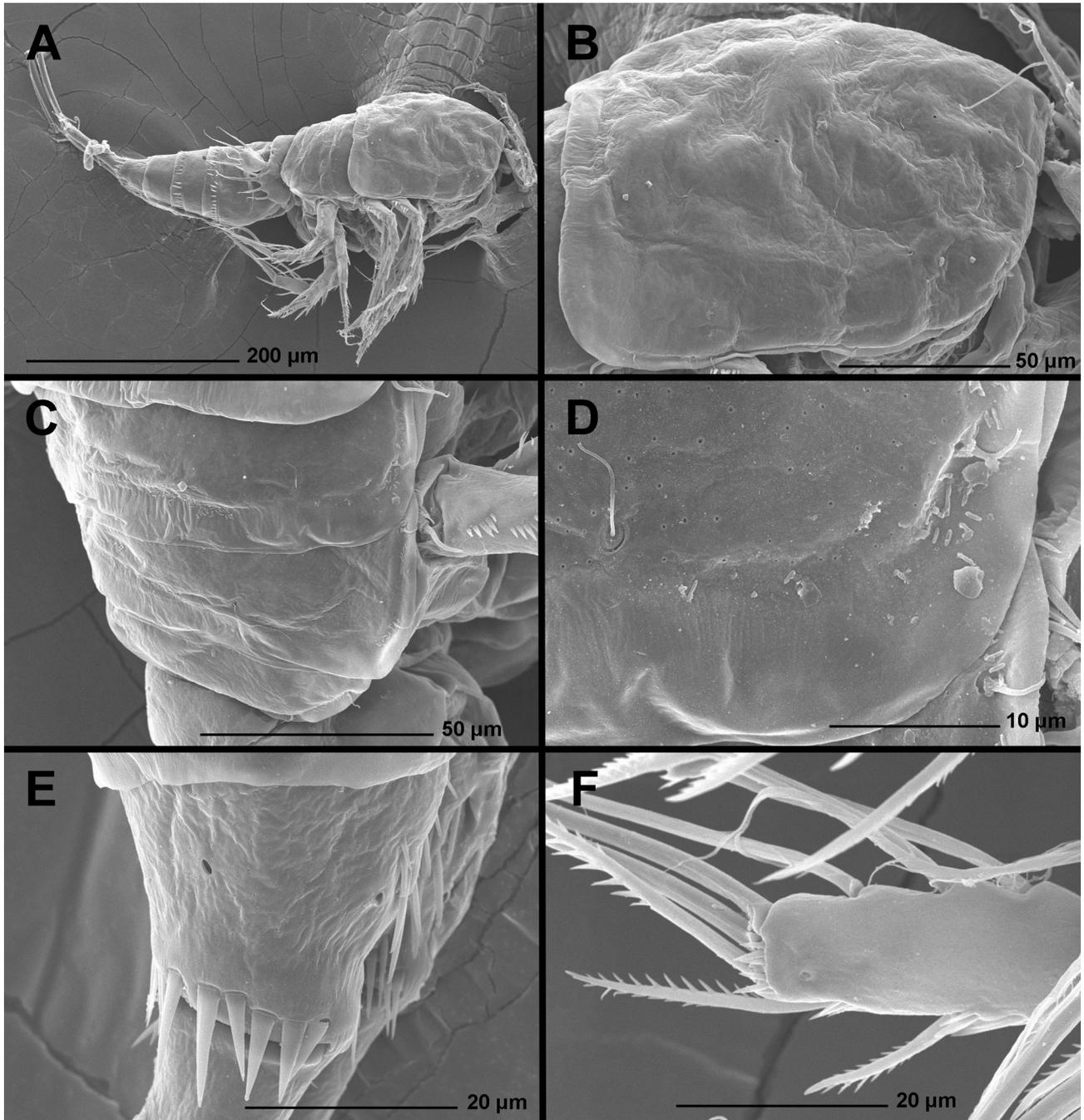


FIGURE 28. *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.**, scanning electron micrographs, A–E female paratype 2, F, male paratype 1: A, habitus, lateral view; B, cephalothoracic shield, lateral view; C, pedigerous somites, lateral view; D, distal lateral corner of second pedigerous somite; E, anal somite, lateral view; F, third exopodal segment of fourth swimming leg, anterior view. Scale bars 10 µm (D), 20 µm (E, F), 50 µm (B, C), and 200 µm (A).

Sixth leg as in *Wellstenhelia calliope*.

Male (based on allotype and three paratypes). Body length from 466 to 492 µm. Habitus, colour, rostrum, shape and ornamentation of cephalothorax, all pedigerous somites, ornamentation of last three urosomites (Fig. 26A, B), caudal rami (Fig. 26A, B), antenna (Fig. 29A), labrum (Fig. 27F), paragnaths, mandibula (Fig. 27F), maxillula (Fig. 27F), maxilla (Fig. 27F), maxilliped (Fig. 27F), first swimming leg, third swimming leg, and coxae, bases, and exopods of second and fourth (Fig. 28F) swimming legs as in female. Prosome/urosome ratio 1.1, greatest width at posterior end of cephalothorax, body length/width ratio about 3.6; cephalothorax twice as wide as genital somite in dorsal view. Genital somite and third urosomite not fused.

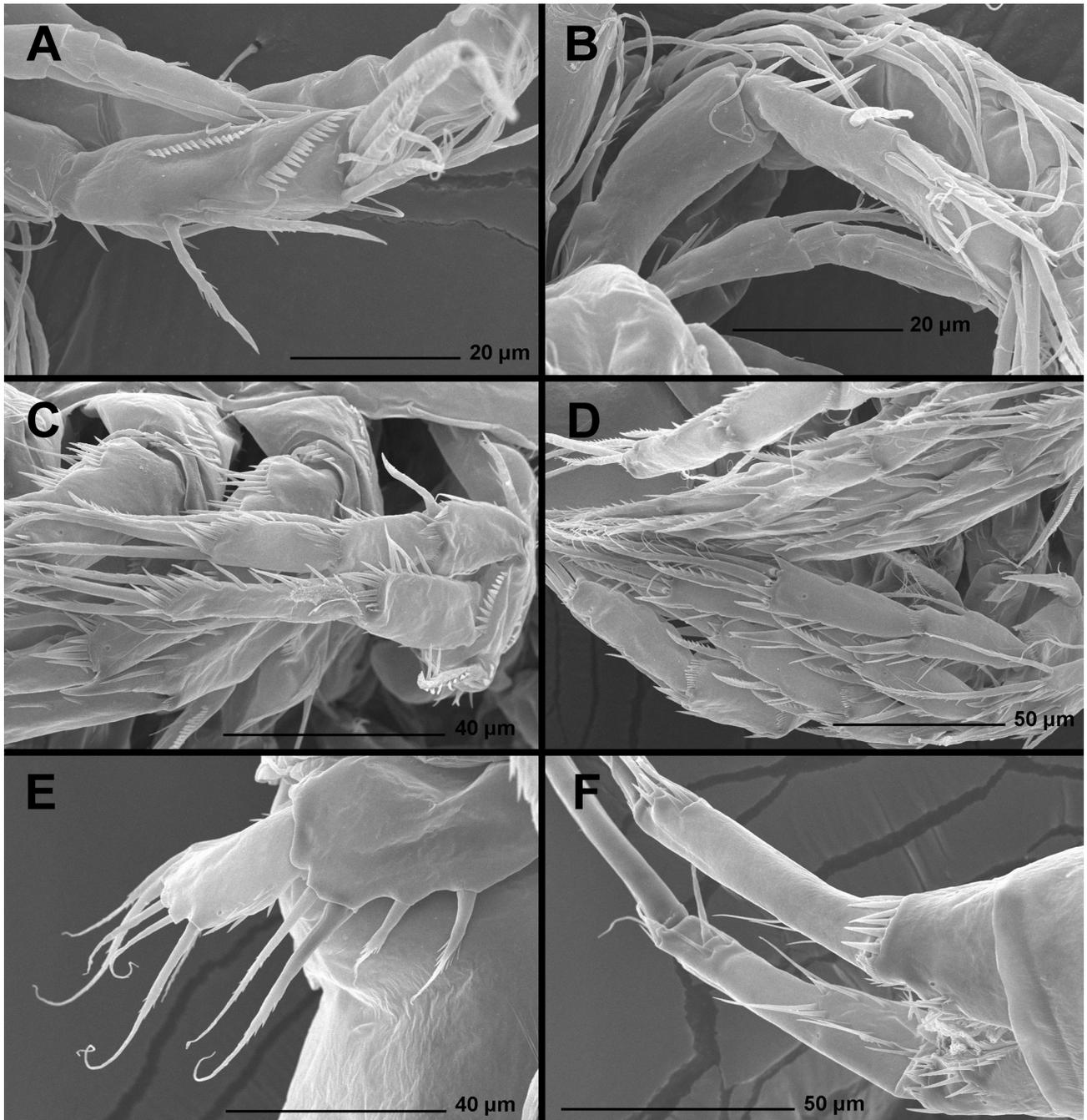


FIGURE 29. *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.**, scanning electron micrographs, A, male paratype 1, B, female paratype 3, C, female paratype 4, D–F, female paratype 5: A, distal part of antenna, posterior view; B, antenna, anterior view; C, first swimming leg and proximal parts of second and third swimming legs, ventral view; D, second to fourth swimming legs, ventro-lateral view; E, fifth leg, ventro-lateral view; F, anal somite and caudal rami, ventro-lateral view. Scale bars 20 µm (A,B), 40 µm (C, E), and 50 µm (D, F).

First urosomite (Fig. 26A, B) slightly narrower and longer than in female but also with three pairs of sensilla (nos. 64, 65, 66) and one pair of pores (no. 63).

Genital somite (Fig. 26A, B) as in *Wellstenhelia calliope*, except lateral pore no. 68 situated somewhat closer to ventral side.

Third urosomite (Fig. 26A, B) as in *Wellstenhelia calliope*, except ventral row of spinules not interrupted between sensilla pair no. 73 (arrowed in Fig. 26B), and those sensilla also more widely spaced.

Antennula (Fig. 26C, D) shape, segmentation, and most armature and ornamentation as in *Wellstenhelia*

calliope, except much shorter generally, especially ultimate segment (arrowed in Fig. 26D), and third and fourth segments with one and two additional setae respectively; setal formula thus 1.11.7+ae.9+ae.1.2.1.4.6+ae.

Endopod of second swimming leg (Fig. 26E) with second and third segments fused, as in *Wellstenhelia calliope*, but with only two apical elements (arrowed in Fig. 26E).

Endopod of fourth swimming leg (Fig. 26F) with inner seta on first segment slender and plumose, as in *Wellstenhelia calliope*, but outer apical element on third segment transformed into powerful claw (arrowed in Fig. 26F).

Fifth leg (Fig. 26A) shape, armature, and ornamentation as in *Wellstenhelia calliope*, except inner exopodal element much stronger and longer (arrowed in Fig. 26A); length ratio of exopodal armature elements, starting from inner side 1 : 0.7 : 0.4.

Sixth leg (Fig. 26A, B) as in *Wellstenhelia calliope*, except middle seta somewhat stronger; length ratio of armature elements, starting from inner side, 1 : 1.5 : 1.

Variability. The middle apical caudal seta can be more or less inflated in female and more or less fused with outer apical seta, and distal part can be completely missing or present as a short slender extension of the inflated part. This seta is less noticeably inflated in males. All other features are extremely conservative.

Morphological affinities. Autapomorphies of *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.** include slender and dense dorsal spinules along distal margin of the anal somite (Fig. 25B), inflated inner principal caudal seta (Fig. 25C), long spinules on the first leg coxa (Fig. 24F), second seta from inner side on the female fifth leg endopod short (Fig. 25E), and very narrow base of the female fifth leg exopod (Fig. 25E). Other unique features include the reduced armature of the male second leg endopod (Fig. 26E) and transformed inner apical seta on the male fourth leg endopod (Fig. 26F), but as mentioned above, males or male characters are unknown in four congeners. The long and slender caudal rami of *Wellstenhelia qingdaoensis* are superficially similar to those of *Wellstenhelia calliope* **sp. nov.** (see above), but they lack spinules along the posterior part of the inner margin in the former species, as well as the posterior pair of ventral pores (no. 83). As mentioned in the affinities section of *Wellstenhelia calliope* (see above) morphological differences between these two species are numerous, and it is quite probable that the elongated caudal rami evolved convergently in these two species. All other congeners have much shorter caudal rami than *Wellstenhelia qingdaoensis*, and each can be distinguished additionally from it by several other differences in the ornamentation of somites or other micro-characters. In fact, this species has a somewhat isolated position in the genus. The Mediterranean *Wellstenhelia bocqueti* (Soyer, 1971) **comb. nov.** has basally confluent principal caudal setae, similar to those of *Wellstenhelia qingdaoensis*, but the former species has much shorter caudal rami, differently shaped female fifth leg, and shorter ventral rows of spinules on urosomites.

***Wellstenhelia euterpe* sp. nov.**

(Figs. 30–33)

Type locality. South Korea, South Sea, Gwangyang Bay, sampling station 2, muddy sediments, 34.881861°N 127.635083°E (Fig. 1).

Specimens examined. Female holotype dissected on one slide (collection number NIBRIV0000232689), female paratype mounted on SEM stub (collection number NIBRIV0000232690), type locality, 39 July 2012, leg. K. Kim.

Etymology. The species is named after Euterpe (Ancient Greek: Εὐτέρπη), one of nine Muses from Greek mythology, who was a patron of lyric poetry and song. The species name is a noun in apposition (in the nominative case).

Description. Female (based on holotype and one paratype). Body length 460 µm and 373 µm respectively. Integument thick and surface smooth, without minute pits. Body segmentation, colour, nauplius eye, and hyaline fringes as in *Wellstenhelia calliope* **sp. nov.** Most somite ornamentation also similar to *Wellstenhelia calliope*, and presumed homologous pore and sensilla numbered with same Arabic numerals (see Figs. 30A, B, 31A, B, C, D, E, 32A) to allow easier comparison. Habitus (Figs. 30A, B, 33A) more robust, with prosome/urosome length ratio 1.3, body length/width ratio about three, cephalothorax twice as wide as genital double-somite.

Rostrum (Fig. 30A, C) similar in shape and ornamentation to *Wellstenhelia calliope* but dorsal pore no. 2 position much more anterior (arrowed in Fig. 30C) and rostrum larger in comparison to cephalothorax.

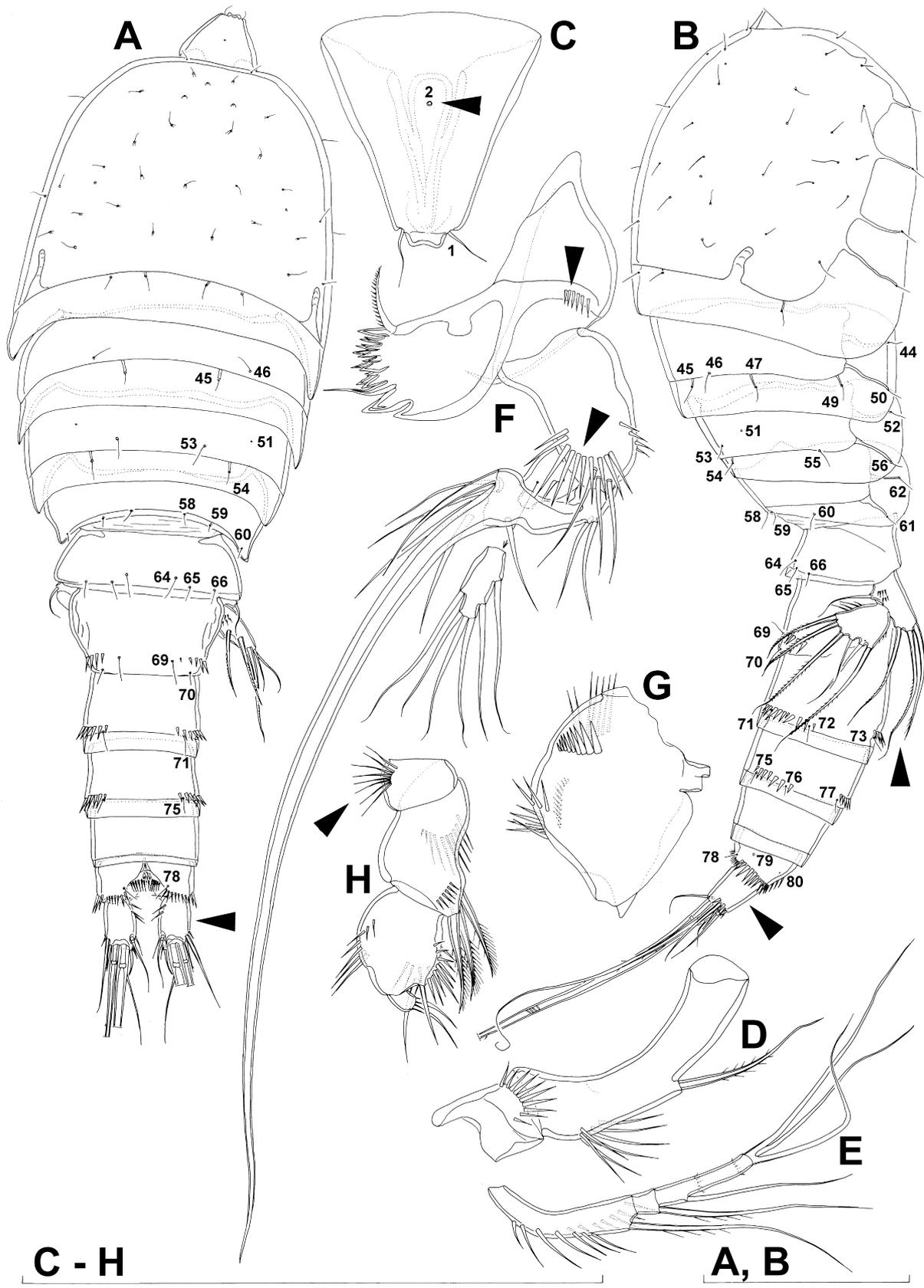


FIGURE 30. *Wellstenhelia euterpe* sp. nov., line drawings, female holotype: A, habitus, dorsal view; B, habitus, lateral view; C, rostrum, dissected and flattened, dorsal view; D, coxa and allobasis of antenna, posterior view; E, exopod of antenna, posterior view; F, mandibula, posterior view (arrow points to separately drawn endopod); G, syncoxa of maxilla, posterior view; H, maxilliped, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

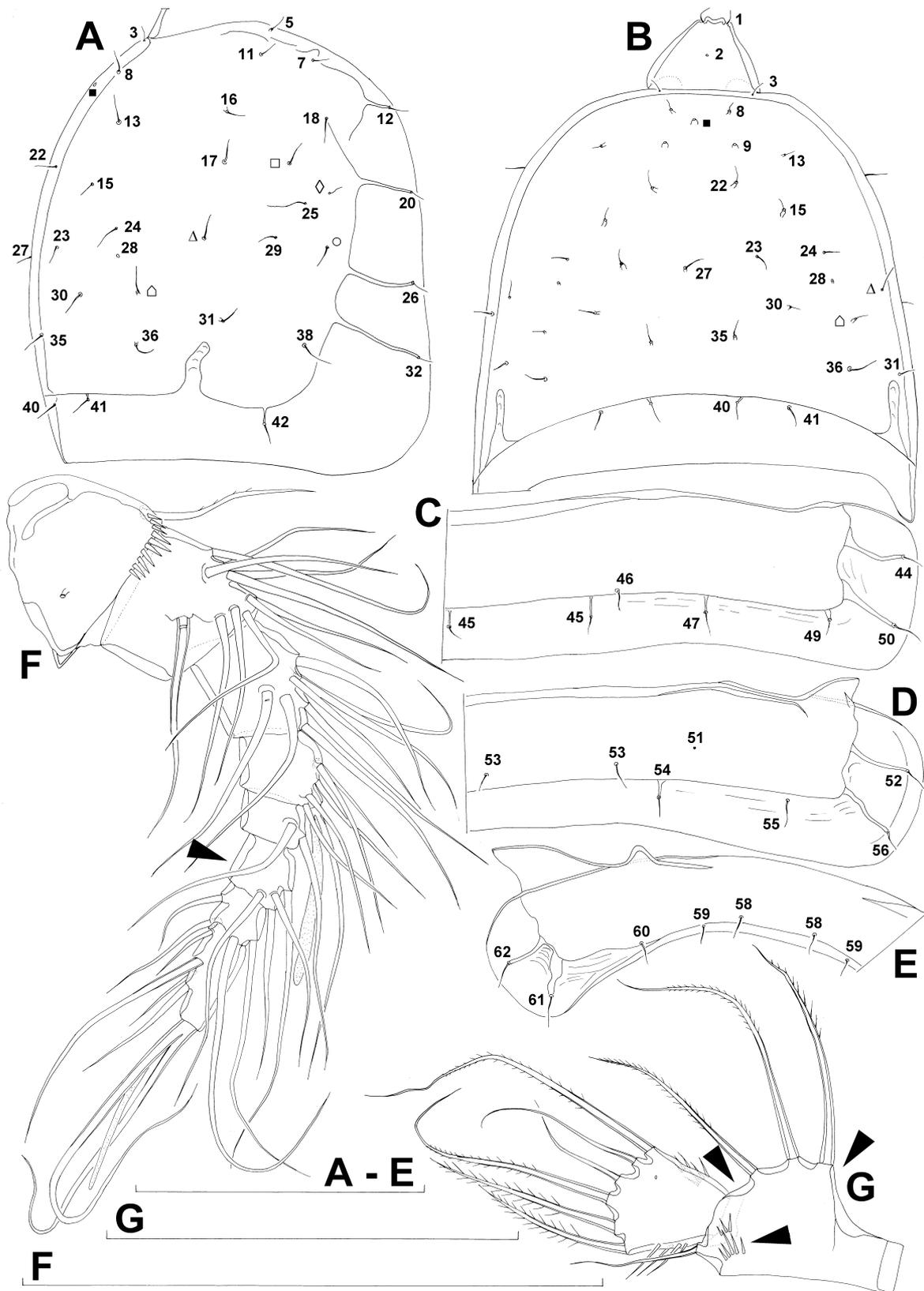


FIGURE 31. *Wellstenhelia euterpe* sp. nov., line drawings, female holotype: A, cephalothoracic shield, lateral view; B, cephalothoracic shield and rostrum, dorsal view; C, pleuron of second pedigerous somite, dissected and flattened; D, pleuron of third pedigerous somite, dissected and flattened; E, pleuron of fourth pedigerous somite, dissected and flattened; F, antennula, dorsal view; G, fifth leg, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Geometric shapes (□, ■, ○, ◇, △, ▽) indicate unique sensilla and pores. Arrowheads point to most prominent specific features. Scale bars 100 μm.

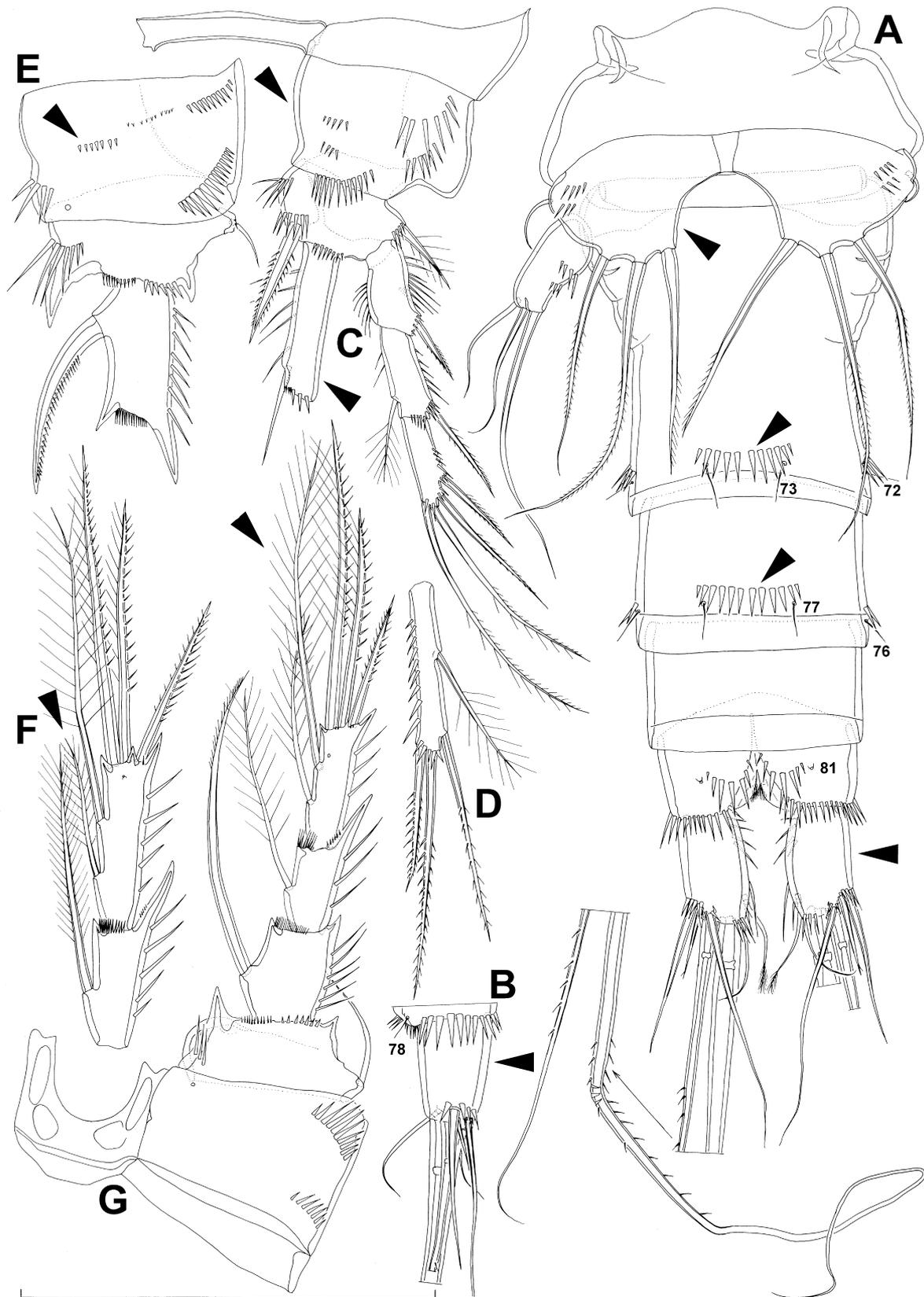


FIGURE 32. *Wellstenhelia euterpe* sp. nov., line drawings, female holotype: A, urosome, ventral view (arrow points to separately drawn distal parts of principal apical caudal setae); B, right caudal ramus, lateral view; C, first swimming leg without second endopodal segment, anterior view; D, second endopodal segment of first leg, anterior view; E, coxa, basis, and first endopodal segment of second swimming leg; F, second and third endopodal segments of second swimming leg; G, fourth swimming leg without exopod. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Arrowheads point to most prominent specific features. Scale bar 100 μ m.

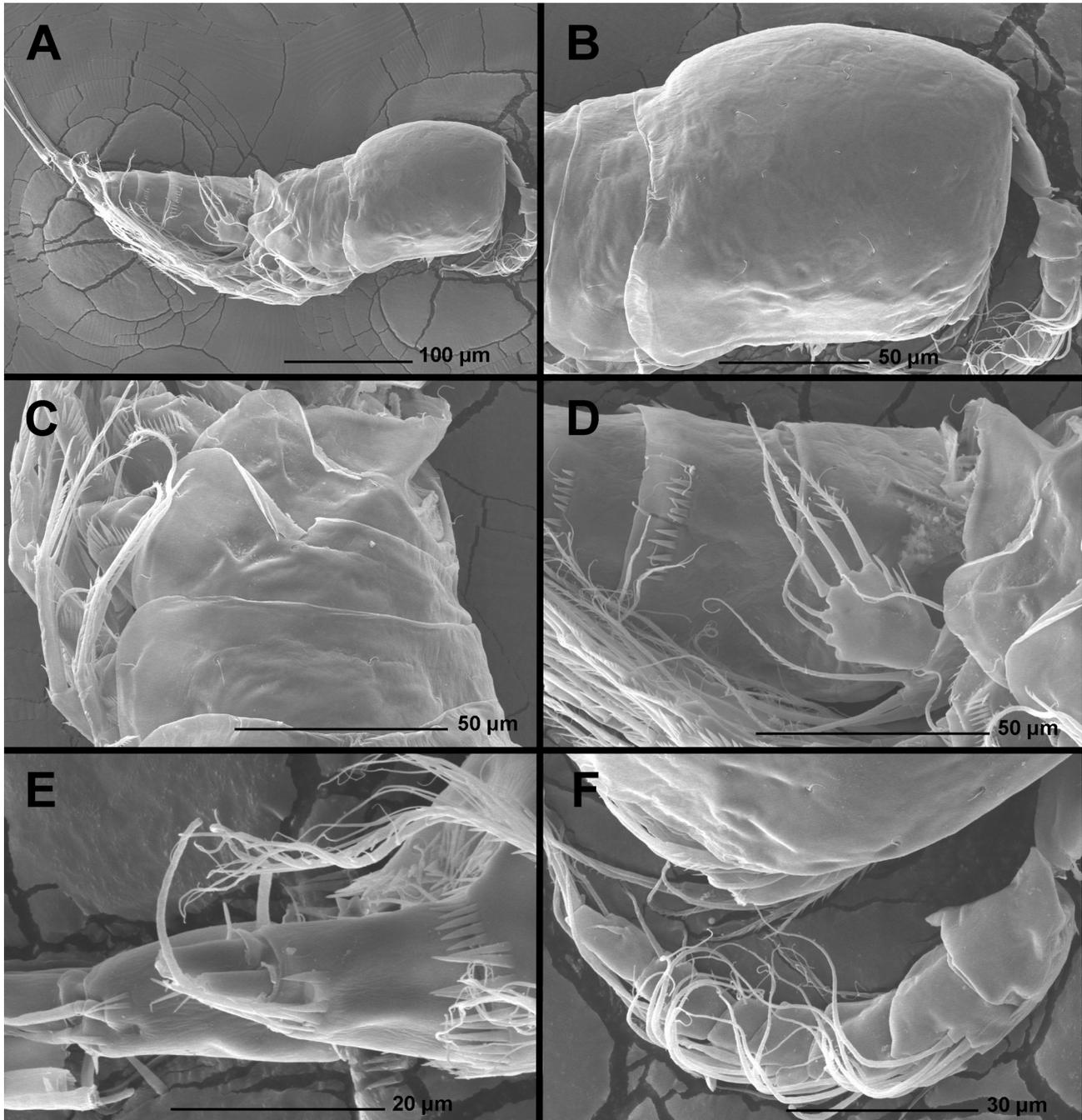


FIGURE 33. *Wellstenhelia euterpe* sp. nov., scanning electron micrographs, female paratype: A, habitus, lateral view; B, cephalothorax, lateral view; C, pedigerous somites, lateral view; D, fifth leg and genital double-somite, lateral view; E, caudal rami, lateral view; F, antennula, dorsal view. Scale bars 20 µm (E); 30 µm (F), 50 µm (B, C, D), and 100 µm (A).

Cephalothorax (Figs. 30A, B, 31A, B, 33B) about 0.85 times as long as wide; comprising 28% of total body length. Surface of cephalothoracic shield with 34 paired or unpaired sensilla and pores, most of which probably homologous to those in *Wellstenhelia calliope* (indicated with Arabic numerals in illustrations), but 12 pores and sensilla missing (nos. 4, 6, 7, 10, 14, 16, 19, 21, 33, 34, 35, 37, 39); absolute and relative positions of some pores and sensilla differ and posterior dorsal sensilla no. 40 paired; six unique pores and sensilla indicated with geometric shapes in Fig. 31A, B.

Pleuron of second pedigerous somite (Figs. 31C, 33C) ornamented as in *Wellstenhelia calliope*, except lateral pair of sensilla no. 48 and anterior pair of pores no. 43 missing.

Pleuron of third pedigerous somite (Figs. 31D, 33C) ornamented as in *Wellstenhelia calliope*, except anterior pair of pores no. 51 more widely spaced.

Pleuron of fourth pedigerous somite (Figs. 31E, 33C) ornamented as in *Wellstenhelia calliope*, except anterior lateral pair of pores no. 57 missing.

First urosomite (Fig. 30A, B) as in *Wellstenhelia calliope*, except pores nos. 63 & 67 missing.

Genital double-somite (Figs. 30A, B, 32A, 33D) as in *Wellstenhelia calliope*, except much more slender, with dorsal pair of sensilla no. 69 more widely spaced, anterior pore no. 68 missing, and shorter ventral row of spinules (arrowed in Fig. 32A).

Last three urosomites (Figs. 30A, B, 32A) as in *Wellstenhelia calliope*, except for shorter ventral row of spinules (arrowed in Fig. 32A) and more closely spaced sensilla pair no. 77 on first of them, as well as somewhat stronger spinules in anal sinus.

Caudal rami (Figs. 30A, B, 32A, B, 33E) short and stout, much shorter than in *Wellstenhelia calliope* (arrowed in Figs. 30A, B, 32A, B), about as long as anal somite, cylindrical, 1.7 times as long as wide (ventral view), parallel, with space between them about one ramus width; most ornamentation and all armature as in *Wellstenhelia calliope*, except both ventral pores (nos. 82, 83) missing.

Antennula (Figs. 31F, 33F) ornamentation and armature as in *Wellstenhelia calliope*, except first segment with more spinules in distal row and sixth segment proportionately shorter (arrowed in Fig. 31F).

Antenna (Fig. 30D, E), labrum, and paragnaths as in *Wellstenhelia calliope*.

Mandibula (Fig. 30F) as in *Wellstenhelia calliope*, except with larger spinules on basis (arrowed in Fig. 30F) and additional row of spinules on coxa (arrowed in Fig. 30F).

Maxillula, maxilla (Fig. 30G), and maxilliped (Fig. 30H) as in *Wellstenhelia calliope*, except maxilliped with row of long and slender spinules on coxa (arrowed in Fig. 30H).

Swimming legs (Fig. 32C, D, E, F, G) segmentation, most ornamentation, most armature, and proportions of various armature elements as in *Wellstenhelia calliope*, except all legs without anterior pore on first endopodal segment, first leg without inner spinules on coxa (arrowed in Fig. 32C), second leg with proximal row of spinules on coxa slightly longer (arrowed in Fig. 32E) and with additional inner seta on third endopodal segment (arrowed in Fig. 32F), and fourth leg with distal inner seta on third endopodal segment less spiniform (arrowed in Fig. 32G).

Fifth leg (Figs. 30B, 31G, 32A, 33D) segmentation, general shape, and most armature and ornamentation as in *Wellstenhelia calliope*, except innermost endopodal seta missing (arrowed in Figs. 30B, 31G, 32A), two additional rows of anterior spinules of basis (arrowed in Fig. 31G), and endopodal lobe without spiniform process at base on exopod (arrowed in Fig. 31G). Length ratio of endopodal setae, starting from inner side, 1 : 1.2 : 0.85. Length ratio of exopodal setae, starting from inner side, 1 : 0.5 : 0.3 : 0.85 : 0.8 : 0.5.

Sixth leg as in *Wellstenhelia calliope*.

Male. Unknown.

Variability. Only two females were studied and no variable morphological feature was observed.

Morphological affinities. *Wellstenhelia euterpe* sp. nov. differs from all congeners by the armature of the female fifth leg endopod, which bears only three setae (Fig. 31G). The complete reduction of the innermost element is considered here a clear autapomorphy. Other unique features of this species include two inner setae on the third endopodal segment of the second swimming leg (Fig. 32F) and slender distal inner seta on the third endopodal segment of the fourth swimming leg (Fig. 32G), but these are plesiomorphic character states in a larger group of stenheiliins. Compared to other congeners, *Wellstenhelia euterpe* has the smallest body, shortest caudal rami (Fig. 32A, B), shortest sixth antennular segment (Fig. 31F), and smoothest and thickest cuticulum. It also has a unique position of the dorsal rostral pore (Fig. 30C), which is much more anterior than in other congeners, but the state of this character is unknown in *Wellstenhelia bocqueti* (Soyer, 1971) **comb. nov.**, *Wellstenhelia hanstromi* (Lang, 1948) **comb. nov.**, and *Wellstenhelia melpomene* sp. nov. (see Lang 1948; Soyer 1971; Kornev & Chertoprud 2008). Other unique features include position and/or presence of several pores and sensilla on somites (Figs. 30A, B, 31A, B, C, D, E), size of spinules on the mandibula (Fig. 30F) and maxilliped (Fig. 30H), and presence of two rows of large spinules on the basal part of the female fifth leg baseoendopod (Fig. 31G). Quite clearly this species has no close relatives among recent congeners. Unfortunately, the males are still unknown.

***Wellstenhelia melpomene* sp. nov.**

Synonymy. *Stenhelia hanstroemi* Lang – Kornev & Chertoprud 2008: p. 201, fig. 5.96.

Type locality. Russia, White Sea, Kandalaksha Gulf, Velikaya Salma Bay, between 30 and 100 m, approximate coordinates 66.497°N 33.621°E.

Type material. Holotype female illustrated by Kornev & Chertoprud (2008) in fig. 5.96, dissected on two slides; paratypes, numerous males and females in alcohol; all deposited at P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia; not examined.

Etymology. The species is named after Melpomene (Ancient Greek: Μελπομένη), one of nine Muses from Greek mythology, who was a patron of tragedy. The species name is a noun in apposition (in the nominative case).

Description. Female as described by Kornev & Chertoprud (2008) from the White Sea, and illustrated in their figure 5.96 as *Stenhelia hanstroemi* Lang, 1948. Male not described or illustrated.

Morphological affinities. Kornev & Chertoprud (2008) state that this species is very common in the White Sea, on muddy bottoms between 30 and 100 m, although it is not clear if they found any males. They provide a brief description and skilful drawings of the female habitus in lateral view, caudal ramus in dorsal view, first swimming leg, fourth swimming leg, and fifth leg. In the armature formula of the swimming legs they state that the third exopodal segment of the first leg bears three outer spines, while their fig. 5.96B shows a normal condition, with two outer spines. We consider the former a lapsus calami. Also the number of setae on the second endopodal segment of the second leg is questionable, as no other member of *Wellstenhelia* **gen. nov.** bears two setae and there is no evidence that either Lang (1948) or Kornev & Chertoprud (2008) studied this appendage in detail. They mention that their population differs slightly from that described by Lang (1948) just in the shape of the fourth leg endopod. However, *Wellstenhelia melpomene* **sp. nov.** and *Wellstenhelia hanstromi* (Lang, 1948) **comb. nov.** differ in at least the following three characters: relative length of the caudal rami (shorter in *Wellstenhelia melpomene*), relative length of the inner seta on the first endopodal segment of fourth leg (longer in *Wellstenhelia melpomene*), and relative length of the female fifth leg armature (all generally longer in *Wellstenhelia melpomene*). In the light of newly discovered diversity of the Korean sympatric stenheliins, these morphological differences cannot be attributed to intraspecific variability. Both species are morphologically most similar to *Wellstenhelia clio* **sp. nov.**, and their affinities are discussed in the remarks section of the latter species (see above).

Genus *Itostenhelia* gen. nov.

Type species. *Itostenhelia polyhymnia* **sp. nov.**

Other species. *Stenhelia* (*Delavalia*) *golikovi* Chislenko, 1978.

Etymology. The new genus name is dedicated to late Dr. Itô Tatsunori, for his contribution to the taxonomy of harpacticoids in general, and stenheliin miraciids in particular. His last name is prefixed to the existing genus name *Stenhelia*.

Diagnosis. Habitus relatively slender in dorsal view, podoplean boundary between prosome and urosome conspicuous. Integument of all somites well sclerotized, prosomites generally smooth and urosomites covered with dense pattern of minute triangular spinules, no cuticular windows or pits. Hyaline fringe of all somites broad and smooth. Rostrum with dorsal transverse suture, bifid tip, pair of dorsal sensilla near tip, and bunch of strong anterior spinules; no dorsal pores. Genital double-somite completely fused along ventral surface but with deep suture indicating original segmentation between genital and third urosomites dorso-laterally, dividing double-somite into shorter anterior and longer posterior parts; anterior part inflated, perfectly rounded laterally (in dorsal view), without sutures or folds; genital apertures placed ventro-laterally. Preanal somite without surface ornamentation, except for minute spinules. Anal somite cleft medially at posterior half, with wide and almost trilobate anal operculum, with pair of large dorsal sensilla on anal operculum, and posterior row of strong spinules on anal somite, without ventral spinules along medial cleft. Caudal rami cylindrical, from 3.5 to four times as long as wide, with several strong inner spinules in anterior third, and with seven setae (three lateral, one dorsal and three apical), all in posterior sixth of ramus length. Female antennula seven-segmented, but traces of ancestral division present on sixth segment, with distal posterior corner of first segment produced into short process, eighth segment

with three lateral and two apical setae; no apical aesthetasc on ultimate segment. Male antennula strongly geniculate and nine-segmented, with additional large aesthetasc on third segment. Antenna composed of short coxa, strong allobasis with few cuticular sutures indicating ancestral segmentation, one-segmented endopod, and three-segmented exopod; endopod with two lateral spines flanking one slender seta. Mandibula without central seta on cutting edge, with six slender setae on small one-segmented endopod, and with two lateral and five apical setae on elongated and curved exopod; three apical exopodal setae strong and spiniform, one of them extremely long. Maxillula composed of praecoxa, coxa, basis, one-segmented endopod, and one-segmented exopod; endopod and exopod not confluent basally, with two and four setae respectively. Maxilla composed of large syncoxa, small basis and even smaller one-segmented endopod; three coxal endites armature formula (starting from dorsal side) 2.3.3; basis with two lateral slender setae and two apical geniculate spines; endopod with four slender setae. Maxilliped not prehensile, four-segmented, with armature formula 0.3.2.2. All swimming legs of similar size and long in comparison to body length, with sharp and long spiniform processes on intercoxal sclerites, spiniform process on inner distal corner of basis of second to fourth leg; all exopods three-segmented, endopod of first leg two-segmented, endopods of second to fourth legs three-segmented, except endopod of second leg in male, which with fused second and third segments and reduced and characteristically modified armature (apical armature consisting of outer spine with distal comb of spinules and two large spinules at midlength, and lateral spiniform seta significantly longer than spine); armature formula of exopods/endopods in female as follows: first leg, 0.1.022/1.211; second leg, 1.1.223/1.2.121; third leg, 1.1.322/1.1.321; fourth leg, 1.1.322/1.1.221; inner seta on first endopodal segments of second and third legs slender; distal inner setae on third exopodal and endopodal segments minute at least in third leg; sexual dimorphism only in second leg. Female fifth legs joined with small triangular intercoxal sclerite, with row of posterior spinules on baseoendopod at base of exopod; endopodal lobe with four setae, two inner ones significantly shorter than outer ones; exopod ovoid, more than twice as long as wide, with row of very long spinules along both inner and outer margins (outer ones especially long), with five setae; innermost exopodal seta longest and strongest, second and third exopodal seta from inner side short and slender, outermost seta hardly longer than neighbouring outer spinules. Male fifth leg with fused endopodal lobes forming slightly convex plate, with four spines (two belonging to each leg, very dissimilar in size, inner at least twice as long as outer), long posterior row of spinules between endopodal armature and exopod; exopod ovoid, with several outer spinules, with three inner setae (all short, slender, and smooth) and two apical spines, inner one fused basally to segment, outermost one strongest and longest. Female sixth leg minute, covering genital aperture, with single pinnate seta at outer distal corner, joined with opposite leg via deep ventral suture into single wide and short flap.

***Itostenhelia polyhymnia* sp. nov.**

(Figs. 34–42)

Type locality. South Korea, South Sea, Gwangyang Bay, sampling station 10, muddy sediments, 34.897056°N 127.757722°E (Fig. 1).

Specimens examined. Female holotype dissected on one slide (collection number NIBRIV0000232691), male allotype dissected on one slide (collection number NIBRIV0000232692), female paratype dissected on one slide (collection number NIBRIV0000232693), one male paratype and three female paratypes together on one SEM stub (collection number NIBRIV0000232694), four male paratypes and seven female paratypes together in ethanol (collection number NIBRIV0000232695), type locality, 18 February 2012, leg. K. Kim.

One male paratype and 15 female paratypes together in ethanol (collection number NIBRIV0000232696), one female destroyed for DNA sequence (amplification unsuccessful), type locality, 18 November 2013, leg. K. Kim.

Three female paratypes (one ovigerous) together in ethanol (collection number NIBRIV0000232697), five females destroyed for DNA sequence (two successful, Codes 0176 & 0273), type locality, 30 July 2012, leg. K. Kim.

Three females (two ovigerous) destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 9, muddy sediments, 34.951389°N 127.734361°E (Fig. 1), 18 November 2012, leg. K. Kim.

One female destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 16, muddy sediments, 34.768889°N 127.783806°E (Fig. 1), 18 November 2012, leg. K. Kim.

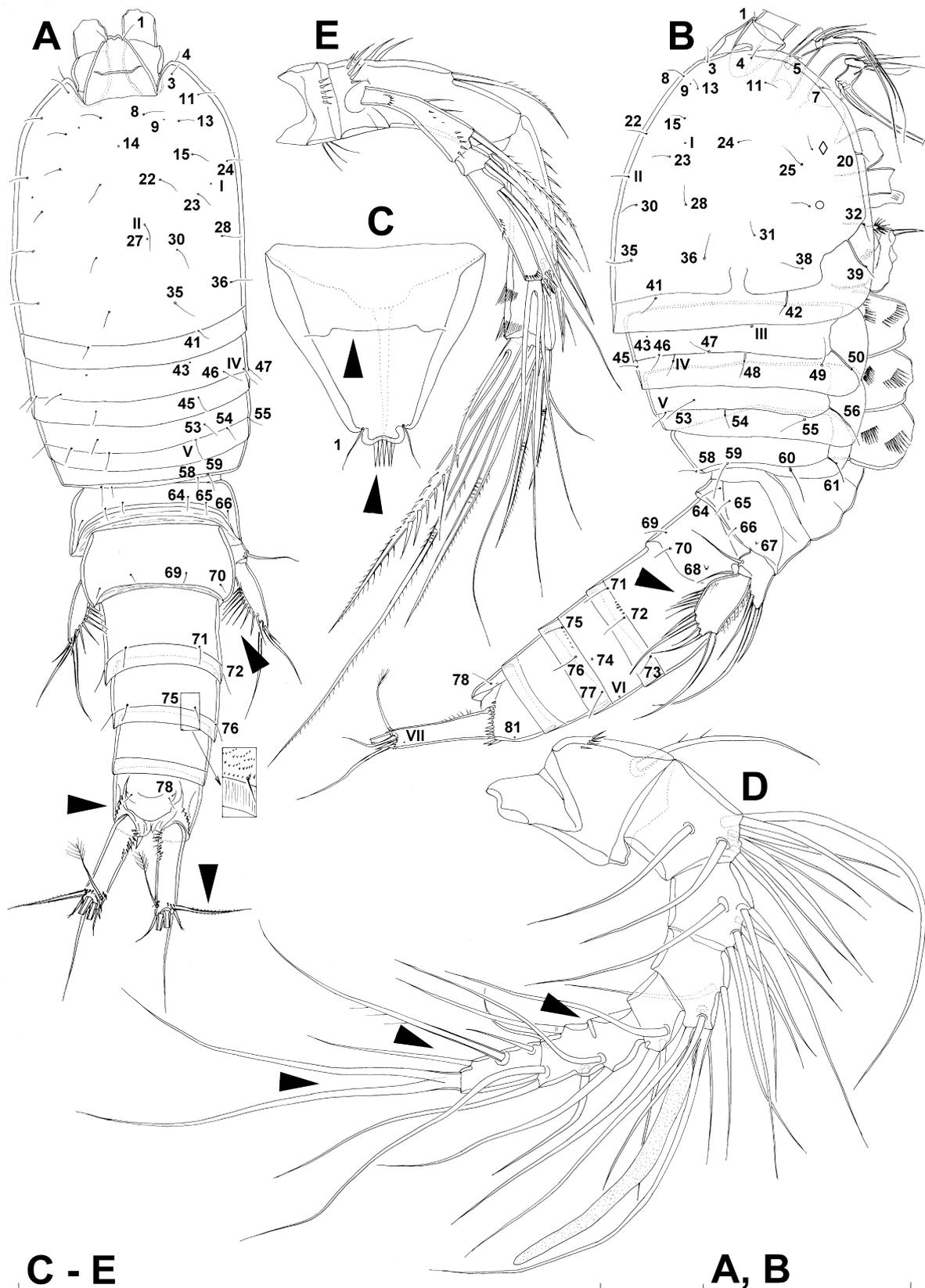


FIGURE 34. *Itostenhelia polyhymnia* sp. nov., line drawings, female holotype: A, habitus, dorsal view; B, habitus, lateral view; C, rostrum, dissected and flattened, dorsal view; D, antennula, dorsal view; E, antenna, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Geometric shapes (\circ , \diamond) indicate sensilla presumably homologous to those in *Wellstenhelia euterpe*. Roman numerals (I–VII) indicate unique sensilla and pores. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

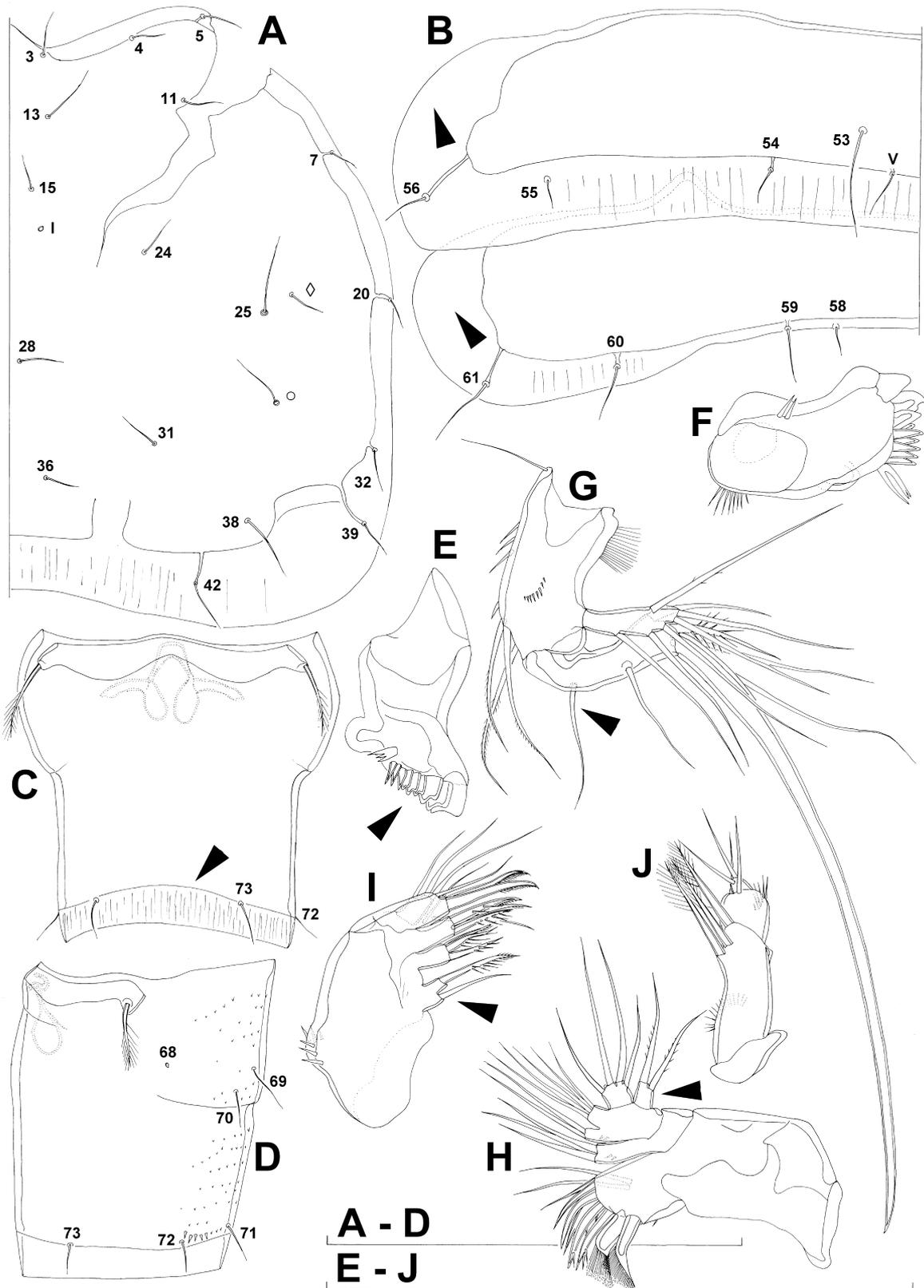


FIGURE 35. *Itostenhelia polyhymnia* sp. nov., line drawings, female holotype: A, right side of cephalothoracic shield, dissected, flattened, and partly broken; B, pleurons of third and fourth pedigerous somites, dissected and flattened; C, genital double-somite, ventral view; D, genital double-somite, lateral view; E, syncoxa of mandibula, antero-ventral view; F, syncoxa of mandibula, posterior view; G, mandibular palp, anterior view; H, maxillula, posterior view; I, mandibula, anterior view; J, maxilliped, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Geometric shapes (○, ◇) indicate sensilla presumably homologous to those in *Wellstenhelia euterpe*. Roman numerals (I, V) indicate unique sensilla and pores. Arrowheads point to most prominent specific features. Scale bars 100 μm.

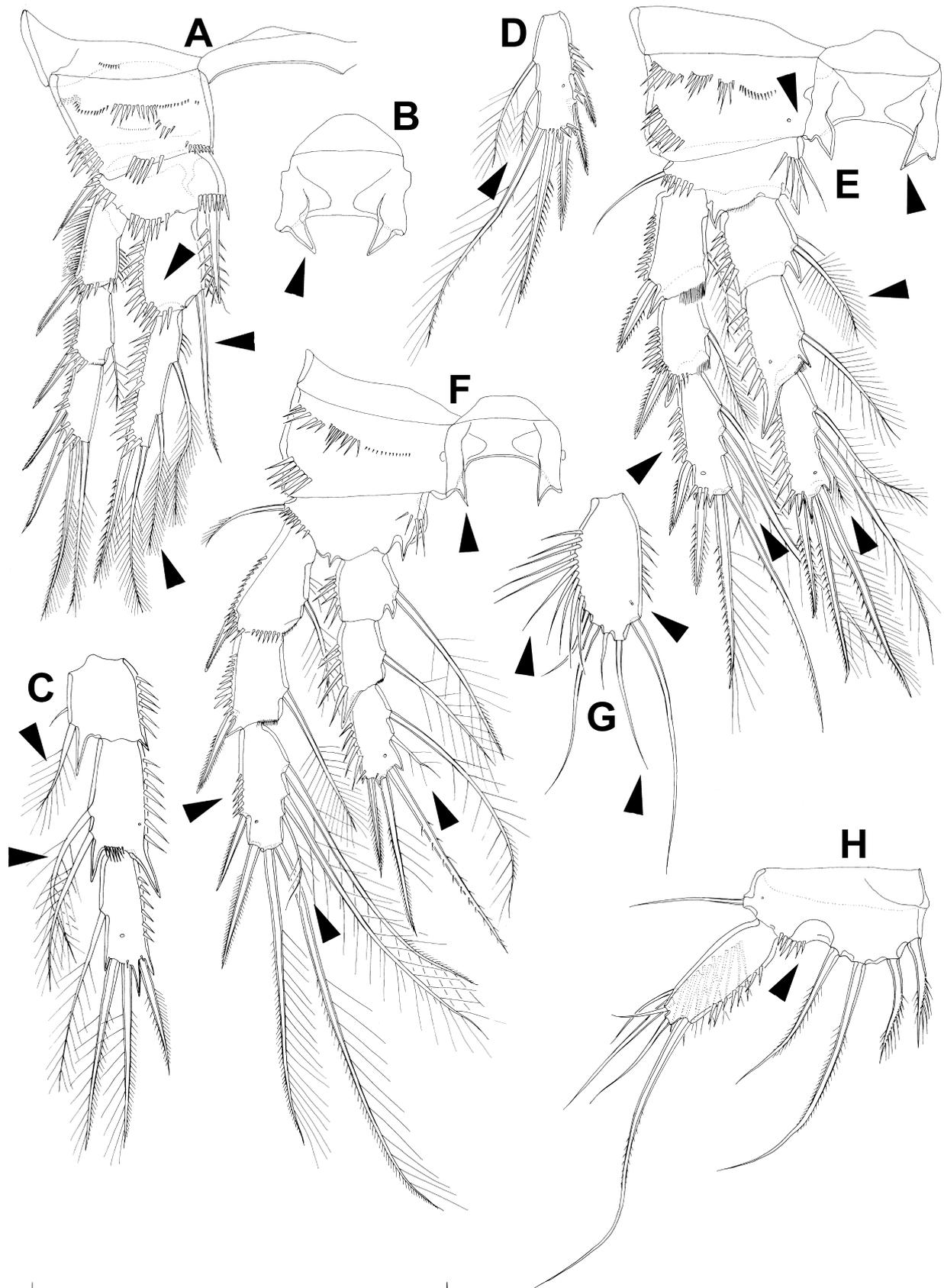


FIGURE 36. *Itostenhelia polyhymnia* sp. nov., line drawings, female holotype: A, first swimming leg, anterior view; B, intercoxal sclerite of second swimming leg, anterior view; C, endopod of second swimming leg, anterior view; D, third exopodal segment of second swimming leg, anterior view; E, third swimming leg, anterior view; F, fourth swimming leg, anterior view; G, exopod of fifth leg, anterior view; H, fifth leg, anterior view;. Arrowheads point to most prominent specific features. Scale bar 100 μ m.

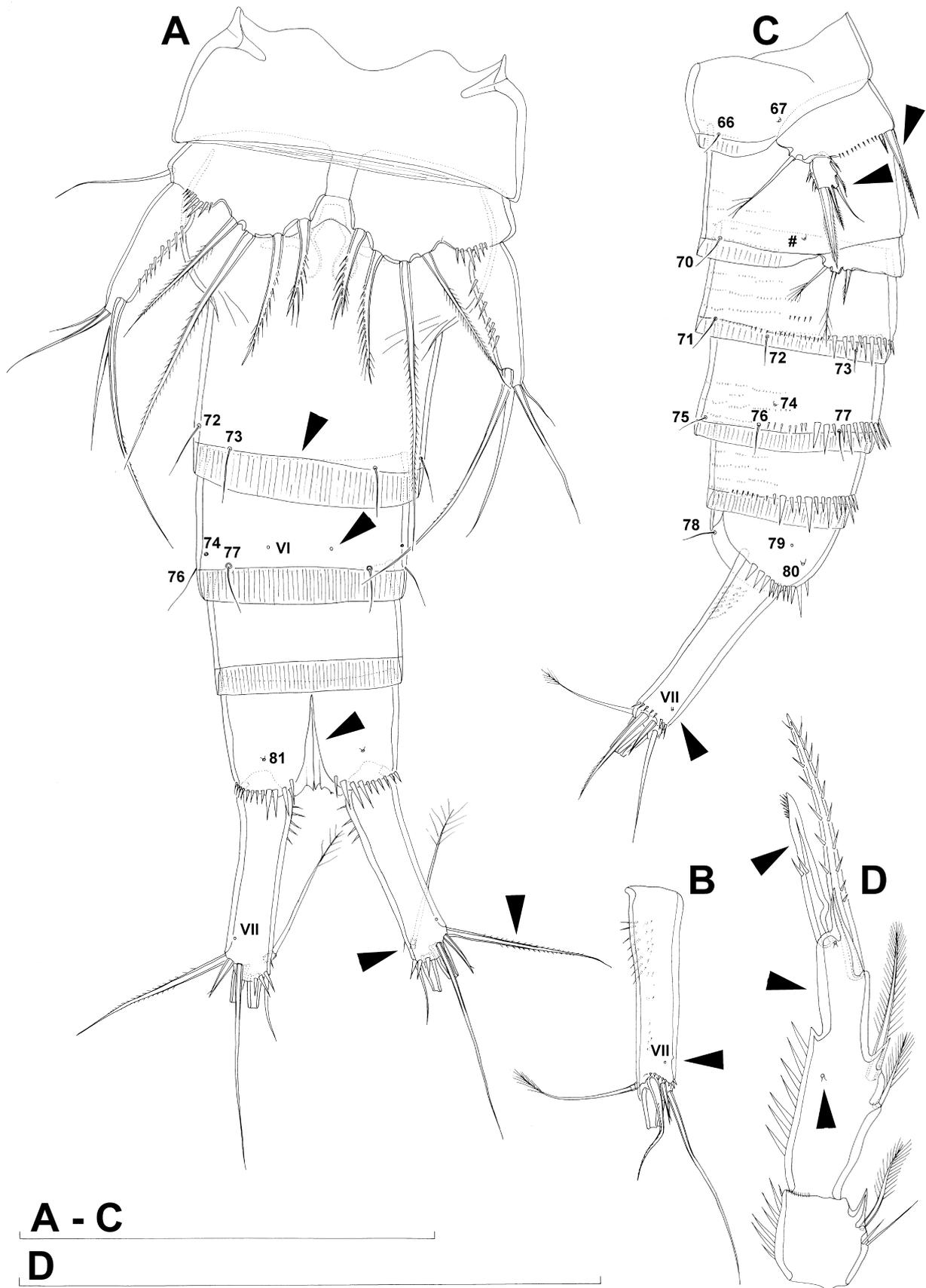


FIGURE 37. *Itostenhelia polyhymnia* sp. nov., line drawings, A–B, female holotype, C–D, male allotype: A, urosome, ventral view; B, right caudal ramus, lateral view; C, urosome, lateral view; D, endopod of second swimming leg, anterior view. Arabic numerals and hash mark (#) indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Roman numerals (VI, VII) indicate unique pores Arrowheads point to most prominent specific features. Scale bars 100 μ m.

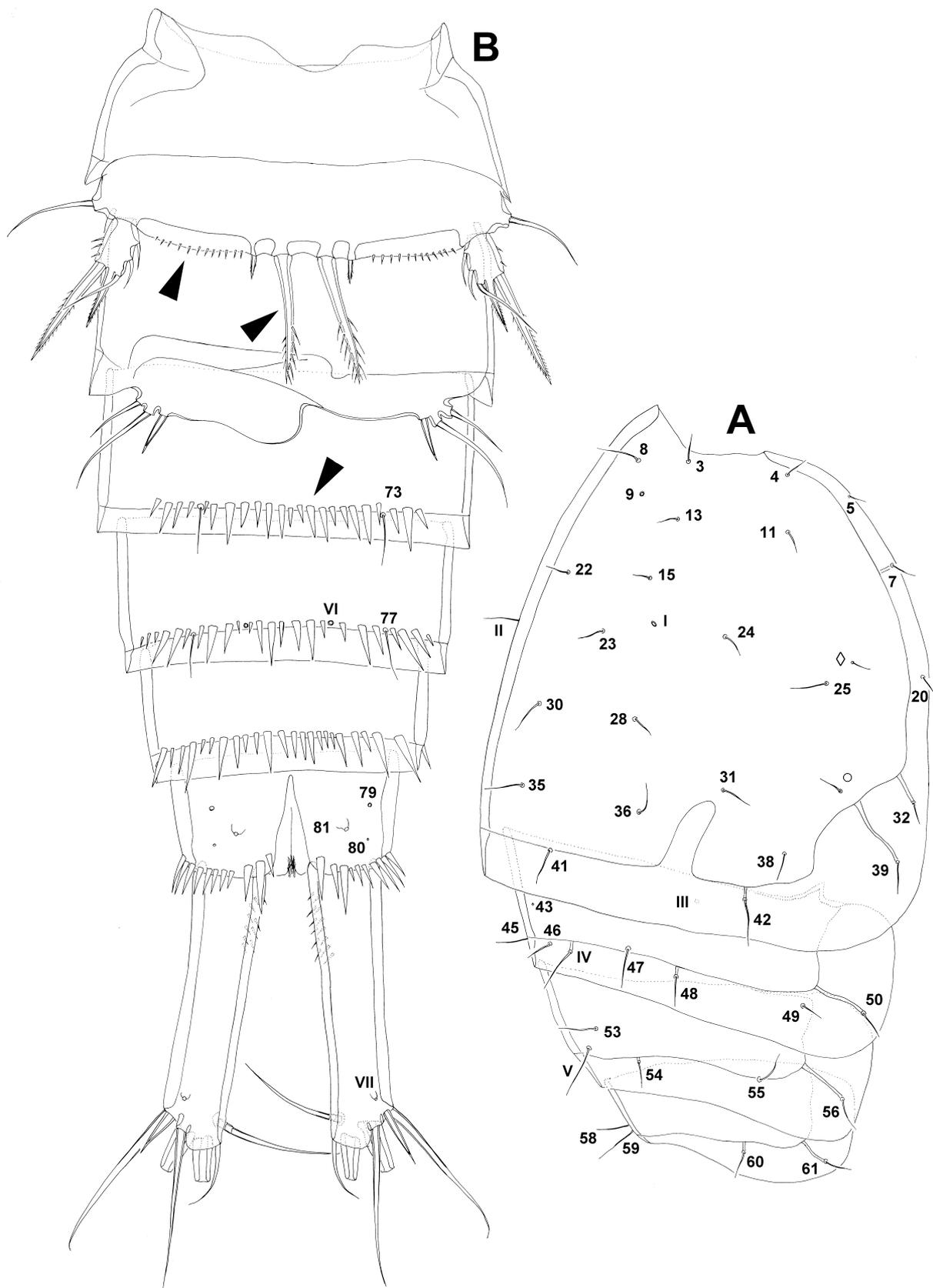


FIGURE 38. *Itostenhelia polyhymnia* sp. nov., line drawings, male allotype: A, cephalothoracic shield and pleurons of second to fourth pedigerous somites, lateral view; B, urosome, ventral view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Geometric shapes (○, ◇) indicate sensilla presumably homologous to those in *Wellstenhelia euterpe*. Roman numerals (I–VII) indicate unique sensilla and pores Arrowheads point to most prominent specific features. Scale bars 100 μm.

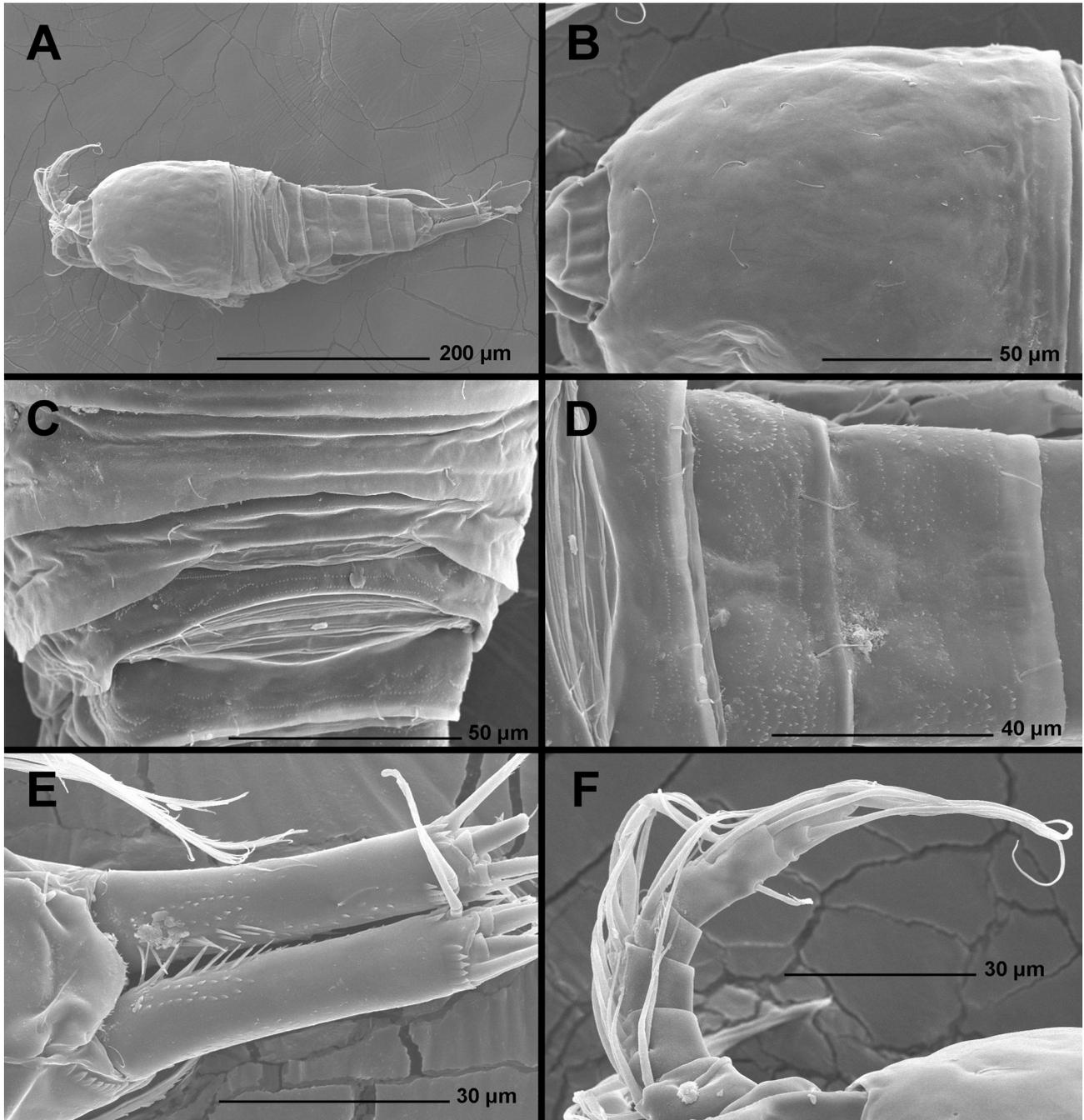


FIGURE 39. *Itostenhelia polyhymnia* sp. nov., scanning electron micrographs, female paratype 1: A, habitus, dorsal view; B, cephalothorax, dorsal view; C, pedigerous somites, dorsal view; D, first urosomite and genital double-somite, dorsal view; E, anal somite and caudal rami, dorsal view; F, antennula, dorsal view. Scale bars 30 µm (E, F), 40 µm (D), 50 µm (B, C), and 200 µm (A).

Etymology. The species is named after Polyhymnia (Ancient Greek: Πολυΰμνια), one of nine Muses from Greek mythology, who was a patron of sacred poetry and song. The species name is a noun in apposition (in the nominative case).

Description. Female (based on holotype and 12 paratypes). Body length from 405 to 428 µm (424 µm in holotype). Body segmentation, colour, nauplius eye, hyaline fringes, integument thickness as in *Wellstenhelia calliope* sp. nov. Surface appearance of prosomites extremely smooth and without minute pits even when examined on highest magnifications with scanning electron microscope; surface of urosomites mostly covered with numerous irregular rows of minute pits dorsally and laterally (see inset in Fig. 34A), except for hyaline fringes which generally smooth and slightly frilled. Most somite ornamentation similar to *Wellstenhelia calliope*, and

presumed homologous pores and sensilla numbered with same Arabic numerals (see Figs. 34A, B, C, 35A, B, C, D, 37A) to allow easier comparison. Habitus (Figs. 34A, B, 39A, 40A, 16A) less robust than in *Wellstenhelia calliope*, prosome/urosoma length ratio about one, body length/width ratio from 3.1 to 3.6, cephalothorax from 1.5 to 1.7 times as wide as genital double-somite.

Rostrum (Figs. 34C, 39B) general shape and position of anterior pair of sensilla no. 1 as in *Wellstenhelia calliope* but with additional bunch of ventral spinules just beyond tip (arrowed in Fig. 34C), with pronounced transverse dorsal suture (arrowed in Fig. 34C), and without dorsal pore no. 2.

Cephalothorax (Figs. 34A, B, 35A, 39B, 40B) about 1.1 times as long as wide; comprising 28% of total body length. Surface of cephalothoracic shield with 30 paired or unpaired sensilla and pores, most probably homologous to those in *Wellstenhelia calliope* (indicated with Arabic numerals in illustrations), 14 pores and sensilla missing (nos. 6, 10, 12, 16, 17, 18, 19, 21, 26, 29, 33, 34, 37, 40); absolute and relative positions of some pores and sensilla different; two lateral pairs of sensilla probably homologous to those in *Wellstenhelia euterge* (indicated with geometric shapes in illustrations); one unique pair of dorsal pores (no. I) and one unique unpaired dorsal sensillum (no. II) located in central part of cephalothorax (also indicated with Roman numerals in illustrations).

Pleuron of second pedigerous somite (Figs. 34A, B, 39C, 40C) ornamented as in *Wellstenhelia calliope*, except anterior lateral pair of sensilla no. 44 missing, unique pair of lateral pores (no. III), and unique pair of dorsal sensilla (no. IV).

Pleuron of third pedigerous somite (Figs. 34A, B, 35B, 39C, 40C) ornamented as in *Wellstenhelia calliope*, except anterior pair of dorsal pores no. 51 and anterior lateral pair of sensilla no. 52 missing (latter arrowed in Fig. 35B), and one unique dorsal pair of sensilla (no. V).

Pleuron of fourth pedigerous somite (Figs. 34A, B, 35B, 39C, 40C) as in *Wellstenhelia calliope*, except pair of anterior lateral pores no. 57 and pair of anterior lateral sensilla no. 62 missing (latter arrowed in Fig. 35B). First urosomite (Figs. 34A, B, 39D, 40D) as in *Wellstenhelia calliope*, except pair of anterior lateral pores no. 63 missing.

Genital double-somite (Figs. 34A, B, 35C, D, 37A, 39D, 40D) as in *Wellstenhelia calliope*, except anterior part less inflated laterally, genital apertures situated more ventrally, all large spinules missing (arrowed in Figs. 35C, 37A), anterior pair of pores no. 68 missing, and dorsal anterior pairs of sensilla nos. 69 & 70 more widely spaced; only more sclerotized part of genital apparatus visible inside and copulatory pores not visible on surface.

Third urosomite (Figs. 34A, B, 37A, 40D) as in *Wellstenhelia calliope*, except all large spinules missing and one unique pair of ventral pores (no. VI) present (arrowed in Fig. 37A).

Preanal somite (Figs. 34A, B, 37A) without pores and sensilla, with numerous rows of minute spinules on dorsal and lateral sides, as in all urosomites.

Anal somite (Figs. 34A, B, 37A, 39E, 40E) general shape and ornamentation as in *Wellstenhelia calliope*, except ventral spinules along medial cleft (arrowed in Fig. 37A) and lateral pores nos. 79 & 80 missing, and anal operculum well developed, broad and smooth, reaching beyond distal margin of anal somite.

Caudal rami (Figs. 34A, B, 37A, B, 39E, 40E) shape and armature very similar to those in *Wellstenhelia calliope*, except dorsalmost lateral setae much stronger and conspicuously directed outwards (arrowed in Fig. 37A); rami cylindrical, about 1.7 times as long as anal somite, 3.5 times as long as wide (ventral view), slightly divergent or parallel, with space between them about one ramus width; ornamentation consisting of several large inner spinules in anterior part, single unique anterior pore in distal part (no. VII; arrowed in Fig. 37B), and several small spinules at base of dorsal and lateral setae and along dorsal and inner surface.

Antennula (Figs. 34D, 39F) similar to that in *Wellstenhelia calliope* but sixth and seventh segments almost completely fused, and eighth segment with only three lateral setae and without apical aesthetasc (all three features arrowed in Fig. 34D); only ornamentation single short row of small spinules in proximal half of first segment, distal row of spinules missing; aesthetasc on fourth segment reaching distal tip of appendage; setal formula 1.10.8.6+ae.3.(2.5).5.

Antenna (Fig. 34E) as in *Wellstenhelia calliope*, except allobasis and first exopodal segment proportionately slightly shorter.

Labrum (Fig. 41A) and paragnaths (Fig. 41A) as in *Wellstenhelia calliope*, except labrum with additional spiniform process on anterior surface near distal margin.

Mandibula (Figs. 35E, F, G, 41A) similar to that in *Wellstenhelia calliope* but cutting edge without central seta (arrowed in Fig. 35E) and exopod with only one proximal seta (arrowed in Fig. 35G); both coxa and basis with more spinules than in *Wellstenhelia calliope*.

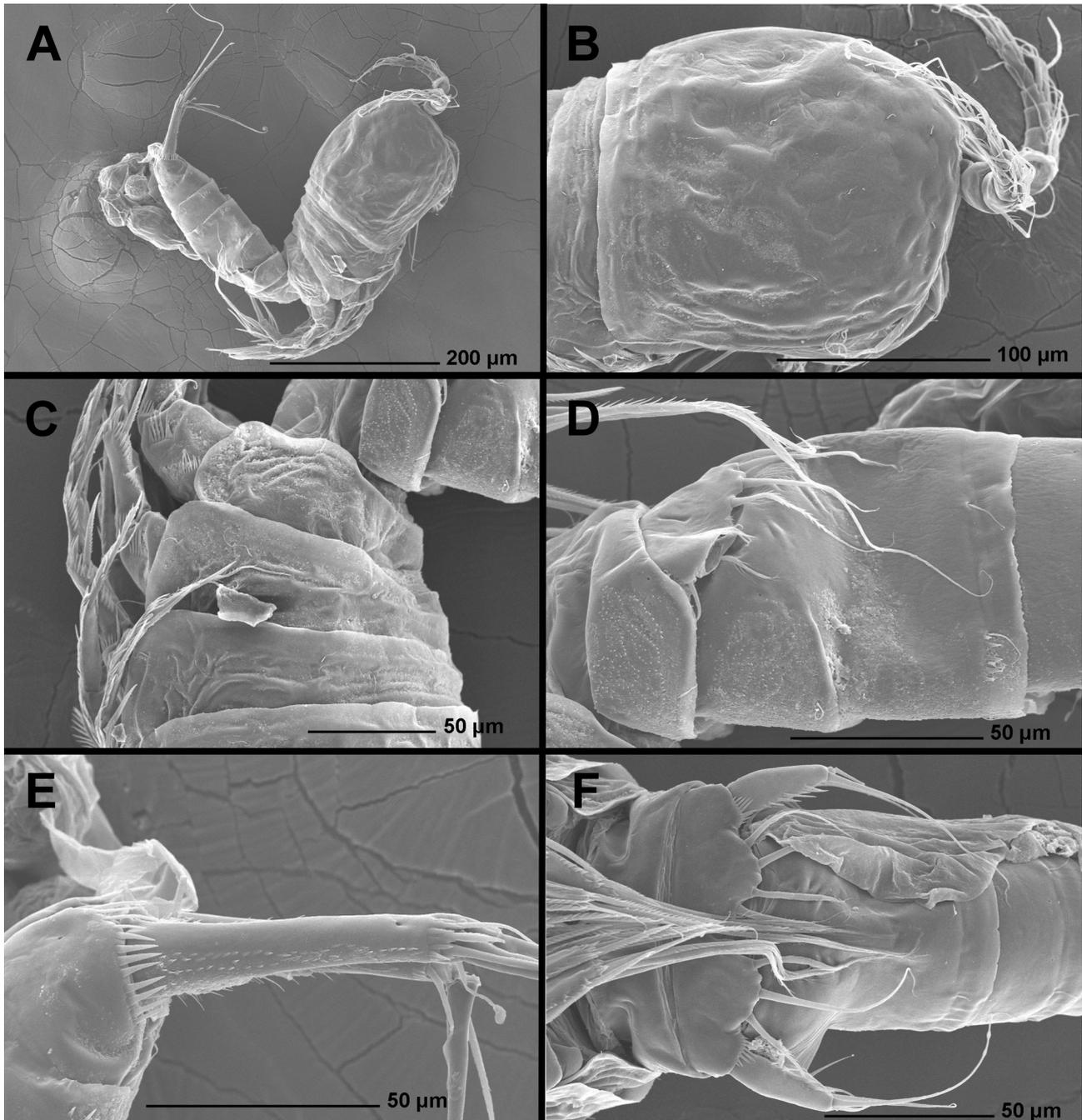


FIGURE 40. *Itostenhelia polyhymnia* sp. nov., scanning electron micrographs, A–E, female paratype 2, F, female paratype 3: A, habitus, lateral view; B, cephalothorax, lateral view; C pedigerous somites, lateral view; D, first urosomite and genital double-somite, lateral view (exopod of fifth leg broken off); E, anal somite and caudal rami, lateral view; F, fifth legs and genital double-somite with one empty egg-sack, ventral view. Scale bars 50 µm (C, D, E, F), 100 µm (B), and 200 µm (A).

Maxillula (Figs. 35H, 41A) as in *Wellstenhelia calliope*, except exopod and endopod not fused (arrowed in Fig. 35H) and coxa without large anterior spinules.

Maxilla (Figs. 35I, 41A) as in *Wellstenhelia calliope*, except dorsal endite on syncoxa with only two setae (arrowed in Fig. 35I), syncoxa with only one arched row of outer spinules, and endopod with only four slender setae.

Maxilliped (Figs. 35J, 41A) segmentation, armature and most ornamentation as in *Wellstenhelia calliope*, but outer distal corner of coxa produced into pronounced and blunt process.

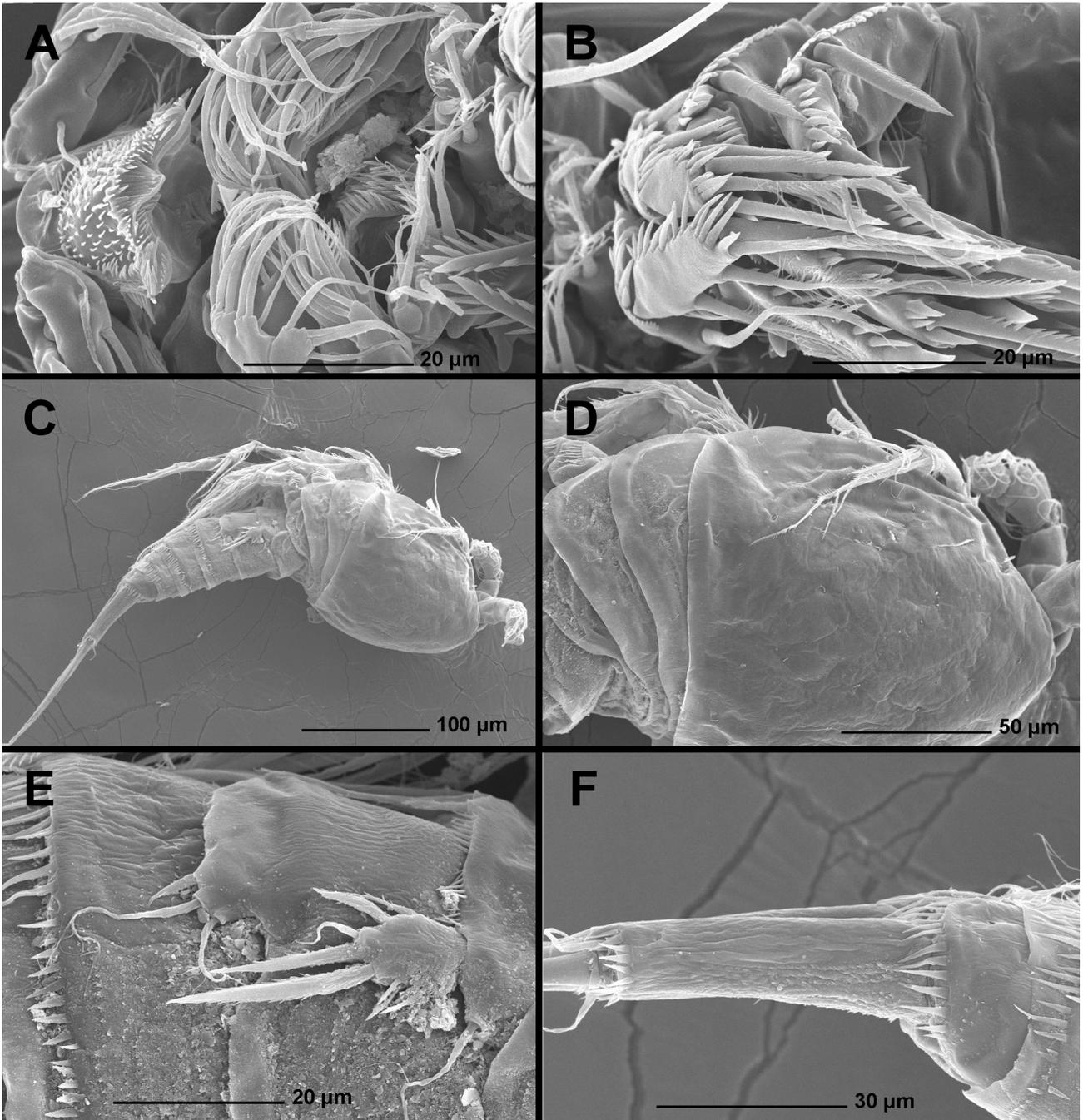


FIGURE 41. *Itostenhelia polyhymnia* sp. nov., scanning electron micrographs, A–B, female paratype 3, C–F, male paratype: A, mouth appendages, ventral view; B, tips of swimming legs, ventral view; C, habitus, lateral view; D, prosome, lateral view; E, second (genital) and third urosomites with fifth and sixth legs, lateral view; F, anal somite and caudal rami, lateral view. Scale bars 20 μm (A, B, E), 30 μm (F), 50 μm (D), and 100 μm (C).

First swimming leg (Figs. 36A, 41B) as in *Wellstenhelia calliope*, except coxa and basis without inner spinules, first endopodal segment much shorter and its inner seta longer and stronger (both arrowed in Fig. 36A), and distal inner seta on second endopodal segment inserted further away from distal margin (arrowed in Fig. 36A).

Second swimming leg (Figs. 36B, C, D, 41B) as in *Wellstenhelia calliope*, except intercoxal sclerite with sharp distal projections (arrowed in Fig. 36B) and smooth, first endopodal segment with slender seta (arrowed in Fig. 36C), second endopodal segment with two inner setae (arrowed in Fig. 36C), and third exopodal segment with shorter distal inner seta (arrowed in Fig. 36D).

Third swimming leg (Figs. 36E, 41B) as in *Wellstenhelia calliope*, except intercoxal sclerite with sharp distal projections (arrowed in Fig. 36E), inner distal row of spinules on coxa missing (arrowed in Fig. 36E), third

exopodal segment with only two outer spines and distal inner seta short and slender (both arrowed in Fig. 36E), first endopodal segment with slender inner seta (arrowed in Fig. 36E), and distal inner seta on third endopodal segment very short and slender (arrowed in Fig. 36E).

Fourth swimming leg (Fig. 36F) as in *Wellstenhelia calliope*, except intercoxal sclerite with sharp distal projections (arrowed in Fig. 36F), third exopodal segment with only two outer spines and distal inner seta short and slender (both arrowed in Fig. 36F), and distal inner seta on third endopodal segment very short and slender (arrowed in Fig. 36F).

Fifth leg (Figs. 34A, B, 36G, H, 37A, 40D, F) segmentation, general shape, and number of armature elements on endopodal lobe as in *Wellstenhelia calliope*, except baseoendopod without spiniform process at base of exopod, with row of strong spinules instead (arrowed in Fig. 36H), additional anterior pore at base of basal seta. Exopod ovoid, about 2.1 times as long as greatest width, with long outer spinules (arrowed in Figs. 34A, B, 36G), shorter inner spinules, and anterior pore, with five armature elements, second from inner side much longer than third (arrowed in Fig. 36G). Length ratio of endopodal setae, starting from inner side, 1 : 1 : 2.4 : 1.5. Length ratio of exopodal setae, starting from inner side, 1 : 0.5 : 0.2 : 0.7 : 0.3.

Sixth legs (Fig. 35C, D) simple cuticular plates covering paired genital apertures, inserted close to anterior margin of genital double-somite ventro-laterally, with single bipinnate seta, joined together into short but wide operculum.

Male (based on allotype and four paratypes). Body length from 357 to 412 μm (382 μm in allotype). Habitus (Fig. 41C), colour, rostrum, shape and ornamentation of cephalothorax (Figs. 38A, 41D), second pedigerous somite (Figs. 38A, 41D), third pedigerous somite (Fig. 38A, 41D), fourth pedigerous somite (Fig. 38A), ornamentation of first urosomite (Fig. 37C), caudal rami (Figs. 37C, 38B, 41F), antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, first swimming leg, third swimming leg, and fourth swimming leg as in female.

Genital somite (Figs. 37C, 38B, 41E) somewhat wider than in *Wellstenhelia calliope* and without large spinules; lateral pore no. 68 missing; additionally ornamented with several rows of minute spinules dorso-laterally. Third urosomite (Figs. 37C, 38B, 41E) as in *Wellstenhelia calliope*, except ventral row of spinules not interrupted between sensilla pair no. 73 (arrowed in Fig. 38B) and these sensilla also more widely spaced; additionally ornamented with several rows of minute spinules dorso-laterally.

Fourth urosomite (Figs. 37C, 38B) pore and sensilla pattern as in female (i.e. unique pore pair no. VI present), but additionally ornamented with ventral row of spinules of various sizes, some quite large.

Fifth urosomite (Figs. 37C, 38B, 41F) without pores or sensilla as in female, but with posterior ventral row of spinules of various sizes, some quite large.

Anal somite (Figs. 37C, 38B, 41F) as in female, except lateral pores nos. 79 & 80 present in allotype (missing in paratypes).

Caudal rami (Figs. 37C, 38B, 41F) about four times as long as wide in ventral view, with two rows of relatively short inner spinules in anterior third.

Antennula (Figs. 41C, D) as in *Itostenhelia terpisichore*, except completely clasped.

Second swimming leg (Fig. 37D) with coxa, basis, and exopod as in female. Endopod significantly transformed, with second and third segment fused (arrowed in Fig. 37D), third segment smaller and without outer spinules (arrowed in Fig. 37D), outer apical spine enlarged, with small inner hump at proximal fifth of its length, mostly smooth, with only two anterior spinules at midlength and short row of slender inner spinules near distal tip; small notch on either side as remnant of ancestral segmentation; proximal seta on ancestral second segment short and slender, about as long as segment's width; inner spiniform element on ancestral third segment also strong but bipinnate and not transformed, about 1.7 times as long as outer apical spine.

Fifth leg (Figs. 37C, 38B, 41E) general shape and segmentation as in *Wellstenhelia calliope* but armature and ornamentation very different; fused endopodal lobes forming slightly convex plate, with four spines (two belonging to each leg; arrowed in Fig. 38B) and long posterior row of spinules between endopodal armature and exopod (arrowed in Fig. 38B); inner endopodal spine almost six times as long as outer one; exopod ovoid, with several outer spinules, with three inner setae (all short, slender, and smooth) and two apical spines, inner one fused basally to segment; outer apical exopodal spine only slightly shorter than inner endopodal spine and length ratio of exopodal armature, starting from inner side, 1 : 0.45 : 0.6 : 0.3 : 0.3.

Sixth legs (Fig. 37C, 38B, 41E) as in *Wellstenhelia calliope*, except right leg distinct at base and more movable.

Variability. Most morphological features are extremely conservative, including the sensilla and pores pattern of somites, and length ratio of different armature on appendages. Except for body length, the only other variable feature was the presence/absence of lateral pores on the male anal somite (Figs. 37C, 38B, 41F).

Morphological affinities. The Korean *Itostenhelia polyhymnia* sp. nov. is morphologically very similar to its only congener, the Russian *Itostenhelia golikovi* (Chislenko, 1978) comb. nov. They show no differences in the antennula, antenna, mouth appendages or swimming legs, and even their sensilla and pores pattern on somites is exactly the same. That, and the fact that the original description of the Russian species by Chislenko (1978) was lacking in detail and contained several inaccuracies, was the reason we redescribe *Itostenhelia golikovi* below, also providing the first description of the male. Most major differences between these two species are all male characters, and they include proportions of the caudal rami (slightly longer in *Itostenhelia polyhymnia*), size of the patch of spinules on the inner margin of the caudal rami (smaller in *Itostenhelia polyhymnia*), relative size of the proximal inner seta on the ancestral second endopodal segment of the second leg (smaller in *Itostenhelia polyhymnia*), relative length of the inner spiniform seta on the ancestral third endopodal segment of the second leg (shorter in *Itostenhelia polyhymnia*), shape of the inner margin of the fused ancestral second and third endopodal segments of the second leg (with a notch in *Itostenhelia polyhymnia*), and length of the outer endopodal seta of the fifth leg (shorter in *Itostenhelia polyhymnia*). The females are extremely similar and can be distinguished mostly by the habitus size (smaller in *Itostenhelia polyhymnia*) and shape (more slender in *Itostenhelia polyhymnia*), in addition to the shape of the sclerotized parts of the genital receptacles (wider posterior parts in *Itostenhelia polyhymnia*). All these differences are arrowed in the drawings of *Itostenhelia golikovi* (see Figs. 43A, 44A, 45A, B, D).

***Itostenhelia polyhymnia* sp. nov. L-form**

(Fig. 42)

Locality. South Korea, South Sea, Gwangyang Bay, sampling station 10, muddy sediments, 34.920944°N 127.785528°E (Fig. 1).

Specimens examined. One female dissected on one slide (collection number NIBRIV0000232698), two females destroyed for DNA sequence (one amplification successful, Code 0271), 30 July 2012, leg. K. Kim.

Remarks. Only three females of this large morphotype were collected, two of which were destroyed for DNA analysis. All were significantly longer and larger than the typical *Itostenhelia polyhymnia*, and the one examined morphologically measured 511 µm. Other differences include somewhat longer caudal rami (arrowed in Fig. 42A), proportionately larger genital double-somite (arrowed in Fig. 42A), and two sensilla on cephalothorax and one on first urosomite missing (all arrowed in Fig. 42A). However, all other morphological details are the same, including the labrum (Fig. 42C) and fifth leg (Fig. 42D), and the COI sequence is indistinguishable too (although it is very short). Thus we have to conclude that this is either dimorphism or a chance mutation. The latter hypothesis seems more likely, as the L-form is very rare compared to the typical form, and all three specimens collected were found in one sample, so there is a chance that they are kin. We have no doubt that these two forms are conspecific, but they are listed separately to better alert readers about their existence.

***Itostenhelia golikovi* (Chislenko, 1978) comb. nov.**

(Figs. 43–47)

Type locality. Russia, Primorsky Krai, Posyet Bay, Minonosok inlet, benthic sands at 3–4 m depth, 42.609258°N 130.861661°E.

Specimens examined. Two females dissected on one slide each (collection numbers NIBRIV0000232699 and NIBRIV0000232700), male dissected on one slide (collection number NIBRIV0000232701), one male and five females together on one SEM stub (collection number NIBRIV0000232702), 10 females (four ovigerous) and two copepodids together in ethanol (collection number NIBRIV0000232703), 10 females together in ethanol (collection number NIBRIV0000232704), four males and 40 females (10 ovigerous) together in ethanol (collection number NIBRIV0000232705), 10 females destroyed for DNA sequence (five amplifications successful, Codes 0734, 0832, 0631, 0330 & 0433), type locality, 06 May 2012, leg. J. Trebyakova.

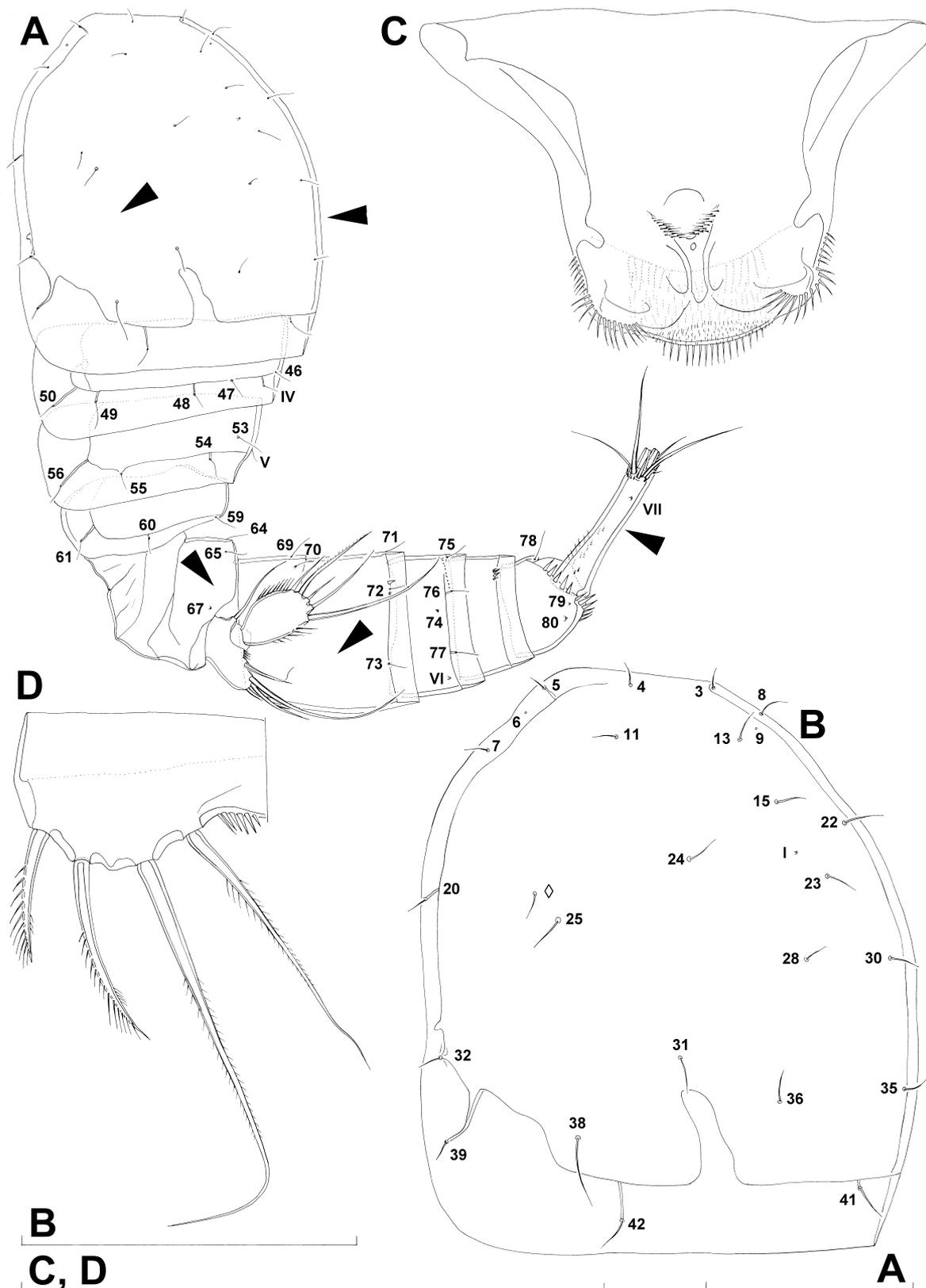


FIGURE 42. *Itostenhelia polyhymnia* sp. nov., L-form, line drawings, female holotype: A, habitus, lateral view; B, cephalothoracic shield, lateral view; C, labrum, dissected and flattened, anterior view; D, baseoendopod of fifth leg, anterior view. Arabic numerals indicating sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Geometric shape (\diamond) indicating sensillum presumably homologous to that in *Wellstenhelia euterpe*. Roman numerals (I, IV–VII) indicating sensilla and pores presumably homologous to those in *Itostenhelia polyhymnia*. Arrowheads pointing most prominent specific features. Scale bars 100 μ m.

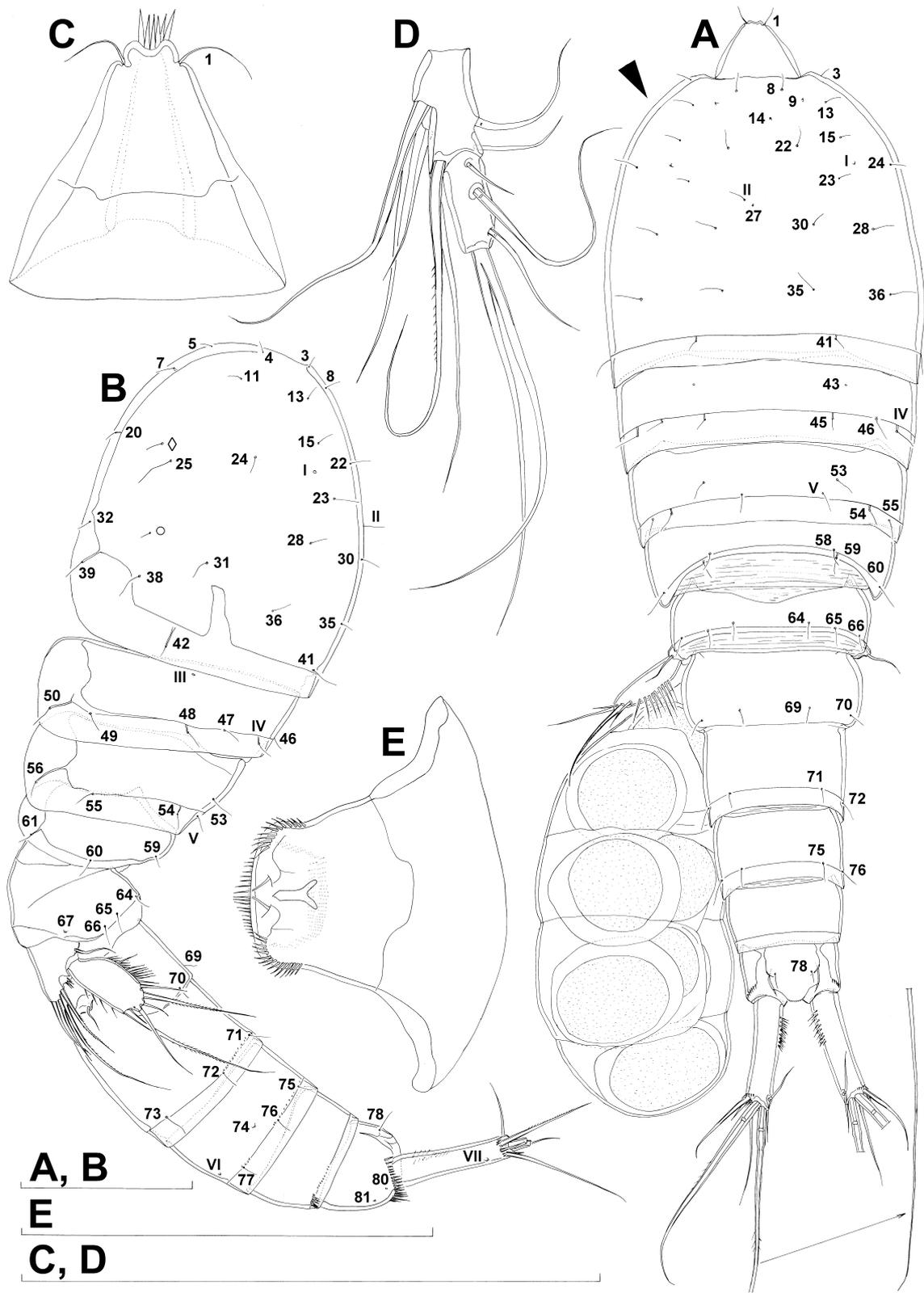


FIGURE 43. *Itostenhelia golikovi* (Chislenko, 1978) **comb. nov.**, line drawings, female holotype: A, habitus, dorsal view (arrow points to separately drawn distal part of inner principal caudal seta); B, habitus, lateral view; C, rostrum, dissected and flattened, dorsal view; D, distal part of antennula, dorsal view; E, labrum, dissected and flattened, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Geometric shapes (\circ , \diamond) indicate sensilla presumably homologous to those in *Wellstenhelia euterpe*. Roman numerals (I–V) indicate sensilla and pores presumably homologous to those in *Itostenhelia polyhymnia*. Arrowhead point to prominent specific feature. Scale bars 100 μ m.

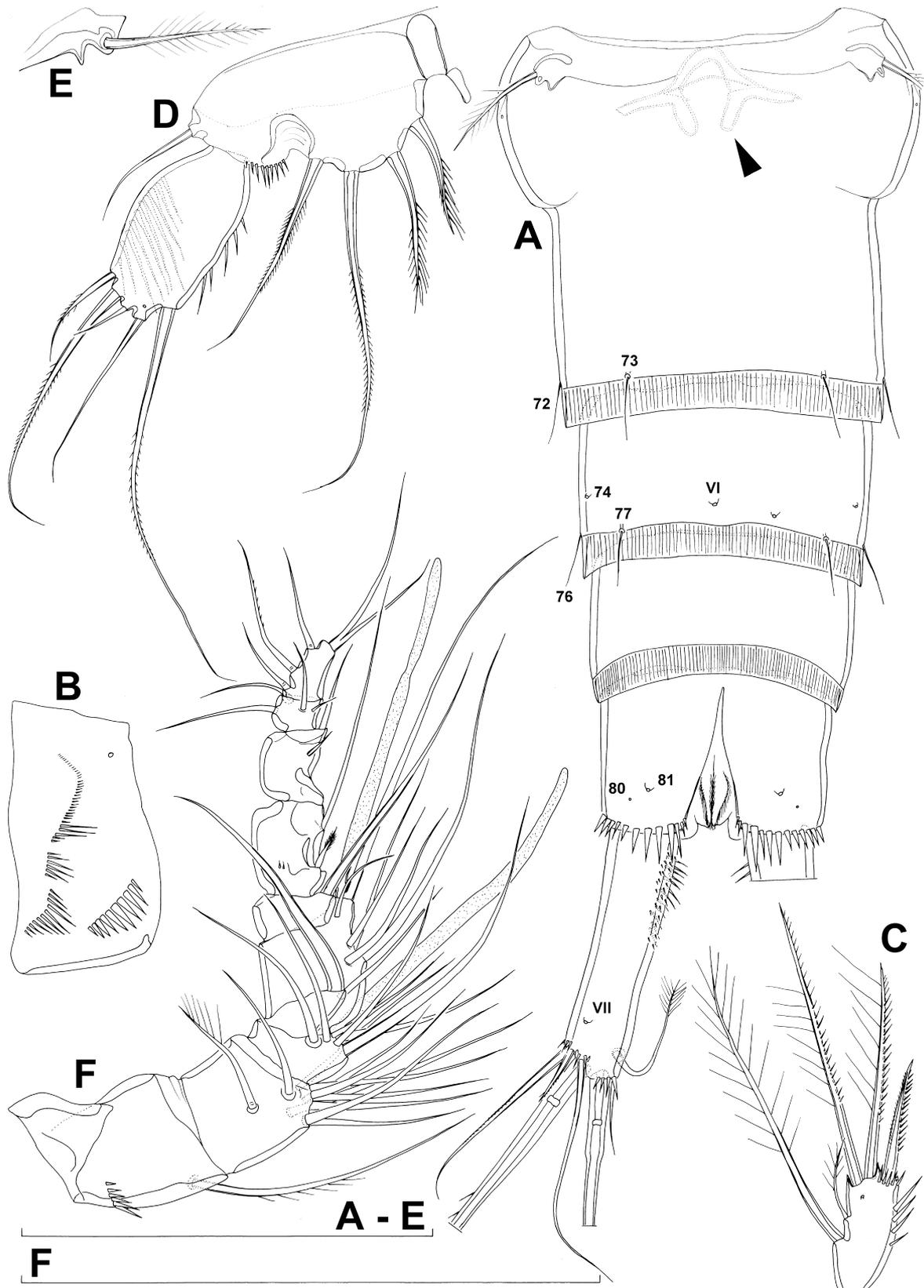


FIGURE 44. *Itostenhelia golikovi* (Chislenko, 1978) **comb. nov.**, line drawings, A–E, female holotype, F, male allotype: A, abdomen, ventral view; B, coxa of third swimming leg, anterior view; C, third endopodal segment of fourth swimming leg, anterior view; D, fifth leg, anterior view; E, sixth leg undissected on genital double-somite, ventro-lateral view; F, antennula, slightly uncoiled and flattened, dorsal view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Roman numerals (VI, VII) indicate sensilla and pores presumably homologous to those in *Itostenhelia polyhymnia*. Arrowhead points to prominent specific feature. Scale bars 100 μ m.

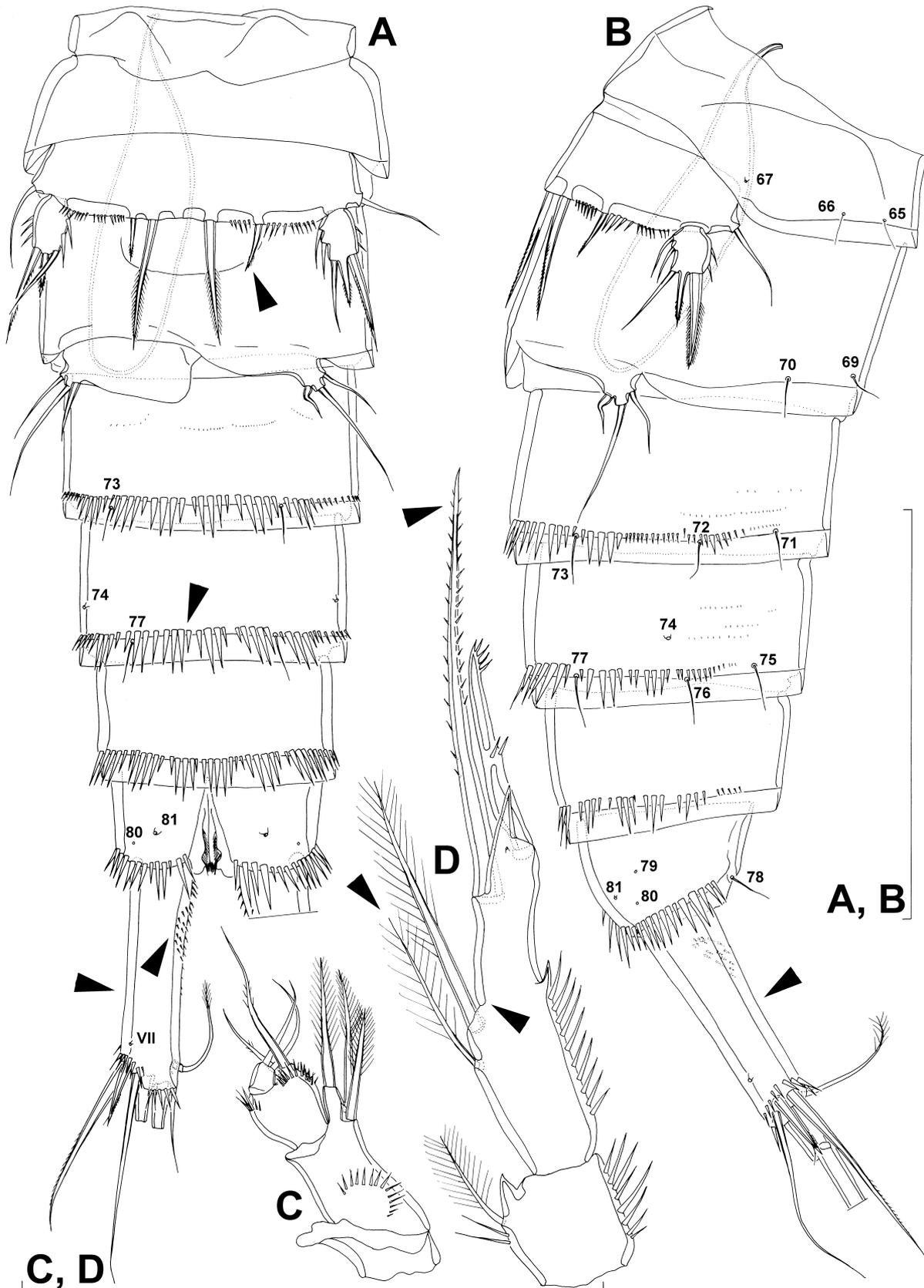


FIGURE 45. *Itostenhelia golikovi* (Chislenko, 1978) **comb. nov.**, line drawings, male allotype: A, urosome with spermatophore visible inside, ventral view; B, urosome with spermatophore visible inside, lateral view; C, maxilliped, posterior view; D, endopod of second swimming leg. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Roman numeral (VII) indicates a pore presumably homologous to that in *Itostenhelia polyhymnia*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

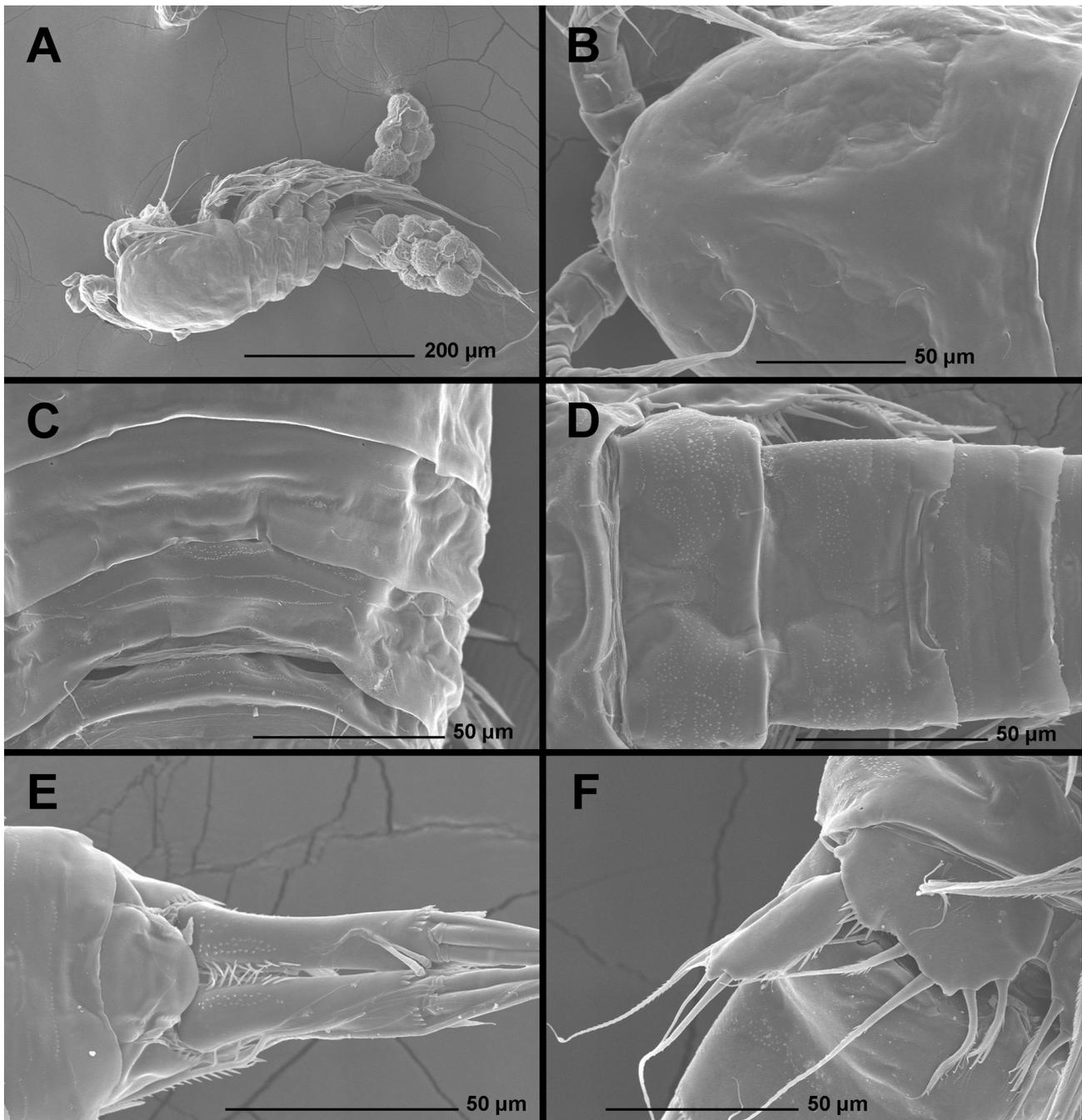


FIGURE 46. *Itostenhelia golikovi* (Chislenko, 1978) **comb. nov.**, scanning electron micrographs, A, female paratype 1, B–E, female paratype 2, F, female paratype 3: A, habitus, lateral view; B, cephalothorax, dorsal view; C, pedigerous somites, dorsal view; D, genital double-somite and subsequent free urosomite, dorsal view; E, anal somite and caudal rami, dorsal view; F, right upper corner of genital somite and fifth leg, ventral view. Scale bars 50 µm (B, C, D, E, F) and 200 µm (A).

Redescription. Female (based on ten specimens). Body length from 545 to 648 µm. Body segmentation, nauplius eye, hyaline fringes, integument thickness, surface appearance of somites, and all somite ornamentation as in *Itostenhelia polyhymnia* **sp. nov.**, including all sensilla and pores, and minute dorso-lateral rows of spinules on urosomites. However, colour of preserved specimens more translucent. Habitus (Figs. 43A, B, 46A) more robust than in *Itostenhelia polyhymnia*, with prosome/urosome length ratio about 1.1, body length/width ratio 3.4, and cephalothorax 1.8 times as wide as genital double-somite. Five specimens with paired egg-sacs, each containing between seven and 10 eggs.

Rostrum (Fig. 43C) as in *Itostenhelia polyhymnia*, including apical bunch of spinules, dorsal suture, position of anterior pair of sensilla no. 1; only slightly smaller in comparison to cephalothorax.

Cephalothorax (Figs. 43A, B, 46B, 47C) about 0.9 times as long as wide; comprising 26% of total body length. Surface of cephalothoracic shield ornamented exactly as in *Delavalia polyhymnia* (all homologous pores and sensilla indicated with Arabic numerals, geometric shapes or Roman numerals in illustrations).

Pleuron of second pedigerous somite (Figs. 43A, B, 46C, 47D), pleuron of third pedigerous somite (Figs. 43A, B, 46C, 47D), and pleuron of fourth pedigerous somite (Figs. 43A, B, 46C, 47D) ornamented exactly as in *Itostenhelia polyhymnia*.

First urosomite (Figs. 34A, B) as in *Itostenhelia polyhymnia*, except slightly narrower both in dorsal and lateral view.

Genital double-somite (Figs. 43A, B, 44A, 46D) as in *Itostenhelia polyhymnia*, except internal structure slightly narrower (arrowed in Fig. 44A).

Third urosomite (Figs. 43A, B, 44A, 46D) and preanal somite (Figs. 43A, B, 44A, 46E) as in *Itostenhelia polyhymnia*.

Anal somite (Figs. 43A, B, 44A, 46E) also as in *Itostenhelia polyhymnia*, except lateral pore no. 80 present.

Caudal rami (Figs. 43A, B, 44A, 46E) as in *Itostenhelia polyhymnia*, except additional field of small spinules present on anterior ventral surface close to inner margin, in addition to large inner spinules.

Antennula (Figs. 43D, 47C) as in *Itostenhelia polyhymnia*, except sixth and seventh segments completely fused.

Antenna, labrum (Figs. 43E, 47A), paragnaths (Fig. 47A), mandibula, maxillula (Fig. 47A), maxilla (Fig. 47B), maxilliped (Fig. 47B), first swimming leg, second swimming leg, third swimming leg (Fig. 44B), and fourth swimming leg (Fig. 44C) as in *Itostenhelia polyhymnia*.

Fifth leg (Figs. 43A, B, 44D, 46F) as in *Itostenhelia polyhymnia*, except pore on basis missing and endopodal lobe slightly more convex. Length ratio of endopodal setae, starting from inner side, 1 : 1.3 : 2.9 : 1.8. Length ratio of exopodal setae, starting from inner side, 1 : 0.5 : 0.15 : 0.7 : 0.3.

Sixth leg (Figs. 44A, E, 46F) as in *Itostenhelia polyhymnia*, except for additional spiniform process next to plumose seta.

Male (based on three specimens). Body length from 548 to 604 µm. Habitus, colour, rostrum, shape and all ornamentation of cephalothorax, shape and ornamentation of second, third, and fourth pedigerous somites, ornamentation of first urosomite (Figs. 45A, B, 47E), caudal rami (Figs. 45A, B, 47F), antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped (Fig. 45C), first swimming leg, third swimming leg, and fourth swimming leg as in female.

Genital somite (Figs. 45A, B, 47E) as in *Itostenhelia polyhymnia*, except lateral pore no. # missing; relatively small spermatophore visible inside, positioned longitudinally on right side, about 3.5 times as long as wide, its neck reaching slightly beyond anterior margin of first urosomite.

Third urosomite (Fig. 45A, B) as in *Itostenhelia polyhymnia*.

Fourth urosomite (Fig. 45A, B) as in *Itostenhelia polyhymnia*, except ventral pair of pores no. VI missing (arrowed in Fig. 45A).

Preanal and anal somites (Figs. 45A, B, 47F) as in *Itostenhelia polyhymnia*.

Caudal rami (Figs. 45A, B, 47F) as in *Itostenhelia polyhymnia*, except slightly shorter (arrowed in Fig. 45A, B) and with additional patch of ventral spinules (arrowed in Fig. 45A), about four times as long as wide in ventral view, with two rows of relatively short inner spinules in anterior third.

Antennula (Fig. 44F) as in *Itostenhelia polyhymnia*, except less clasped; general shape and segmentation as in *Wellstenhelia calliope*; only ornamentation proximal row of spinules on first segment and two dorsal spinules on sixth segment; aesthetascs on third and fourth segments long and slender, no aesthetasc on ninth segment; setal formula 1.10.6+ae.8+ae.1.2.2.4.5.

Second swimming leg coxa, basis, and exopod as in female; endopod (Fig. 45D) as in *Itostenhelia polyhymnia*, except inner spiniform process marking ancestral boundary between second and third segment missing (arrowed in Fig. 45D), proximal seta on ancestral second segment proportionately longer (arrowed in Fig. 45D), and inner spiniform element on ancestral third segment also proportionately longer (arrowed in Fig. 45D).

Fifth leg (Figs. 45A, B, 47E) as in *Itostenhelia polyhymnia*, except outer endopodal spine proportionately much longer (arrowed in Fig. 45A).

Sixth legs (Figs. 45A, B, 47E) as in *Itostenhelia polyhymnia*.

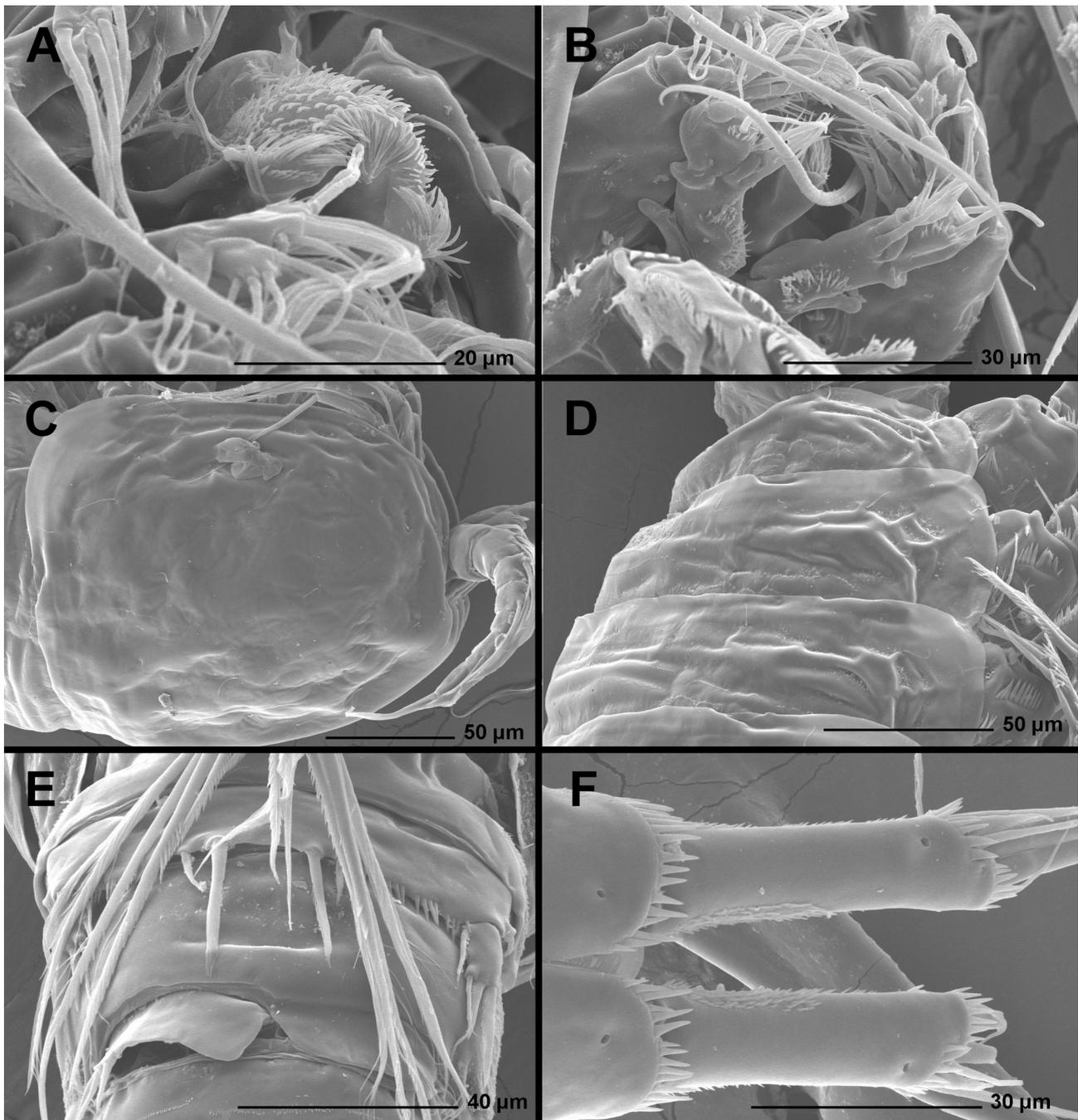


FIGURE 47. *Itostenhelia golikovi* (Chislenko, 1978) **comb. nov.**, scanning electron micrographs, A–B, female paratype 3, C–D, female paratype 4, E–F, male paratype: A, labrum and maxillular palp, ventral view; B, mouth appendages, ventral view; C, cephalothorax, lateral view; D, second to fourth pedigerous somites, lateral view; E, first and second urosomites, ventral view; F, anal somite and caudal rami, ventral view. Scale bars 20 µm (A), 30 µm (B, F), 40 µm (E), and 50 µm (C, D).

Variability. One male has the inner spine on left sixth leg curled, while the same element on right sixth leg is straight (Fig. 45A, B).

Remarks. Chislenko (1978) reports a different armature formula of the swimming legs for this species than what we have found, with the minute inner distal setae missing on the third endopodal and exopodal segments of the fourth leg, as well as no inner seta on the first and second exopodal segments of the second leg. We examined all newly collected specimens from the type locality for these characters and found these setae always present. This implies that Chislenko (1978) either overlooked these setae (perhaps they were broken off on his specimen), or he was dealing with an aberrant specimen. We are inclined to favour the former, as Chislenko (1978) also provides a drawing of a maxilliped with only two setae on the basis, while all stenheliins have three setae here. Given the

similarity of other features between our specimens and those studied by Chislenko (1978), the fact that our specimens were collected exactly from the type locality, and the apparent low diversity of stenheliins there, we believe that there is no chance that we are dealing with a different biological species.

Itostenhelia golikovi (Chislenko, 1978) **comb. nov.** shows very few morphological differences from its Korean congener, *Itostenhelia polyhymnia* **sp. nov.**, and they are all pointed out in the affinities of the latter species (see above) and also indicated with arrowheads in Figs. 43, 44, 45.

Genus *Willenstenhelia* gen. nov.

Type species. *Willenstenhelia thalia* **sp. nov.**

Other species. *Delavalia minuta* A. Scott, 1902; *Stehelia (Delavalia) unisetosa* Wells, 1967; *Willenstenhelia urania* **sp. nov.**; *Willenstenhelia terpsichore* **sp. nov.**

Etymology. The new genus name is dedicated to Dr. Elke Willen, formerly of the Deutsches Zentrum für Marine Biodiversitätsforschung, University of Oldenburg, Germany, for her contribution to the taxonomy and phylogeny of stenheliin miraciids. Her last name is prefixed to the existing genus name *Stenhelia*.

Diagnosis. Habitus robust but not spindle shaped in dorsal view, widest at posterior end of cephalothorax but with also very wide first two urosomites; podoplean boundary between prosome and urosome very conspicuous. Integument of all somites relatively weakly sclerotized, prosomites generally very smooth and urosomites with several parallel transverse rows of minute spinules, without cuticular windows or pits. Hyaline fringe of somites broad and smooth. Rostrum with dorsal transverse suture, bifid tip, pair of dorsal sensilla near tip, and pair of dorso-lateral pores near midlength; no spinules. Genital double-somite in female completely fused along ventral surface but with deep suture indicating original segmentation between genital and second urosomites dorso-laterally, dividing double-somite into equally long halves; anterior part inflated and with sharp and posteriorly directed cuticular process in vicinity of laterally placed genital apertures. Preanal somite with large and small spinules. Anal somite clefted medially at posterior half, with wide and almost trilobate anal operculum; ornamented with pair of large dorsal sensilla on anal operculum, posterior row of strong spinules on anal somite, and several large ventral spinules along medial cleft. Caudal rami more or less cylindrical, with slightly wider base, from three to five times as long as wide, completely smooth, and with seven setae (three lateral, one dorsal and three apical), all in posterior sixth of ramus length. Female antennula seven-segmented, but traces of ancestral division present on sixth segment, with distal posterior corner of first segment without spiniform process, and eighth segment with three lateral and two apical setae; no apical aesthetasc on ultimate segment. Male antennula strongly geniculate, nine-segmented, with additional large aesthetasc on third segment. Antenna composed of short coxa, strong allobasis, one-segmented endopod, and three-segmented exopod; endopod with two lateral spines flanking one slender seta. Mandibula without central seta on cutting edge, with six slender setae on small one-segmented endopod, and with three lateral and six apical setae on elongated and curved exopod; four apical exopodal setae strong and spiniform, one of them extremely long. Maxillula composed of praecoxa, coxa, basis, one-segmented endopod, and one-segmented exopod; endopod and exopod fused basally to basis, with two and four setae respectively; endopod wide distally. Maxilla composed of large syncoxa, small basis and even smaller one-segmented endopod; three coxal endites armature formula (starting from dorsal side) 2.3.3; basis with two lateral slender setae and two apical geniculate spines; endopod with four slender setae. Maxilliped not prehensile, three-segmented (two endopodal segments fused), with armature formula 0.3.4. All swimming legs of similar size and long in comparison to body length, with short spiniform processes on intercoxal sclerite and inner distal corner of basis of second to fourth leg, with all exopods three-segmented, endopod of first leg two-segmented, endopods of second to fourth legs three-segmented, except endopod of second leg in male with fused second and third segments; armature formula of exopods/endopods in female as follows: first leg, 0.1.022/1.211; second leg, 0.1.123/1.2.121; third leg, 0.1.223/1.1.121; fourth leg, 0.1.1(2)22(3)/1.0.121; inner seta on first endopodal segments of second and third legs slender; inner seta on first endopodal segment of fourth leg extremely strong and long; no sexual dimorphism in third leg; male second leg with three elements on ancestral third endopodal segment and inner apical seta shorter than outer spine; male fourth leg with very strong and characteristically curved outer spine on second exopodal segment. Female fifth legs fused medially, without posterior spinules or spiniform process on baseoendopod at base of exopod; endopodal lobe with only three elements but with large gap between

innermost and two other ones; exopod more or less rectangular in shape, with wide base, about 1.5 times as long as wide, with five setae; innermost exopodal seta inserted on inner margin, while others more or less apical; central exopodal seta short and slender. Male fifth leg with fused endopodal lobes forming slightly convex plate, with two or three dissimilar spines on very narrow bump close to medial line and long posterior row of spinules between endopodal armature and exopod; exopod rectangular, with four or five elements, innermost one always inserted on inner margin, outermost one strong and spiniform. Female sixth leg minute flap covering genital aperture, with single short seta and two minute spines; sixth legs not joined with ventral suture, ventral surface of genital double-somite completely smooth.

***Willstenhelia thalia* sp. nov.**

(Figs. 48–54)

Type locality. South Korea, South Sea, Gwangyang Bay, sampling station 10, muddy sediments, 37.539231°N 126.343417°E.

Specimens examined. Female holotype dissected on one slide (collection number NIBRIV0000232706), male allotype dissected on one slide (collection number NIBRIV0000232707), two male paratypes and four female paratypes together on one SEM stub (collection number NIBRIV0000232708), three males and four females destroyed for DNA sequence (four females amplification successful, Codes 0245, 0444, 0146 & 0348), type locality, 18 November 2012, leg. K. Kim.

Two male paratypes and seven female paratypes together in ethanol (collection number NIBRIV0000232709), three females destroyed for DNA sequence (amplification successful, Codes 0143, 0241 & 0342), type locality, 30 July 2012, leg. K. Kim.

Thirty male paratypes and 30 female paratypes together in ethanol (collection number NIBRIV0000232710), one female destroyed for DNA sequence (amplification successful, Code 0547), South Korea, South Sea, Gwangyang Bay, sampling station 10, muddy sediments, 34.920944°N 127.785528°E, 18 November 2012, leg. K. Kim (Fig. 1).

Three male paratypes and 12 female paratypes together in ethanol (collection number NIBRIV0000232711), one female destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 10, muddy sediments, 34.920944°N 127.785528°E, 18 February 2012, leg. K. Kim.

One female destroyed for DNA sequence (amplification unsuccessful), South Korea, South Sea, Gwangyang Bay, sampling station 15, muddy sediments, 34.797194°N 127.786444°E, 18 November 2012, leg. K. Kim (Fig. 1).

Etymology. The species is named after Thalia (Ancient Greek: Θάλεια), one of nine Muses from Greek mythology, who was a patron of comedy. The species name is a noun in apposition (in the nominative case).

Description. Female (based on holotype and six paratypes). Body length from 373 to 441 μm (428 μm in holotype). Body segmentation, colour, nauplius eye, hyaline fringes, integument thickness as in *Wellstenhelia calliope* **sp. nov.** Surface appearance of prosomites extremely smooth and without minute pits even when examined on highest magnifications with scanning electron microscope; surface of urosomites mostly covered with numerous irregular rows of minute pits on dorsal and lateral sides, except for hyaline fringes which generally smooth and slightly frilled. Most somite ornamentation also similar to *Wellstenhelia calliope*, and presumed homologous pore and sensilla numbered with same Arabic numerals (see Figs. 48A, B, C, 49A, B, C, D) to allow easier comparison. Habitus (Figs. 48A, B, 53A) less robust than in *Wellstenhelia calliope*, with prosome/urosome length ratio about 1.1, body length/width ratio from 2.6 to 2.9, and cephalothorax from 1.6 to 1.7 times as wide as genital double-somite.

Rostrum (Figs. 48A, B, C, 53B) general shape and position of anterior pair of sensilla no. 1 as in *Wellstenhelia calliope* but without dorsal pore no. 2 and with two dorso-lateral pores centrally (no. α).

Cephalothorax (Figs. 48A, B, 49C, 53B, 54A, C) about 0.9 times as long as wide; comprising 30% of total body length. Surface of cephalothoracic shield with 28 unpaired and paired sensilla and pores, most of which probably homologous to those in *Wellstenhelia calliope* (indicated with Arabic numerals in illustrations), but 17 pores and sensilla missing (nos. 3, 6, 10, 14, 16, 17, 18, 19, 21, 23, 26, 27, 29, 33, 34, 37, 40); absolute and relative positions of some pores and sensilla differ; one lateral pair of sensilla probably homologous to that in *Wellstenhelia euterpe* (indicated with geometric shape in illustrations); one unpaired dorsal sensillum (no. II) probably

homologous to that in *Itostenhelia polyhymnia*; three unique pairs of pores located in anterior half, one lateral (no. β) and two dorsal (nos. γ , δ).

Pleuron of second pedigerous somite (Figs. 48A, B, 49D) relatively narrow, with only four pairs of posterior sensilla, three probably homologous to *Wellstenhelia calliope* (nos. 46, 49, 50) and one probably homologous to *Wellstenhelia euterpe* (no. IV).

Pleuron of third pedigerous somite (Figs. 48A, B, 49D) similar to second pedigerous somite in shape and ornamentation, with only four pairs of posterior sensilla, all probably homologous to those in *Wellstenhelia calliope* (nos. 53, 54, 55, 56).

Pleuron of fourth pedigerous somite (Fig. 48A, B) with only three pairs of posterior sensilla, all homologous to those in *Wellstenhelia calliope* (nos. 59, 60, 61).

First urosomite (Figs. 48A, B, 53C, F) as in *Wellstenhelia calliope*, except pair of anterior lateral pores no. 63 and pair of dorso-lateral sensilla no. 66 missing; dorsal surface additionally ornamented with several rows of minute spinules, while ventral surface smooth.

Genital double-somite (Figs. 48A, B, 49A, B, 53C, F) shape as in *Wellstenhelia calliope*, except anterior part much more inflated laterally, almost as wide as first urosomite, with lateral expansions produced into posteriorly directed, large spiniform processes (arrowed in Figs. 48B, 49A); paired copulatory pores small ovoid holes in anterior part, situated ventro-laterally; paired genital apertures situated laterally, covered by reduced sixth legs; only more sclerotized part of genital apparatus visible inside; ornamentation similar to that in *Wellstenhelia calliope*, except most large spinules missing (only three at base of ventral sensillum no. 73, arrowed in Fig. 49A, and two close to dorsal sensillum no. 71), lateral pair of sensilla no. 72 also missing, and dorsal anterior pairs of sensilla nos. 69 & 70 more widely spaced; dorsal surface additionally ornamented with many parallel rows of minute spinules, ventral surface smooth; no ventral suture between genital apertures.

Third urosomite (Figs. 48A, B, 49A) as in *Wellstenhelia calliope*, except lateral pair of sensilla no. 76 and most large spinules missing, two or three large spinules only at base of sensilla; dorsal surface additionally ornamented with four parallel rows of minute spinules, while ventral surface smooth.

Preanal somite (Figs. 48A, B, 49A, 53D) without sensilla as in *Wellstenhelia calliope* but with pair of unique lateral pores (no. ϵ), two large posterior spinules dorso-laterally on each side, and three parallel rows of minute dorsal spinules.

Anal somite (Figs. 48A, B, 49A, 53D, 54B) general shape and ornamentation as in *Wellstenhelia calliope*, except for fewer spinules along medial cleft and distal margin, lateral pores nos. 79 & 80 missing, and anal operculum well developed, broad and smooth, reaching beyond distal margin of anal somite.

Caudal rami (Figs. 48A, B, 49A, 53D, 54B) shape and armature similar to those in *Wellstenhelia calliope*, except more elongated, middle lateral seta much shorter and more slender, inner margin without spinules, anterior ventral pore no. 82 moved more towards outer margin (arrowed in Fig. 49A), and posterior ventral pore no. 83 missing; rami cylindrical, about 1.9 times as long as anal somite, 4.6 times as long as wide (ventral view), slightly divergent or parallel, and with space between them about one ramus width.

Antennula (Figs. 48D, 49E, F, 53B) similar to that in *Wellstenhelia calliope* but sixth and seventh segments almost completely fused, and eighth segment with only three lateral setae and without apical aesthetasc; only ornamentation short row of small spinules in proximal half of first segment and one central row of minute dorsal spinules, distal row of spinules and spiniform process missing; aesthetasc on fourth segment just reaching distal tip of appendage; setal formula 1.10.9.6+ae.3.(4.4).5.

Antenna (Fig. 48E) as in *Wellstenhelia calliope*, except allobasis and first exopodal segment proportionately shorter, endopod with single slender lateral seta, and inner apical fused seta much longer, spiniform, and geniculate.

Labrum (Fig. 53E) and paragnaths (Fig. 53E) as in *Wellstenhelia calliope*.

Mandibula (Figs. 50A, B, 53E) similar to that in *Wellstenhelia calliope*, except cutting edge without central seta and with shorter dorsalmost seta, basis with additional row of slender spinules, and exopod with three lateral setae inserted much closer to each other.

Maxillula (Figs. 48F, 49G, 53E) as in *Wellstenhelia calliope*, except cutting edge with stronger combs on two ventralmost spines (arrowed in Fig. 48F), basis almost completely fused with endopod and exopod, and endopod much wider distally (arrowed in Fig. 49G).

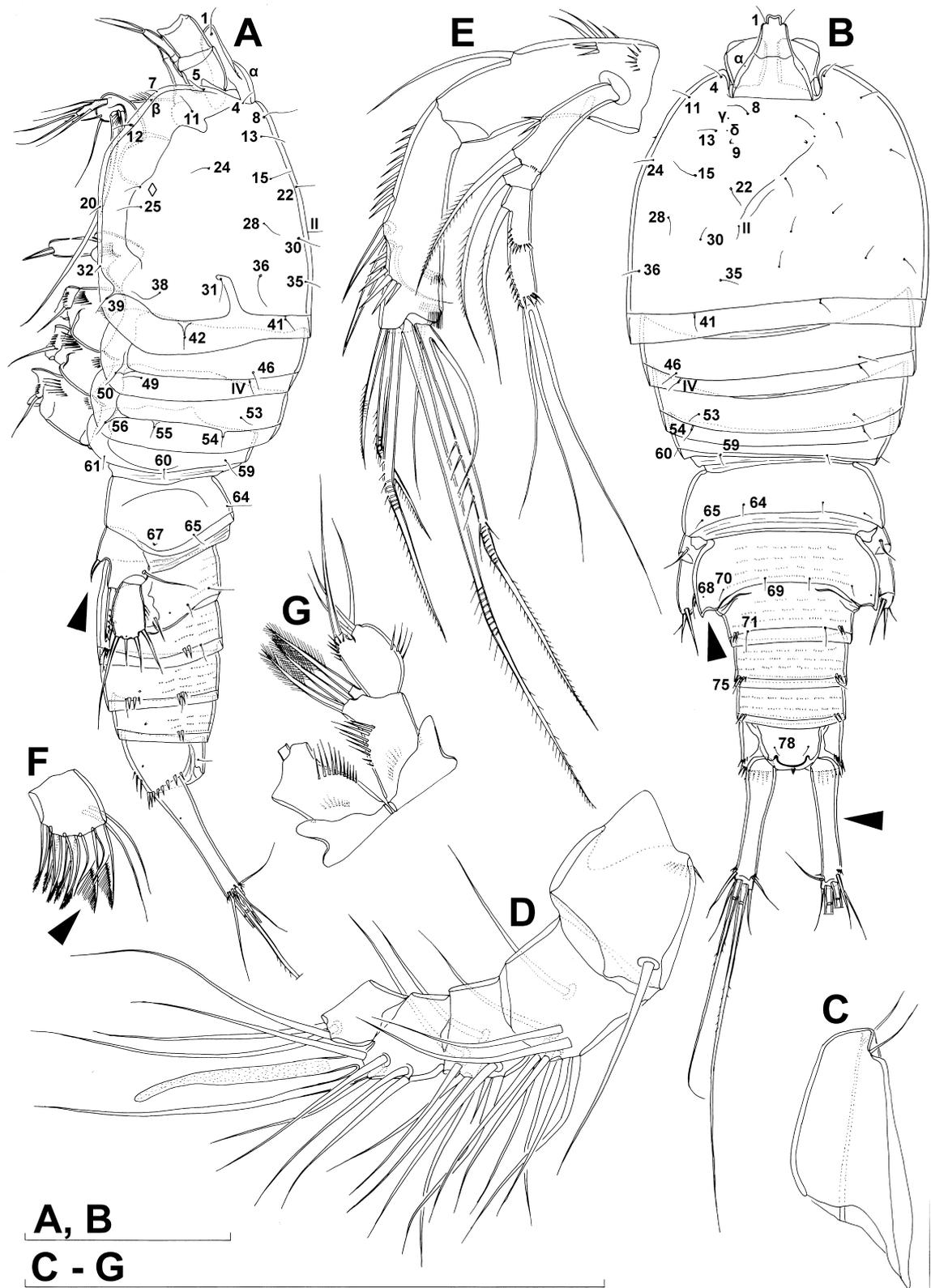


FIGURE 48. *Willstenhelia thalia* sp. nov., line drawings, female holotype: A, habitus, lateral view; B, habitus, dorsal view; C, rostrum, dissected and partly flattened, lateral view; D, proximal part of antennula, ventral view; E, antenna, anterior view; F, praecoxa of maxillula, posterior view; G, maxillipeds, posterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Willstenhelia calliope*. Geometric shape (◊) indicates sensillum presumably homologous to that in *Willstenhelia euterpe*. Roman numerals (II, IV) indicate sensilla presumably homologous to those in *Itostenhelia polyhymnia*. Greek letters (α, β, γ, δ) indicate unique sensilla and pores. Arrowheads point to most prominent specific features. Scale bars 100 μm.

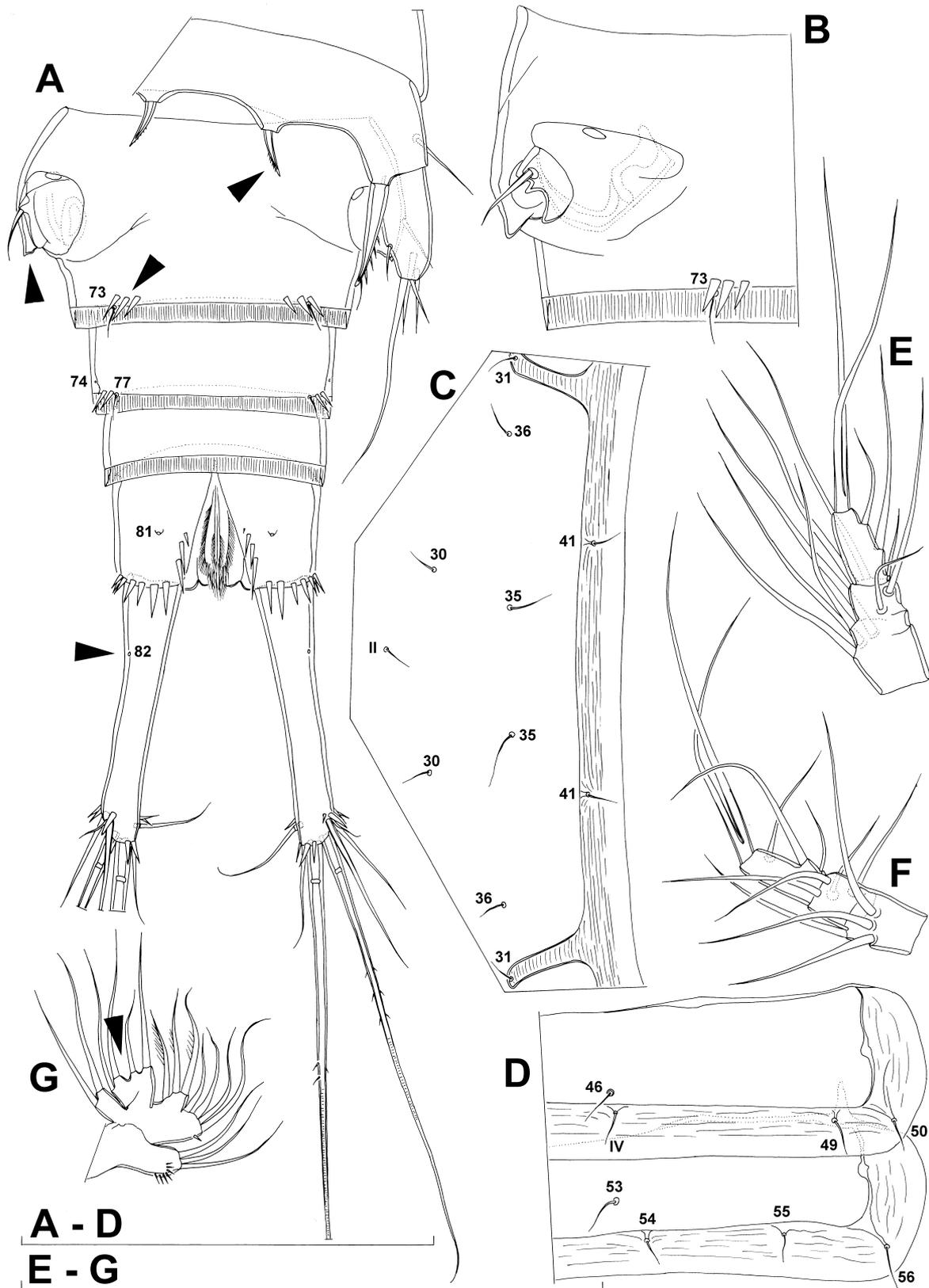


FIGURE 49. *Willenstenhelia thalia* sp. nov., line drawings, female holotype: A, urosome, ventral view; B, right part of genital double-somite, ventro-lateral view; C, posterior central part of cephalothoracic shield, dissected and flattened; D, pleurons of second and third pedigerous somites, dissected and flattened; E, distal part of antennula, ventral view; F, distal part of antennula, dorso-anterior view; G, maxillular palp, anterior view. Arabic numerals indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Roman numerals (II, IV) indicate sensilla presumably homologous to those in *Itostenhelia polyhymnia*. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

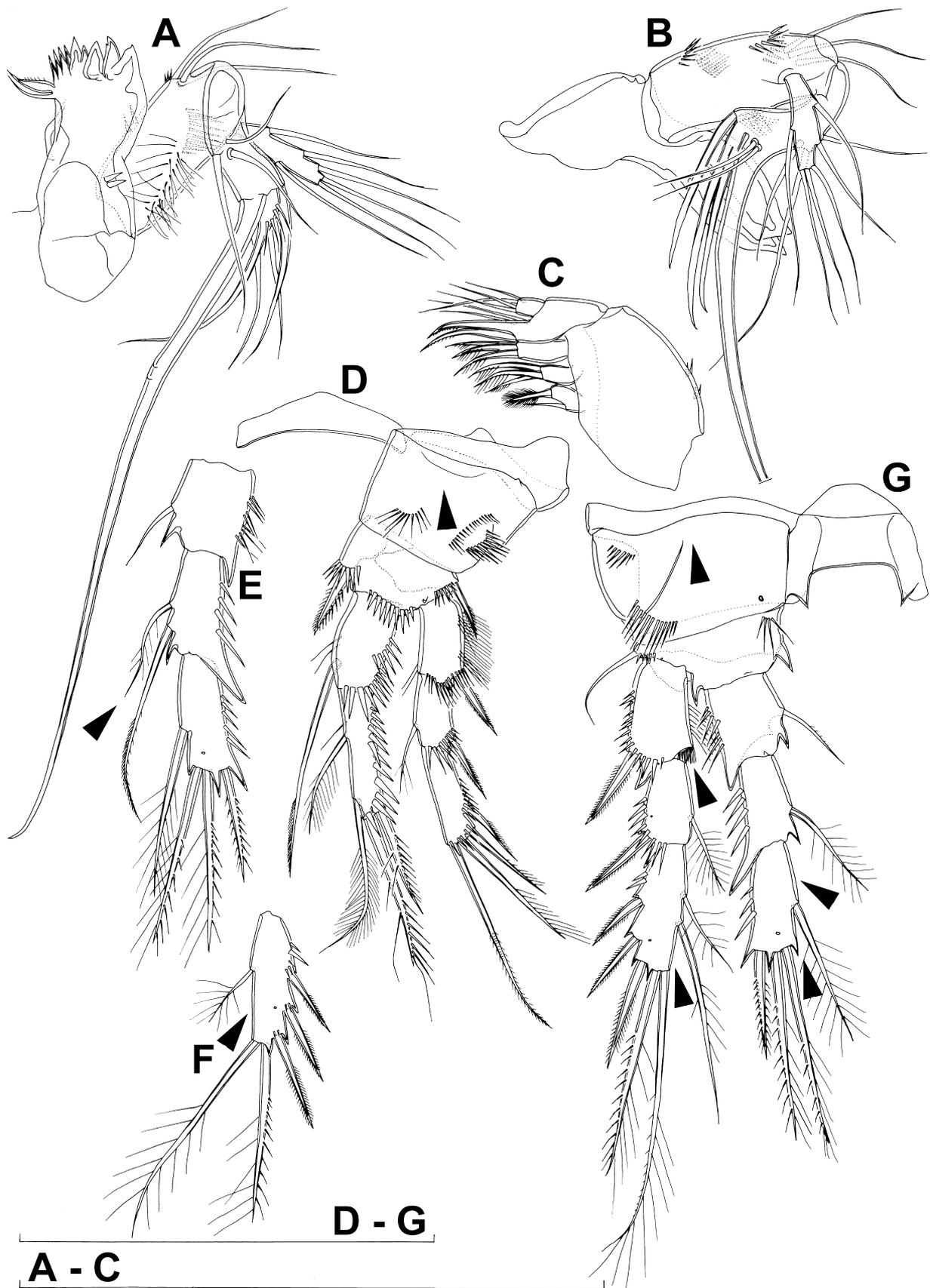


FIGURE 50. *Willenstenhelia thalia* sp. nov., line drawings, female holotype: A, mandibula, posterior view; B, mandibula, antero-ventral view; C, maxilla, posterior view; D, first swimming leg, anterior view; E, endopod of second swimming leg, anterior view; F, third exopodal segment of second swimming leg, anterior view; G, third swimming leg, anterior view. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

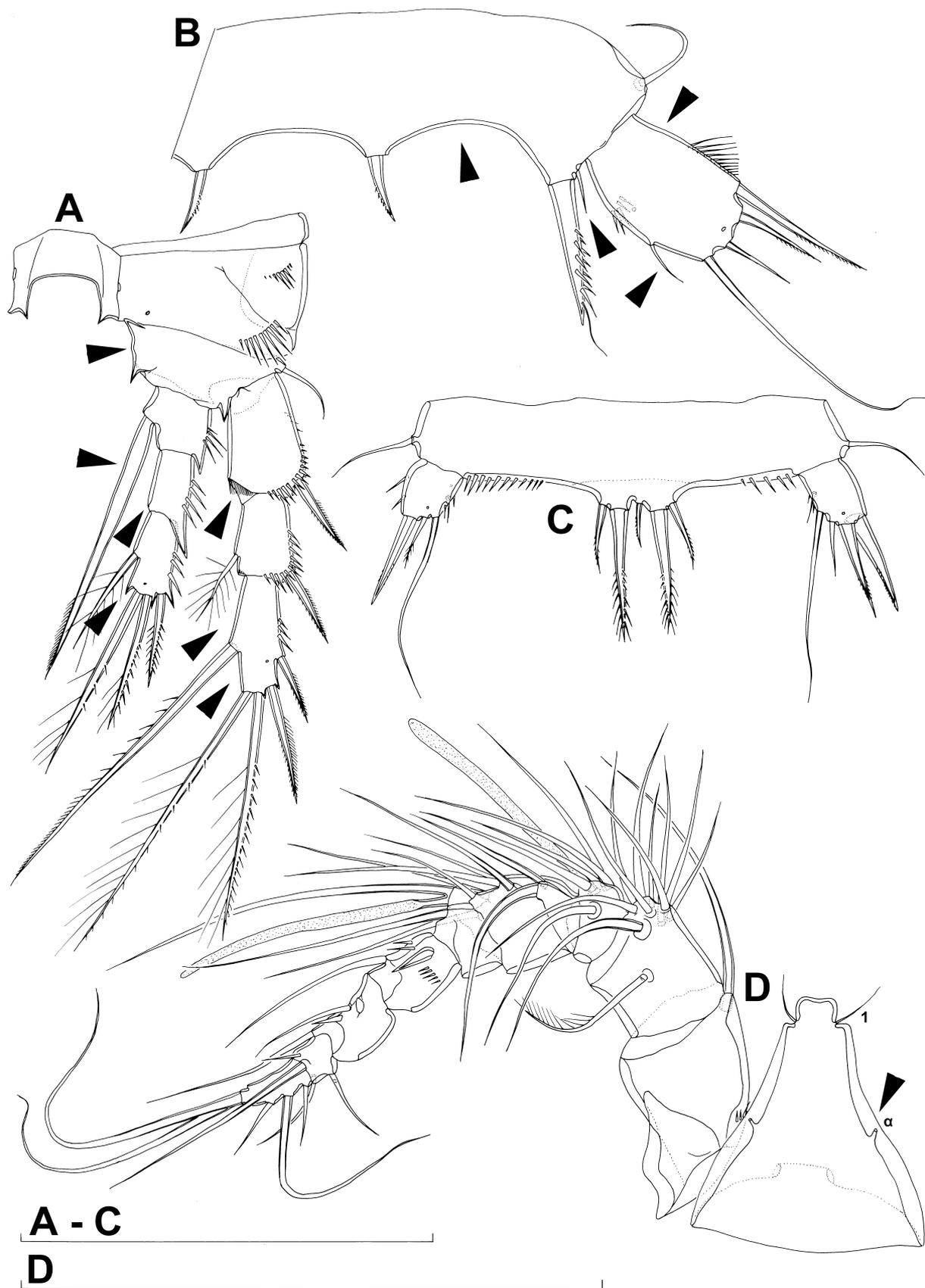


FIGURE 51. *Willenstenhelia thalia* sp. nov., line drawings, A–B, female holotype, C–D, male allotype: A, fourth swimming leg, anterior view; B, fifth swimming leg, anterior view; C, fifth swimming legs, anterior view; D, rostrum and antennula, dorsal view. Arabic numeral indicates sensillum presumably homologous to that in *Itostenhelia polyhymnia*. Greek letter (α) indicates a unique pore. Arrowheads point to most prominent specific features. Scale bars 100 μ m.

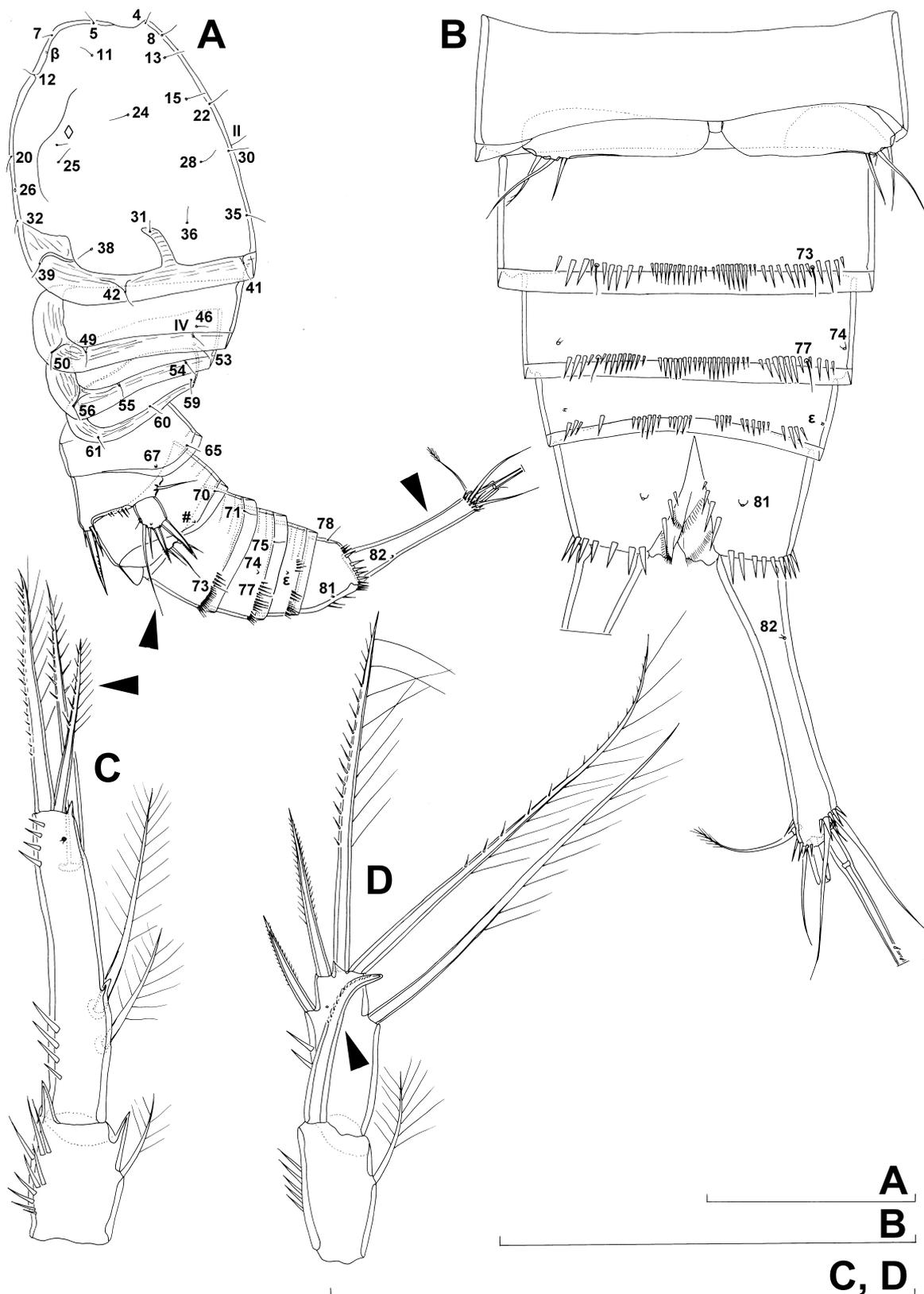


FIGURE 52. *Willstenhelia thalia* sp. nov., line drawings, male allotype: A, habitus, lateral view; B, urosome, ventral view; C, endopod of second swimming leg, anterior view; D, last two exopodal segment of fourth swimming leg, anterior view. Arabic numerals and hash mark (#) indicate sensilla and pores presumably homologous to those in *Wellstenhelia calliope*. Geometric shape (◊) indicates sensillum presumably homologous to that in *Wellstenhelia euterpe*. Roman numerals (II, IV) indicate sensilla presumably homologous to those in *Itostenhelia polyhymnia*. Greek letters (β, ε) indicate unique sensilla and pores. Arrowheads point to most prominent specific features. Scale bars 100 μm.

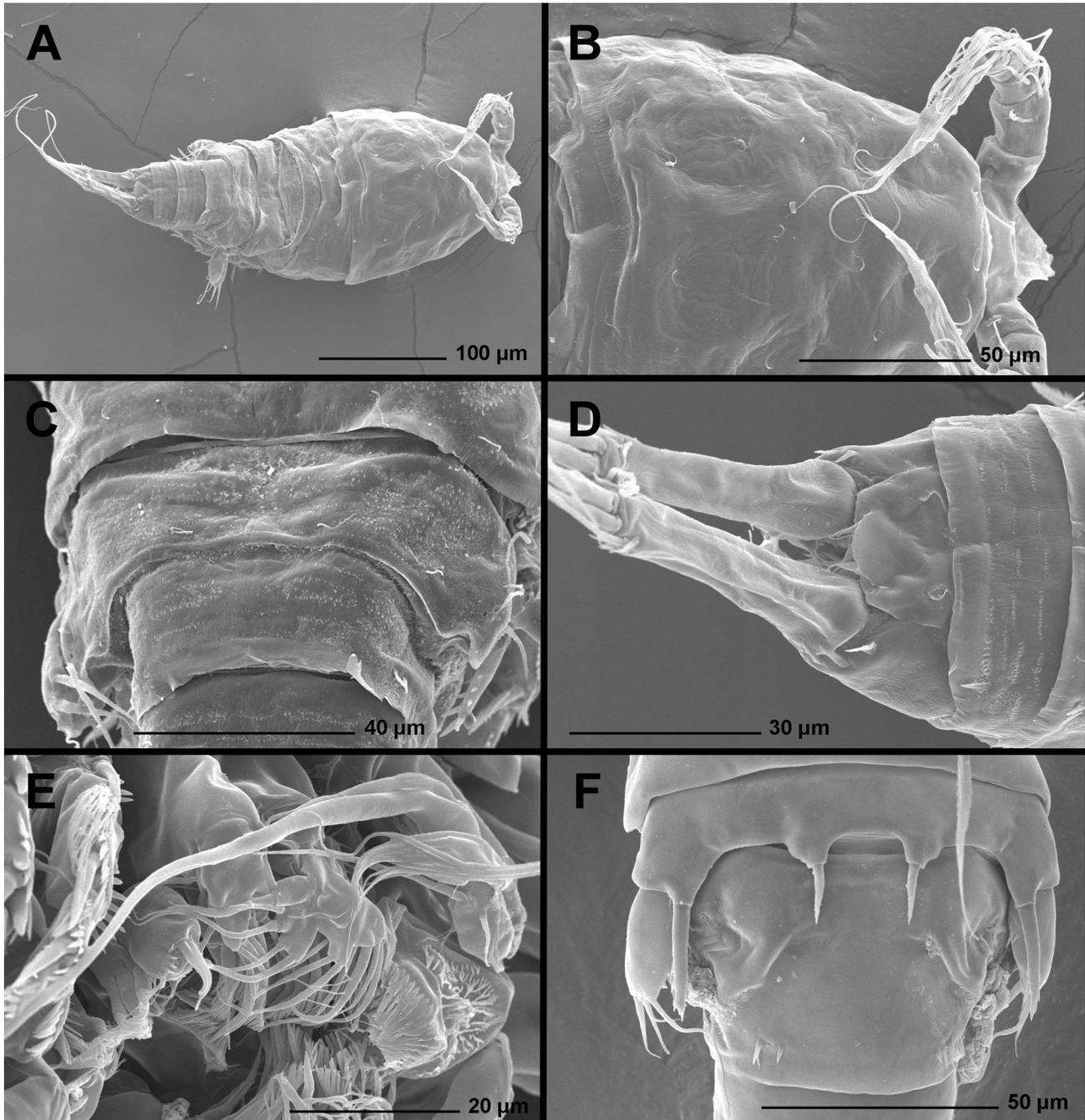


FIGURE 53. *Willstenhelia thalia* sp. nov., scanning electron micrographs, A–D, female paratype 1, E–F, female paratype 2: A, habitus, dorsal view; B, cephalothorax, dorsal view; C, genital double-somite, dorsal view; D, preanal and anal somites and caudal rami, dorsal view; E, mouth appendages, ventral view; F, genital double-somite and fifth legs, ventral view. Scale bars 20 µm (E), 30 µm (D), 40 µm (C), 50 µm (B, F), and 100 µm (A).

Maxilla (Figs. 50C, 53E, 41A) as in *Wellstenhelia calliope*, except dorsal endite on syncoxa with only two setae, syncoxa with only several outer spinules, and endopod with only four slender setae.

Maxilliped (Figs. 48G, 53E) segmentation, armature and most ornamentation as in *Wellstenhelia calliope*, except outer distal corner of coxa produced into pronounced and blunt process and second endopodal segment fused basally to first endopodal; also setae on first endopodal segment proportionately much longer.

First swimming leg (Fig. 50D) as in *Itostenhelia polyhymnia*, except coxa without proximal row of anterior spinules (arrowed in Fig. 50D) and distal inner seta on second endopodal segment inserted closer to distal margin.

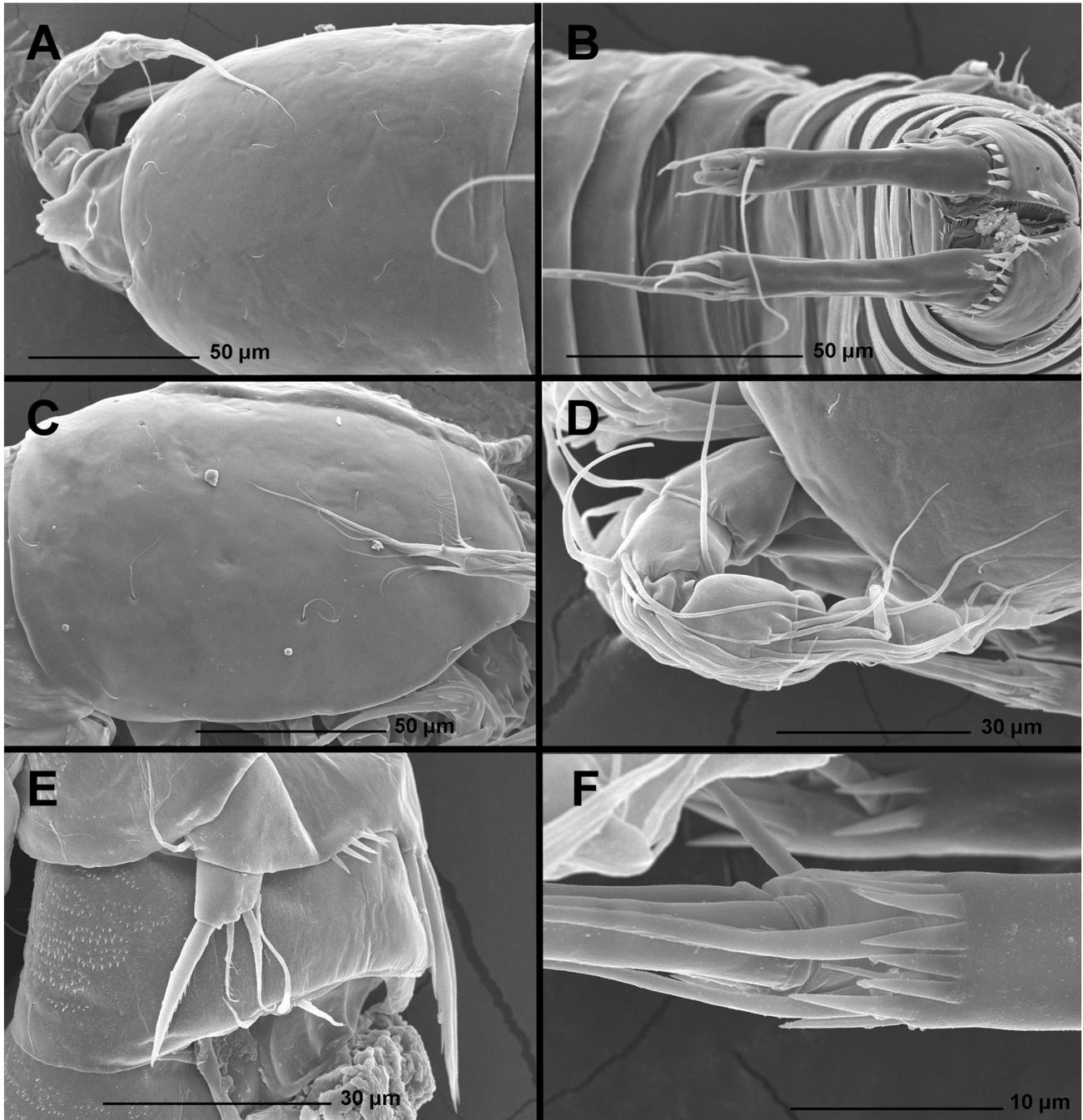


FIGURE 54. *Willenstenhelia thalia* sp. nov., scanning electron micrographs, A–B, female paratype 3, C, female paratype 4, D–F, male paratype: A, cephalothorax, dorsal view; B, anal somite and caudal rami, posterior view; C, cephalothorax, lateral view; D, antennula, lateral view; E, genital somite and fifth leg, lateral view; F, posterior part of caudal rami, lateral view. Scale bars 10 μ m (F), 30 μ m (D, E), and 50 μ m (A, B, C).

Second swimming leg (Fig. 50E, F) as in *Itostenhelia polyhymnia*, except first exopodal segment without inner seta, third exopodal segment without distal inner seta (arrowed in Fig. 50F) and second endopodal segment with shorter proximal seta (arrowed in Fig. 50E).

Third swimming leg (Fig. 50G) as in *Itostenhelia polyhymnia*, except intercoxal sclerite with shorter distal projections, coxa without proximal row of spinules (arrowed in Fig. 50G), first exopodal segment without inner seta (arrowed in Fig. 50G), third exopodal segment without distal exopodal setae (arrowed in Fig. 50G) and with three outer spines, and third endopodal segment without proximal or distal inner setae (both positions arrowed in Fig. 50G).

Fourth swimming leg (Fig. 51A) as in *Wellstenhelia calliope*, except intercoxal sclerite with sharp distal

projections, basis without inner spinules, first exopodal segment without inner setae (arrowed in Fig. 51A), third exopodal segment with only two outer spines and without proximal or distal inner setae (both arrowed in Fig. 51A), first endopodal segment smaller and with longer and stronger inner seta (arrowed in Fig. 51A), second endopodal segment without inner seta (arrowed in Fig. 51A), and third endopodal segment with only one inner seta (arrowed in Fig. 51A).

Fifth leg (Figs. 49A, 51B, 53F) segmentation as in *Wellstenhelia calliope* but general shape, armature, and ornamentation very different. Endopodal lobes completely fused, each with three elements, with enormous gap (arrowed in Fig. 51B) between two inner spiniform ones; outer element minute, smooth, and slender (arrowed in Fig. 51B); middle element strongest, unipinnate along outer margin, twice as long as inner element, and 3.5 times as long as outer slender seta. Exopod almost rectangular (arrowed in Fig. 51B), 1.5 times as long as wide, with longitudinal row of outer spinules in distal part, transverse row of inner spinules, one anterior pore and one posterior pore, with five setae, innermost one larger than some spinules (arrowed in Fig. 51B). Length ratio of exopodal setae, starting from inner side, 1 : 5.5 : 1.5 : 1.8 : 3.1.

Sixth leg (Fig. 49B) simple small cuticular plate covering genital aperture, inserted at midlength of genital double-somite laterally, with single smooth seta flanking short spiniform process.

Male (based on allotype and 16 paratypes). Body length from 375 to 403 μm (385 μm in allotype). Habitus (Fig. 52A), colour, rostrum (Fig. 52D), shape and ornamentation of cephalothorax (Figs. 52A, 54A, C), second pedigerous somite (Figs. 52A), third pedigerous somite (Fig. 52A), fourth pedigerous somite (Fig. 52A), ornamentation of first urosomite (Figs. 52A, B, 54E), anal somite (Fig. 52A, B), caudal rami (Figs. 52A, B, 54F), antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, first swimming leg, and third swimming leg as in female.

Genital somite (Figs. 52A, B, 54E) shorter and wider than in *Wellstenhelia calliope* and without large spinules; lateral pore no. 68 missing; additionally ornamented with several rows of minute spinules dorso-laterally.

Third urosomite (Fig. 52A, B) as in *Wellstenhelia calliope*, except lateral pair of sensilla no. 72 missing, ventral row of spinules not interrupted between sensilla pair no. 73, and these sensilla also more widely spaced; additionally ornamented with several rows of minute spinules dorso-laterally.

Fourth urosomite (Fig. 52A, B) pore and sensilla pattern as in female (i.e. lateral sensilla no. 76 missing), except for continuous ventral posterior row of large spinules.

Fifth urosomite (Fig. 52A, B) with lateral pore (no. ϵ) as in female, but with posterior ventral row of spinules of various sizes.

Caudal rami (Figs. 52A, B, 54F) long and slender (arrowed in Fig. 52A), about 4.5 times as long as wide in ventral view, with middle lateral seta hardly longer than spinules that flank it.

Antennula (Figs. 51D, 54D) as in *Itostenhelia terpisichore*, except aesthetascs on third and fourth segment shorter, sixth segment with more spinules, and seventh segment with one more seta; setal formula 1.11.5+ae.9+ae.1.2.3.4.5.

Second swimming leg (Fig. 52C) with coxa, basis, and exopod as in female. Endopod with second and third segment fused, with only three elements on ancestral segment, and with inner apical element (arrowed in Fig. 52C) shorter than outer.

Fourth swimming leg (Fig. 52D) as in female, except outer spine on second exopodal segment strongly curved and sclerotized, highly characteristic and visible even on undissected specimens (arrowed in Fig. 52D).

Fifth leg (Figs. 51C, 52A, 54E) general shape, segmentation, and most armature and ornamentation as in *Itostenhelia polyhymnia*, except endopodal lobes slightly more pronounced, exopod slightly larger, and number of exopodal and endopodal armature elements often asymmetrical. Endopodal lobe mostly with two elements, inner one twice as long as outer one; third element always innermost and smallest. Exopod 1.4 times as long as wide, with outer margin smooth or with several strong spinules, inner margin always with several small spinules, with four or five armature elements; innermost armature element as in female minute and slender seta, next one longest and slender seta (arrowed in Fig. 52A), third short and slender seta, followed by one or two strong and equally long apical spines. Length ratio of exopodal armature, from inner side, 1: 6.8 : 2 : 3.5.

Sixth legs (Figs. 52B, 54E) as in *Itostenhelia polyhymnia*, except both legs distinct at base.

Variability. Fusion between sixth and seventh antennular segment in female is variable, but is never complete (Fig. 49E, F). Male fifth leg is often asymmetrical (Fig. 51C), with more or less spinules on the endopodal lobe, with or without spinules on the outer margin of exopod, with two or three endopodal armature elements, and with

four or five exopodal armature elements. Most morphological features are, however, extremely conservative, including the sensilla and pores pattern of somites, and length ratio of different armature on appendages.

Morphological affinities. *Willenstenhelia thalia* **sp. nov.** differs from all congeners by the minute inner seta on the female fifth leg exopod (Fig. 51B), minute outermost seta on the female fifth leg endopod (Fig. 51B), and robust and spiniform second seta from outer side on the female fifth leg endopod (Fig. 51B), which can all be considered as autapomorphic character states. It also has a more elongated female fifth leg exopod than any other congener, but this may be a plesiomorphy in a larger group of stenheliins. Posteriorly pointed, large spiniform processes on the anterior part of the genital double-somite (Figs. 48B, 49A, B) also may be an autapomorphy, but this feature was not described or illustrated in at least two congeners. All these characters would suggest a somewhat isolated position of *Willenstenhelia thalia* in the genus *Willenstenhelia* **gen. nov.**, which is not surprising given that this is the only Pacific representative. Other congeners include *Willenstenhelia unisetosa* (Wells, 1967) **comb. nov.** from Mozambique (Indian Ocean), *Willenstenhelia urania* **sp. nov.** from the Mediterranean Coast of Israel, *Willenstenhelia terpsichore* **sp. nov.** from the Slovenian Coast of the Adriatic Sea (northern Mediterranean), and *Willenstenhelia minuta* T. Scott, 1902 from the Indian Ocean and the Suez Canal (see below and Scott 1902; Gurney 1927; Lang 1948; Por 1964; Wells 1967; Marinov & Apostolov 1981). The males are still unknown for *Willenstenhelia minuta* and *Willenstenhelia urania*, and those for *Willenstenhelia terpsichore* are described quite incompletely. However, the latter species apparently has both exopodal and endopodal spines (or spiniform setae?) on the male fifth leg fused basally, forming strong spiniform processes, which is very different from the male fifth legs of *Willenstenhelia thalia* and *Willenstenhelia unisetosa*. Similarities in the male fifth leg between the latter two species, in addition to an identical armature formula of both male and female swimming legs, and a very similar anal operculum, may suggest that they are more closely related to each other than to other congeners, while the other three species seem to form a relatively compact group, at least as one can judge from a limited set of morphological characters given in their original reports.

Willenstenhelia thalia differs from *Willenstenhelia unisetosa* additionally by much longer caudal rami, more slender habitus, shorter and more spiniform innermost seta on the female fifth leg endopod, larger and more deeply concave space between two inner setae on the female fifth leg endopod, much shorter outer endopodal element on the male fifth leg endopod, and much longer second seta from inner side on the male fifth leg exopod. Wells (1967) also reported only three endopodal setae on the maxilliped and only one setae on the mandibular basis, but this may be because some setae may have been broken off on his specimen, as all other well-studied stenheliids have four endopodal setae on the maxilliped and three basal setae on the mandibula.

Willenstenhelia thalia differs from *Willenstenhelia minuta*, *Willenstenhelia urania*, and *Willenstenhelia terpsichore* additionally by the spiniform nature of the innermost element on the female fifth leg endopod, shorter second seta from outer side on the female fifth leg exopod, and presence of long spinules on the female fifth leg exopod. Its caudal rami are also significantly longer than those in *Willenstenhelia minuta* and *Willenstenhelia terpsichore*, but comparable in size to those in *Willenstenhelia urania*.

***Willenstenhelia urania* sp. nov.**

Synonymy. *Stenhelia aff. minuta* A. Scott – Por 1964: p. 83, pl. 12, figs. 111, 112.

Type locality. Israel, Mediterranean Sea, off Netanya, muddy bottom, 300 m depth, approximate coordinates 32.3257°N 34.593°E.

Type material. Holotype female illustrated by Por (1964) in figs. 111 and 112, dissected on a slide, collected on 8 October 1961, deposited at the Zoology Department of the Hebrew University, Jerusalem, Israel; not examined.

Etymology. The species is named after Urania (Ancient Greek: Οὐρανία), one of nine Muses from Greek mythology, who was a patron of tragedy. The species name is a noun in apposition (in the nominative case).

Description. Female as described by Por (1964) from Israel, and illustrated in his figures 111 and 112 as *Stenhelia aff. minuta* A. Scott, 1902. Male unknown.

Remarks. Por (1964) was aware that his single female specimen from the Mediterranean Coast of Israel differed from those of *Willenstenhelia minuta* (A. Scott, 1902) **comb. nov.** originally described from the Indian

Ocean by Scott (1902) and subsequently reported from the Suez Canal in Egypt by Gurney (1927) (see also Lang 1948), which he expressed both by using the abbreviation “aff.” in front of the species name and by listing three major morphological differences between them: relative length of the caudal rami, armature of the second exopodal segment of the first swimming leg, and armature of the female fifth leg endopodal lobe. In light of the newly discovered diversity of the Korean sympatric stenheiliins, these morphological differences cannot be attributed to intraspecific variability. Both species are, however, described only by a very limited set of morphological characters, and their relationship, as well as those between them and other three congeners, cannot be properly assessed without a thorough redescription. At the moment it seems that *Willenstenhelia urania* **sp. nov.** is most closely related to *Willenstenhelia minuta* and *Willenstenhelia terpsichore* **sp. nov.** (see below). Their affinities to *Willenstenhelia thalia* **sp. nov.** are discussed above, and they all differ from the Mozambique *Willenstenhelia unisetosa* (Wells, 1967) **comb. nov.** by much longer caudal rami.

***Willenstenhelia terpsichore* sp. nov.**

Synonymy. *Stenhelia* (*Delavalia*) *minuta* A. Scott – Marinov & Apostolov 1981: p. 66, pl. I, figs. 1–9.

Type locality. Slovenia, Adriatic Sea, Piran, muddy bottom, 15 m depth, approximate coordinates 45.5387°N 13.539°E.

Type material. Holotype female as illustrated by Marinov & Apostolov (1981) in figs. 1, 2, 3, 7, 9, dissected on a slide; female paratype as illustrated by Marinov & Apostolov (1981) in fig. 4, dissected on a slide; male allotype as illustrated by Marinov & Apostolov (1981) in figs. 5, 6, 8, dissected on a slide; all collected on 7 August 1971, originally deposited at the the Institut de Pêche, Varna, Bulgaria, but since then lost (Dr. Apostol Apostolov pers. comm.); not examined.

Etymology. The species is named after Terpsichore (Ancient Greek: Τερψιχόρη), one of nine Muses from Greek mythology, who was a patron of dance. The species name is a noun in apposition (in the nominative case).

Description. Female as described by Marinov & Apostolov (1981) from Slovenia, and illustrated in their figures 1, 2, 3, 4, 7 and 9 as *Stenhelia* (*Delavalia*) *minuta* A. Scott, 1902. Male as described by by Marinov & Apostolov (1981) from Slovenia, and illustrated in their figures 5, 6 and 8 as *Stenhelia* (*Delavalia*) *minuta* A. Scott, 1902.

Remarks. Marinov & Apostolov (1981) were aware that their two female specimens from Slovenia differed from those of *Willenstenhelia minuta* (A. Scott, 1902) **comb. nov.** in the relative length of the caudal rami (with the length/width index of four). However, they considered that to be a case of intraspecific variability, assuming that their specimens occupy an intermediate position between the typical *W. minuta* from the Indian Ocean and Suez Canal (with the l/w index of three) and those reported by Por (1964) from the Mediterranean Coast of Israel (with the l/w index of five). As a further evidence of the extreme variability of this supposedly widely distributed species they mentioned and illustrated armature of the female second leg endopod, with or without an inner seta on the third segment. As males were not recorded in the Indian Ocean, Suez or Israeli populations, their characters naturally could not be compared.

In our view, and in light of the newly discovered diversity of the Korean sympatric stenheiliins, these morphological differences cannot be attributed to intraspecific variability. Thus we name this Adriatic population reported by Marinov & Apostolov (1981) as *Willenstenhelia terpsichore* **sp. nov.** Although the caudal rami length of this species has an intermediate value, its geographic position is not intermediate, which means that we are not dealing with a cline. As mentioned above, it would seem that its closest relatives are *Willenstenhelia minuta* and *Willenstenhelia urania* **sp. nov.**, but all three species are known from a very limited set of morphological characters and they would need to be redescribed in detail if we are to assess their phylogenetic relationships. In addition to the differences in the length/width ratio of the caudal rami, there are also some differences in the shape of the female fifth leg, as well as in the proportions of different armature elements on this appendage, at least as far as can be judged from their published drawings. Affinities and differences between *Willenstenhelia terpsichore* and *Willenstenhelia thalia* **sp. nov.** are discussed in the affinities section of the latter species, and they both differ from the Mozambique *Willenstenhelia unisetosa* (Wells, 1967) **comb. nov.** by much longer caudal rami.

TABLE 1. List of copepod specimens for which mtCOI fragment was successfully amplified; see text for authors of the specific names. Note: *Stenhelia sp. 1* is an undescribed new species from South Korea.

Code	Species	Country	Station	Date	Bases	GenBank
0330	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	448	KF524863
0433	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	515	KF524864
0631	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	514	KF524865
0734	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	503	KF524866
0832	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	493	KF524867
0176	<i>Itostenhelia polyhymnia</i>	Korea	10	30 Jul 2012	660	KF524868
0273	<i>Itostenhelia polyhymnia</i>	Korea	10	30 Jul 2012	664	KF524869
0271	<i>Itostenhelia polyhymnia</i> L-form	Korea	10	30 Jul 2012	278	KF524883
8417	<i>Schizopera leptafurca</i>	Australia	YYAC0016A	20 Mar 2010	517	JQ390578
0152	<i>Stenhelia pubescens</i>	Russia	Posyet Bay	06 May 2012	659	KF524870
0254	<i>Stenhelia pubescens</i>	Russia	Posyet Bay	06 May 2012	647	KF524871
0163	<i>Stenhelia sp. 1</i>	Korea	16	18 Nov 2012	558	KF524884
0167	<i>Stenhelia sp. 1</i>	Korea	16	18 Nov 2012	662	KF524885
0122	<i>Wellstenhelia calliope</i>	Korea	5	30 Jul 2012	576	KF524872
0187	<i>Wellstenhelia clio</i>	Korea	10	30 Jul 2012	519	KF524873
0113	<i>Wellstenhelia qingdaoensis</i>	Korea	15	18 Nov 2012	518	KF524874
0143	<i>Willenstenhelia thalia</i>	Korea	10	30 Jul 2012	657	KF524875
0146	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	664	KF524878
0241	<i>Willenstenhelia thalia</i>	Korea	10	30 Jul 2012	524	KF524876
0245	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	662	KF524879
0342	<i>Willenstenhelia thalia</i>	Korea	10	30 Jul 2012	330	KF524877
0348	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	660	KF524880
0444	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	667	KF524881
0547	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	661	KF524882

TABLE 2. Average pairwise maximum likelihood distances (TN model) among mtCOI sequences between each morpho-species (lower diagonal) and within morpho-species (diagonal).

Species	1	2	3	4	5	6	7	8	9
1. <i>Wellstenhelia calliope</i>	-								
2. <i>Itostenhelia polyhymnia</i>	0.271	0.000							
3. <i>Wellstenhelia qingdaoensis</i>	0.267	0.228	-						
4. <i>Wellstenhelia clio</i>	0.202	0.328	0.245	-					
5. <i>Itostenhelia golikovi</i>	0.218	0.071	0.278	0.267	0.006				
6. <i>Willenstenhelia thalia</i>	0.285	0.201	0.291	0.338	0.181	0.008			
7. <i>Schizopera leptafurca</i>	0.302	0.241	0.376	0.344	0.270	0.199	-		
8. <i>Stenhelia sp. 1</i>	0.317	0.193	0.342	0.240	0.170	0.169	0.245	0.000	
9. <i>Stenhelia pubescens</i>	0.318	0.220	0.352	0.311	0.201	0.173	0.311	0.101	0.000

Molecular results

DNA was extracted and the mtCOI fragment successfully PCR-amplified from 23 stenheliin copepod specimens (Table 1), belonging to eight different morpho-species. Unfortunately, despite repeated attempts, we were not able to successfully amplify mtCOI fragment of *Wellstenhelia erato* **sp. nov.**, and for *Wellstenhelia euterpe* **sp. nov.** we did not have enough material for both morphological and molecular analysis. All the sequences were translated into protein using MEGA and were shown to have no evidence of stop codons, ambiguities or insertions–deletions indicative of non-functional copies of mtCOI. BLAST analyses of GenBank revealed that the obtained sequences are copepod in origin and not contaminants, and one of the GenBank COI sequences (JQ390578.1) from the species *Shizopera leptafurca* Karanovic & Cooper, 2012 was included in our phylogenetic analyses.

Average pairwise distances between morpho-species were found to be very high, with the lowest divergence (7.1%) between the Korean *Itostenhelia polyhymnia* **sp. nov.** and the Russian *Itostenhelia golikovi* (Chislenko, 1978) **comb. nov.** (Table 2). Second (10.1 %) and third (16.9 %) lowest divergences were found between *Stenhelia sp. 1* and *Stenhelia pubescens* Chislenko, 1978 and between *Stenhelia sp. 1* and *Willenstenhelia thalia* **sp. nov.**, while those between all other taxa were in excess of 17%. These high divergence values are generally indicative of distinct species by comparison with other crustaceans (Lefébure et al. 2006) and other harpacticoid copepods (Karanovic & Cooper 2011a, 2012). Average pairwise distances among the four stenheliin genera were between 17 % and 33.8 %, indicating only a remote relationship, and are comparable to those among some well accepted canthocamptid and parastenocaridid genera (Karanovic & Cooper 2011a, b). They were certainly comparable to those between *Schizopera leptafurca* and the four stenhellid genera (from 19.9 % to 37.6%), although the former belongs to a different subfamily of miraciid harpacticoids.

The highest divergences within morpho-taxa were those between eight specimens of *Willenstenhelia thalia* (0.8 %), which all came from the same sampling station (St. 10; Fig. 1), although collected on two separate occasions. Divergences between five specimens of *Itostenhelia golikovi* were about 0.6 %. (Table 2). These are all indicative of intraspecific variability (Lefébure et al., 2006). Sequences of all other species where we had more than one specimen showed zero divergence, although being of different length (Table 1). The L-form of *Itostenhelia polyhymnia* shows no molecular divergence from the normal form of this species, despite their morphological difference in size and some cuticular ornamentation (see above), although the amplified fragment was very short (Table 1).

All analyses (Fig. 55) supported the presence of at least nine highly divergent lineages and all five of the multisample lineages were supported with high bootstrap values (>74% for ML). The tree topology in our NJ analysis was the same as in the ML analysis (Fig. 55), except the bootstrap values were generally slightly higher. Our MP analysis resulted in two equally parsimonious trees, each 61 steps long, and their consensus also had a very similar topology to our ML tree, except that bootstrap values were generally slightly lower; also the terminal clade in *Willenstenhelia thalia* was not supported in our MP analysis, nor was the sister relationship between *Wellstenhelia calliope* **sp. nov.** and *Wellstenhelia clio* **sp. nov.** (instead a sister relationship was suggested between *Wellstenhelia qingdaoensis* (Ma & Li, 2011) **comb. nov.** and *Wellstenhelia clio*, but the bootstrap value for this clade was only 39%). Our morphological analyses suggested that *Wellstenhelia clio* is more closely related to *Wellstenhelia calliope* than to *Wellstenhelia qingdaoensis* (see above), which is why we have more confidence in our ML analysis than in our MP analysis, and all further molecular results and subsequent discussion will refer to the former (Fig. 55).

All basal nodes are supported only by moderate bootstrap values (between 52 % and 75 %), which could be explained by the low phylogenetic resolution of the mtCOI gene in basal nodes of the trees, possibly due to saturation at third codon positions (Karanovic & Cooper 2012) and also by various lengths of the fragments amplified (see Table 1). Nevertheless, all four stenheliin genera are well defined. A sister group relationship of *Itostenhelia golikovi* and *Itostenhelia polyhymnia* has the lowest support (52%), yet these two morpho-species are only distinguishable by several settled morphological features, and so different from any other stenheliin that there is no doubt about their sister-species relationship (see above). Another moderately supported lineage is that uniting the three *Wellstenhelia* **gen. nov.** species (53%), but it was recovered in all analyses despite each species being represented with a single sequence (Table 1); divergences between morpho-species are much higher than in the genus *Itostenhelia* **gen. nov.**, which is in complete accordance with the observed morphological evidence. There is also a strongly supported sister group relationship of *Stenhelia pubescens* and *Stenhelia sp. 1* (bootstrap support

75%). Genera *Itostenhelia* and *Wellstenhelia* form a moderately supported clade (60%), with a similar level of support suggested for the lineage formed by these two genera and the genus *Stenhelia*. All our analyses showed *Willenstenhelia* **gen. nov.** as a sister group to all other stenheliins, suggesting only a remote relationship; although this was not apparent from the divergence values (Table 2), it is strongly supported by the above studied morphological data.

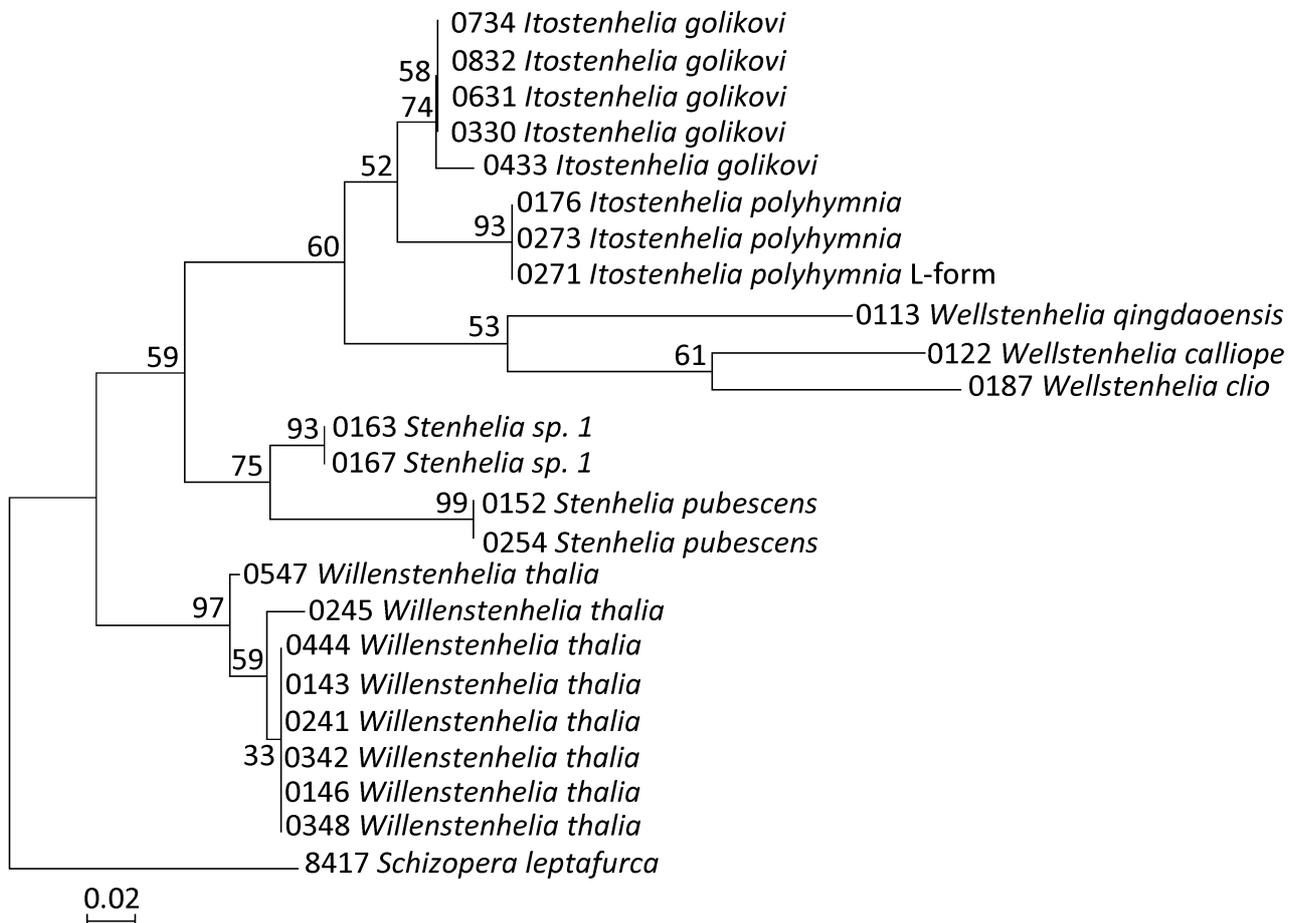


FIGURE 55. Maximum likelihood (ML) tree based on mtCOI sequence data of 23 stenheliin specimens from Gwangyang Bay (South Korea) and Posyet Bay (Russia), constructed using MEGA v 5.0.3 and an HKY+G model of evolution, with numbers on the branches representing bootstrap values from 500 pseudoreplicates. The tree is rooted with *Schizopera leptafurca* Karanovic & Cooper, 2012 from Western Australia. The cladogram is drawn to scale and the specimen codes correspond to those in Table 1.

Discussion

Phylogeny of stenheliins. This study is the first ever attempt at a molecular analysis of stenheliin copepods, and our amplification success rates were extremely low (just below 22%) even with specially designed nested primers (see material examined of each species above). This may be due to the very small size of the specimens and correspondingly low amount of DNA isolate, but it is probably also because we are yet to find an optimal procedure and combination of primers for this group.

However, our phylogenetic analysis (Fig. 55) resulted in demonstrating a polyphyly of the genus *Delavalia* Brady, 1869, as postulated by Mu & Huys (2002), because all species described or redescribed in this paper would traditionally be (and some indeed used to be) classified as belonging to this genus. However, the position of the genus *Stenhelia* Boeck, 1865 deep inside this stenheliin group suggests that the two-segmented endopod must have originated independently at least in *Willenstenhelia* **gen. nov.** and *Itostenhelia* **gen. nov.**/*Wellstenhelia* **gen. nov.** The simplicity of the genus-group division based on this morphological character alone was recently demonstrated in the closely related subfamily Diosaccinae Sars, 1906 by Karanovic & Cooper (2012), also based on the

combined molecular and morphological approach. Of course, a more robust phylogeny of miraciids in general and stenheliins in particular would have to be based on a wider taxon sampling and more genes (including some slower evolving nuclear ones, such as 18S; see Karanovic & Krajcicek 2012a), but the initial congruent data between morphology and genes are encouraging for this group of harpacticoid copepods with very few species being resampled after their initial description and many with even their types lost (see above). Also encouraging was the fact that the topology of our trees changed very little depending on the method used (with essentially no difference between NJ and ML analyses), which may suggest that our data are robust (i.e. phylogenetically informative), despite a relatively short segment of the mtCOI gene (especially in some specimens; see Table 1).

The smallest average divergence values in mtCOI gene (Table 2), and smallest morphological differences, were observed between two allopatric (Korea/Russia) species pairs: *Itostenhelia polyhymnia* sp. nov./*Itostenhelia golikovi* (Chislenko, 1978) comb. nov. and *Stenhelia* sp. 1/*Stenhelia pubescens* Chislenko, 1978 (7.1 % and 10.1% respectively). Average divergence values between all sympatric Korean stenheliins were very high (all in excess of 16.9%), which suggests a long independent evolutionary history. This is also reflected in their numerous morphological differences. To us this suggests a potential for niche partitioning with minimal competition for resources, and is very similar to some recently observed examples of sympatric Australian diosaccins (Karanovic & Cooper 2012). It means that multiple colonisations are a better model for explaining this unprecedented diversity in a small Korean bay than is an explosive radiation, despite the fact that surrounding areas do not hold a high diversity currently. However, without any fossil record we can only guess what the diversity of this group in East Asia was historically. Anthropogenic translocation may also be a contributing factor, as for some other copepod groups (see Karanovic & Krajcicek 2012a), and especially through ships' ballast water discharge (Reid & Pinto-Coelho 1994; Lee 1999). However, this is just a speculation at this stage, but the presence of *Willenstenhelia minuta* (A. Scott, 1902) comb. nov. in the Suez Canal in Egypt (Gurney 1927) is a sign that these animals are easily dispersed even in artificial habitats.

Usefulness of microcharacters in harpacticoid species delineation and their phylogenetic value. Lang (1965) was the first to start paying special attention to somite ornamentation in harpacticoids, and to use it as a diagnostic character in species descriptions and delineations, especially in regard to the spinules pattern on urosomites. Pores and sensilla pattern have not been used in harpacticoid taxonomy until recently, despite their usefulness being demonstrated in distinguishing closely related species of both calanoid (Fleminger 1973; Mauchline 1977; Malt 1983; Koomen 1992; Galassi et al. 1998) and cyclopoid copepods (Strickler 1975; Baribwegure & Dumont 1991; Baribwegure et al. 2001; Baribwegure & Mirabdullayev 2003; Alekseev et al. 2006; Karanovic & Krajcicek 2012a; Karanovic et al. 2012). Initial studies in harpacticoids showed different results in different groups. In the freshwater family Parastenocarididae Chappuis, 1940 a combined morphological and molecular approach showed that spinules ornamentation on urosomites can be used to distinguish between closely related sister species (Karanovic & Cooper 2011a); however, sensilla pattern seems to be extremely conservative within certain lineages (Karanovic & Cooper 2011a; Karanovic et al. 2012; Karanovic & Lee 2012), thus being potentially useful in reconstructing their phylogenetic relationships. Several examined species of the parastenocaridid genus *Proserpinicaris* Jakobi, 1972 all have 45 pairs of sensilla on their body (Karanovic et al. 2012), while those of the genus *Parastenocaris* Kessler, 1913 have only 40 pairs of sensilla (Karanovic & Lee 2012). Their homologisation seems to be relatively uncomplicated, and may prove useful in future revisions of this problematic family. In the family Ameiridae Monard, 1927, a study of several marine species showed a greater diversity of sensilla and pores pattern even between closely related species (Karanovic & Lee 2012), suggesting them as very useful characters for species delineation. Predictably, their homologisation proved to be much more difficult.

In this study, one of our aims was to examine pores and sensilla pattern on somites in different groups of stenheliins. For this purpose we carefully dissected and mounted (flattened) the cephalothoracic shield and pleurons of prosomites (see, for example Fig. 3) for examination under a compound light microscope, in addition to taking numerous SEM photographs. As in previous studies on harpacticoids, the intraspecific variability proved to be almost non-existent, except for the two forms of *Itostenhelia polyhymnia* (compare Figs. 34B and 42A, B). Sexual dimorphism was also weakly pronounced in most species for this character, except for the loss of the lateral pore no. # in females that resulted from the segmental fusion on the genital double-somite (compare, for example, Figs. 2B and 9B), as well as several additional pores or sensilla being present on the male cephalothoracic shield in some species (compare, for example Figs. 3A and 8A, or Figs. 12A and 14E), but not in others (compare Figs. 34B and

38A). The interspecific variability was different in different genera. In the genus *Itostenhelia* the two species examined have exactly the same sensilla and pores pattern on somites (compare Figs 34A, B and 43A, B), while in *Wellstenhelia* differences between species are much more pronounced, not only in the presence/absence of some sensilla or pores but also in the relative position of homologous structures (compare for example positions of the pores nos. 10 & 28 in *Wellstenhelia calliope* **sp. nov.** and *Wellstenhelia clio* **sp. nov.**; Figs. 2B, 12A). Interestingly, this is also reflected in their molecular divergence values (see above, Fig. 55, Table 2). *Wellstenhelia euterpe* **sp. nov.** seems to be the most extreme example, with many pores and sensilla missing and also many novel ones, making the homologisation of different elements according to their relative position in its congeners extremely difficult (Fig. 31A, B). Differences between all three stenheliin genera examined in this study are quite significant, yet a great majority of pores and sensilla can be homologised without many problems, suggesting a potential use of these structures in future phylogenetic reconstructions of harpacticoid copepods. However, many more families would have to be studied before this could happen. Even so, these preliminary studies in three of the four largest harpacticoid families (Boxshall & Halsey 2004) suggest that these characters hold a huge potential for phylogenetic studies, especially where traditional morphological macro-characters are extremely conservative (family Parastenocarididae, for example) or where they show a great number of homoplastic changes (in most subterranean taxa; see Karanovic & Hancock 2009; Karanovic 2010).

Morphology of *Wellstenhelia*. Synapomorphies of the species included in this genus (i.e. generic autapomorphies) include the following features: very strong and curved setae on the first endopodal segments of the second and third leg; settled dimorphism in the swimming legs, with some setae on the third and fourth leg more slender in male than in female; exopod of the male fifth leg with only three elements, the innermost one being the strongest; and endopodal lobe of the male fifth leg without armature or ornamentation. Species of *Wellstenhelia* also share exactly the same armature formula of all swimming legs in the female, as well as the shape and armature of the female fifth leg exopod, but most of these are plesiomorphic features. All species also have a very narrow and membranous anal operculum, but this character has been poorly studied in the past and it may have originated convergently in several other stenheliin lineages. Interspecific morphological affinities among the *Wellstenhelia* congeners are discussed above after species descriptions/redescriptions, along with their distinguishing features. However, several problematic issues still remain unsolved in this genus.

Lang (1948) stated that the swimming legs armature formula of the Swedish *Wellstenhelia hanstromi* (Lang, 1948) **comb. nov.** is as in *Beatricella aemula* (T. Scott, 1893), but this is questionable as all other species of *Wellstenhelia* have only one seta on the second endopodal segment of the second leg. No one has ever provided a drawing of this appendage for *Wellstenhelia hanstromi*, but Kornev & Cheroprud (2008) repeated this statement in the swimming legs armature formula they included in the redescription of a population of this species from the White Sea, in Russia. Unfortunately, their formula is quite problematic. For example, they state that the third exopodal segment of the first leg bears five elements, while their fig. 5.96B shows only four elements on this segment (i.e. a normal condition). There is no indication that they actually studied the second leg of their population. We believe the reduction to one seta on the second endopodal segment of this leg may prove to be another autapomorphy of this genus, but that will have to be checked for *Wellstenhelia hanstromi*, and it certainly originated convergently in several lineages of stenheliins.

Kornev & Chertoprud (2008) did study in detail several morphological features of their population and provided skilful drawings of those (see above), but only mentioned casually that their population differs slightly from that described by Lang (1948) in the shape of the fourth leg endopod. However, it is clear from the drawings published that these two populations differ at least in the following three characters: relative length of the caudal rami, relative length of the inner seta on the first endopodal segment of fourth leg, and relative length of the female fifth leg armature. In the light of the newly discovered diversity of the Korean sympatric stenheliins, these morphological differences cannot be attributed to intraspecific variability, which is why we describe above the population from the White Sea as a new species, *Wellstenhelia melpomene* **sp. nov.** Both species are morphologically very similar to the Korean *Wellstenhelia clio*, but assessment of their phylogenetic relationships will have to await detailed redescriptions and DNA sequencing of the former.

Another problematic issue in this genus is that males (or male characters) are still unknown for four species: *Wellstenhelia hanstromi*, *Wellstenhelia melpomene*, *Wellstenhelia euterpe*, and *Wellstenhelia bocqueti* (Soyer, 1971) **comb. nov.** *Delavalia arctica* T. Scott, 1899 is one of many *Delavalia* species described from a very limited set of female morphological characters, and we do not know the condition of setae on the first endopodal segment of

the second and third legs in this species. However, it allegedly has a similar armature formula to members of *Wellstenhelia* (see Lang 1948), and a very similar female fifth leg. At this stage, however, we do not have enough empirical data to include this species in *Wellstenhelia*, and Lang (1948) also stated that it has two setae on the second endopodal segment of the second leg.

As noted by Mu & Huys (2002), *Muohuysia hylophila* (Hicks, 1988) is the only other stenheliin that exhibits spiniform curved setae on the first endopodal segments of the second and third leg. We think it is conceivable that *Muohuysia* Ozdiken, 2009 and *Wellstenhelia* represent sister clades, which would imply that the two-segmented endopod of the first leg in *Wellstenhelia* evolved independently from that in other *Delavalia* species, because *Muohuysia* has a three-segmented (i.e. plesiomorphic) state of this character. Mu & Huys (2002) cited this hypothesis as a possible support for the polyphyletic nature of *Delavalia*. In the absence of molecular data for *Muohuysia*, this will have to remain a hypothesis, but our molecular phylogeny of the Russian and Korean stenheliins (Fig. 55) indicate that *Delavalia* is indeed polyphyletic (see above).

Morphology of *Itostenhelia*. Autapomorphies of this genus include the following morphological features: rostrum with an anterior bunch of large spinules; baseoendopod of the female fifth leg with a row of spinules at the base of exopod; female fifth leg exopod more than twice as long as wide, ovoid, with long spinules along both inner and outer margins (those along outer margin especially long), with five setae, outermost one hardly longer than neighbouring spinules; female fifth leg endopodal lobe with four setae, two inner ones significantly shorter than the outer ones. Beside these characters, the two species currently included in *Itostenhelia* share many other morphological features, including: smoothly rounded anterior part of the genital double-somite in dorsal (or ventral) view, with genital apertures positioned ventro-laterally; broad and almost trilobate anal operculum; long and slender caudal rami; female antennula with the ancestral sixth and seventh segments partly or completely fused; short first endopodal segment of the first swimming leg; armature formula of all swimming legs, with minute distal inner setae on last exopodal and endopodal segment of at least the third leg; last exopodal segment of third and fourth leg with only two outer spines; armature formula and even proportions of armature elements on the female fifth leg, etc. Some of these characters are plesiomorphies, some arose convergently in a number of different stenheliin lineages, while some are synapomorphies of a larger group of species currently considered members of *Delavalia*. The latter group includes *Delavalia adriatica* (Marinov & Apostolov, 1981), *Delavalia elisabethae* (Por, 1960), *Delavalia hirtipes* (Wells & Rao, 1987), *Delavalia latioferulata* (Itô, 1981), *Delavalia mixta* (Wells & Rao, 1987), *Delavalia normani* T. Scott, 1905, *Delavalia oblonga* (Lang, 1965), *Delavalia polluta* (Monard, 1928), and even maybe *Delavalia gundulae* (Willen, 2003) and *Delavalia nuwukensis* (Wilson, 1965). Unfortunately, the males are still unknown for *Delavalia adriatica* and *D. nuwukensis*, and most species are known from a limited set of morphological characters; especially very little is known about the ornamentation of somites, but for some we do not even have information on the proportion of setae on some swimming legs or armature of some mouth appendages (see Lang 1948, 1965; Por 1960; Wilson 1965; Itô 1981; Marinov & Apostolov 1981; Wells & Rao 1987; Willen 2003). Even so, it seems that at least three species (*Delavalia hirtipes*, *Delavalia latioferulata* and *Delavalia mixta*) form a monophyletic group, that may be recognised as a separate genus in the future, which may represent a sister clade to *Itostenhelia*. *Delavalia elisabethae* seems to be closely related to *Delavalia oblonga*.

None of the abovementioned species, however, can be included in the genus *Itostenhelia*, because they differ by a combination of plesiomorphic and apomorphic morphological features, in addition to those outlined above as autapomorphies of the new genus. Plesiomorphies include: short caudal rami (in *Delavalia adriatica*, *Delavalia elisabethae*, *Delavalia gundulae*, *Delavalia normani*, *Delavalia nuwukensis*, *Delavalia oblonga*, *Delavalia polluta*); eight-segmented female antennula (*Delavalia adriatica*, *Delavalia gundulae*, *Delavalia normani*, *Delavalia nuwukensis*, *Delavalia oblonga*); mandibular endopod with three lateral setae (*Delavalia gundulae*, *Delavalia nuwukensis*); dorsal endite of maxilla with more than two setae (*Delavalia gundulae*, *Delavalia nuwukensis*); distal inner seta on the second endopodal segment of the first leg inserted close to distal margin (*Delavalia gundulae*, *Delavalia nuwukensis*); three outer spines on the third exopodal segment of third leg (*Delavalia adriatica*, *Delavalia elisabethae*, *Delavalia gundulae*, *Delavalia hirtipes*, *Delavalia latioferulata*, *Delavalia mixta*, *Delavalia nuwukensis*, *Delavalia oblonga*); distal seta on third endopodal segment of the third leg long (*Delavalia gundulae*, *Delavalia hirtipes*, *Delavalia mixta*); distal seta on third endopodal segment of the second leg long (*Delavalia nuwukensis*); three outer spines on the third exopodal segment of the fourth leg (*Delavalia adriatica*, *Delavalia hirtipes*, *Delavalia mixta*, *Delavalia oblonga*, *Delavalia polluta*); distal seta on the

third exopodal segment of the fourth leg long (*Delavalia nuwukensis*); distal seta on the third endopodal segment of the fourth leg long (*Delavalia hirtipes*, *Delavalia latioferculata*, *Delavalia mixta*, *Delavalia nuwukensis*, *Delavalia polluta*); and exopod of the female fifth leg short (*Delavalia nuwukensis*, *Delavalia polluta*). Autapomorphies include: rostrum with rounded or pointed tip (in *Delavalia elisabethae* and *Delavalia oblonga*); endopod and exopod of the maxillula confluent at base (*Delavalia gundulae*, *Delavalia nuwukensis*, *Delavalia oblonga*); maxilliped prehensile (*Delavalia gundulae*, *Delavalia nuwukensis*); second endopodal segment of the maxilliped fused to the first endopodal (*Delavalia elisabethae*, *Delavalia mixta*, *Delavalia oblonga*); distal seta on the third exopodal segment of the second, third, and fourth legs missing (*Delavalia gundulae*); large field of slender spinules on the second exopodal segment of the first leg (*Delavalia hirtipes*); baseoendopods of the female fifth leg fused medially (*Delavalia hirtipes*, *Delavalia latioferculata*, *Delavalia mixta*); inner margin of the female fifth leg exopod smooth (*Delavalia elisabethae*, *Delavalia gundulae*, *Delavalia hirtipes*, *Delavalia latioferculata*, *Delavalia mixta*, *Delavalia normani*, *Delavalia oblonga*); exopod of the male fifth leg fused to baseoendopod (*Delavalia elisabethae*, *Delavalia gundulae*, *Delavalia hirtipes*, *Delavalia normani*, *Delavalia oblonga*, *Delavalia polluta*); only four elements on the male fifth leg exopod (*Delavalia mixta*); and possibly outer margin of the female fifth leg smooth (*Delavalia adriatica*).

Morphology of *Willenstenhelia*. Autapomorphies of this genus include the following morphological features: inner apical seta on the male second endopodal segment of the second leg shorter than outer spine (see Fig. 52C); outer spine on the male second exopodal segment of the fourth leg more sclerotized than other spines and strongly curved inwards (Fig. 52D); baseoendopod of the female fifth leg with only three elements and with a large gap between the innermost one and other two (Fig. 51B); second endopodal segment of the fourth leg without inner seta (Fig. 51A); and female fifth leg exopod with only five setae and innermost seta moved to the inner margin (Fig. 51B). The latter two characters, however, originated probably convergently in several other stenheliins. For example, *Muohuysia hylophila* (Hicks, 1988) lacks seta on the second endopodal segment of the fourth leg but has a three-segmented endopod of the first leg and six setae on the female fifth leg exopod (see Hicks 1988; Mu & Huys 2002). Possibly, we can add to the generic characters a reduced armature of the second, third, and fourth swimming legs, but this has happened apparently convergently several times in the subfamily, and it would be hard to distinguish synapomorphies from symplesiomorphies, especially considering the fact that many such species are only known from a limited set of morphological characters.

In addition to the type species, *Willenstenhelia thalia* **sp. nov.**, we also include in this genus *Willenstenhelia unisetosa* (Wells, 1967) **comb. nov.** from Mozambique (Indian Ocean), *Willenstenhelia urania* **sp. nov.** from the Mediterranean Coast of Israel, *Willenstenhelia terpsichore* **sp. nov.** from the Slovenian Coast of the Adriatic Sea (northern Mediterranean), and *Willenstenhelia minuta* from the Indian Ocean and the Suez Canal (see above and Scott 1902; Gurney 1927; Lang 1948; Por 1964; Wells 1967; Marinov & Apostolov 1981). Descriptions of both *Willenstenhelia urania* and *Willenstenhelia terpsichore* are based on published records and redescriptions of the supposedly widely distributed and very variable *Willenstenhelia minuta*. Unfortunately, the males are still unknown for *Willenstenhelia minuta* and *Willenstenhelia urania*, and those for *Willenstenhelia terpsichore* are described quite incompletely. Marinov & Apostolov (1981) illustrated the latter with a characteristically curved spine on the second exopodal segment of the fourth leg, but a very different shape of the fifth leg and endopod of the second leg than in either *Willenstenhelia thalia* or *Willenstenhelia unisetosa*. They also reported variability in the armature of the third endopodal segment of the female second leg, so it is possible that they unknowingly examined and illustrated two different sympatric species. This will have to be checked on newly collected material, as the type material of *Willenstenhelia terpsichore* is unfortunately lost (Dr. Apostolov pers. comm.). *Willenstenhelia minuta* supposedly has two inner setae and three outer spines on the third exopodal segment of the fourth leg (see Lang 1948), but there are no published drawings of this segment anywhere. If true, this would distinguish this species at once from other congeners, but it is a plesiomorphic character state and thus without phylogenetic importance. This would also have to be examined in the future, adding to the list of unresolved issues in this genus. *Delavalia palustris* Brady, 1868 and *Delavalia palustris bispinosa* (Bodin, 1970) could possibly be distant relatives of *Willenstenhelia*, because they share the peculiar shape of the female fifth leg. However, they have a number of morphological differences that suggest a long independent evolutionary history. Six setae on the female fifth leg exopod, two inner setae on the female third exopodal segment of the fourth leg, inner seta on the second endopodal segment of the fourth leg, and absence of a peculiarly transformed spine on the male second exopodal segment of the fourth leg are all most probably plesiomorphic features when compared to *Willenstenhelia*. Other differences

are most probably apomorphies accumulated during independent evolution and they include: lack of lateral seta on the second endopodal segment of the first leg, only one seta on the second endopodal segment of the male second leg, completely fused baseonendopod and exopod of the male fifth leg, and lack of armature on the male fifth leg endopodal lobe. Thus, it is quite possible that the peculiar shape of the female fifth leg in these taxa is also a result of convergent evolution. *Delavalia palustris* is the type species of the genus *Delavalia*, but apart from *Delavalia palustris bispinosa* (which could actually be a separate species) has no close relatives among extant species; however, this species is widely distributed, with reported geographic variability (see Lang 1948; Bodin 1970; Apostolov & Marinov 1988; Kornev & Chertoprud 2008), and future detailed study of its morphology and DNA may reveal that we are dealing with a species-complex, as is the case with many supposedly very widely distributed copepods (see Bláha et al. 2010; Karanovic & Krajcicek 2012a, b; Hamrova et al. 2012).

Delavalia clavus (Wells & Rao, 1987) and *Delavalia paraclavus* (Wells & Rao, 1987) from the Andaman Islands in the Indian Ocean could also be distantly related to *Willenstenhelia*, as they have a similar armature formula of the swimming legs, and in particular absent seta on the second endopodal segment of the fourth leg. They also have a number of differences, which could be interpreted either as plesiomorphic (female fifth leg endopodal lobe with four setae, and absence of the curved spine on the second exopodal segment of the male fourth leg) or apomorphic features (spiniform process on the fifth leg exopod both in male and female, and only four setae on the second endopodal segment of the male second leg) when compared to the members of *Willenstenhelia*. These two species certainly represent a monophyletic unit among the currently known members of *Delavalia*, and all other species of this genus are even more distantly related to *Willenstenhelia*. The only other *Delavalia* without a seta on the second endopodal segment of the fourth leg is *Delavalia valens* (Wells & Rao, 1987), also from the Andaman Islands (Wells & Rao 1987), but it differs from *Willenstenhelia* in many characters, which probably suggest that the reduction of this seta occurred in stenheliins several times independently.

Two species currently assigned to the genus *Onychostenhelia* Itô, 1979 share with *Willenstenhelia* sexual dimorphism on the fourth leg exopod, but the transformation of this ramus in males of the former involves also a peculiar outgrowth of the proximal part of the third segment, in addition to the curved spine on the second segment (Itô 1979; Huys & Mu 2008). Although this structure may have the same function in both genera, numerous morphological differences between them in the armature and segmentation of the swimming legs, as well as transformations of the fifth leg, suggest that superficial similarities in the male fourth leg exopod could be a product of convergent evolution.

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References

- Alekseev, V., Dumont, H.J., Pensaert, J., Baribwegure, D. & Vanfleteren, J.R. (2006) A redescription of *Eucyclops serrulatus* (Fischer, 1851) (Crustacea: Copepoda: Cyclopoida) and some related taxa, with a phylogeny of the *E. serrulatus*-group. *Zoologica Scripta*, 35, 123–147.
<http://dx.doi.org/10.1111/j.1463-6409.2006.00223.x>
- Apostolov, A.M. & Marinov, T.M. (1988) *Copepoda, Harpacticoida (morski harpaktikoidi)*. Fauna na Bulgaria 18, Sofia, 383 pp. [in Bulgarian]

- Baribwegure, D. & Dumont, H.J. (1999) The use of integumental pore signature in the characterisation of species of the genus *Thermocyclops* Kiefer, 1927: The case of *Thermocyclops emini* (Mrázek, 1895) (Crustacea: Copepoda: Cyclopoida). *Belgian Journal of Zoology*, 129, 187–200.
- Baribwegure, D. & Mirabdullayev, I.M. (2003) *Thermocyclops dumonti* sp. n. (Crustacea, Copepoda), from a temporary waterbody in China. *International Review of Hydrobiology*, 88, 201–211.
- Baribwegure, D., Thirion, C. & Dumont, H.J. (2001) The integumental pore signature of *Thermocyclops oblongatus* (Sars, 1927) and *T. neglectus* (Sars, 1909), with the description of *Thermocyclops africae* new species, and a comparison with *T. emini* (Mrázek, 1895). *Hydrobiologia*, 458, 201–220.
<http://dx.doi.org/10.1023/b:hydr.0000007216.58971.38>
- Bláha, M., Hulák, M., Slouková, J. & Těšitel, J. (2010) Molecular and morphological patterns across *Acanthocyclops vernalis-robustus* species complex (Copepoda, Cyclopoida). *Zoologica Scripta*, 39, 259–268.
<http://dx.doi.org/10.1111/j.1463-6409.2010.00422.x>
- Bodin, P. (1970) Copépodes Harpacticoides marins des environs de La Rochelle, 1 – Espèces de la vase intertidale de Chatelaillon. *Tethys*, 2, 385–436.
- Boxshall, G.A. & Halsey, S.H. (2004) *An Introduction to Copepod Diversity*. The Ray Society, London, 966 pp.
- Burgess, R. (2001) An improved protocol for separating meiofauna from sediments using colloidal silica soils. *Marine Ecology Progress Series*, 214, 161–165.
- Chislenko, L.L. (1978) New species of harpacticoid copepods (Copepoda, Harpacticoida) from Posyet Bay, Sea of Japan. *Trudy Zoologicheskogo Instituta, Akademii Nauk SSSR, Leningrad*, 61, 161–192. [in Russian]
- Coull, B.C. (1976) A revised key to *Stenhelia* (*Delavalia*) (Copepoda: Harpacticoida) including a new species from South Carolina, U.S.A. *Zoological Journal of the Linnean Society*, 59, 353–364.
<http://dx.doi.org/10.1111/j.1096-3642.1976.tb01018.x>
- Dahms, H.U. & Bresciani, J. (1993) Naupliar development of *Stenhelia* (*D.*) *palustris* (Copepoda, Harpacticoida). *Ophelia*, 37, 101–116.
<http://dx.doi.org/10.1080/00785326.1993.10429911>
- Dussart, B.H. & Defaye, D. (2001) *Introduction to the Copepoda. 2nd edition. Guide to the identification of the microinvertebrates of the continental waters of the world, No. 16*. Backhuys Publishers, Leiden, 344 pp.
- Fleminger, A. (1973) Pattern, number, variability, and taxonomic significance of integumental organs (sensilla and glandular pores) in the genus *Eucalamus* (Copepoda, Calanoida). *Fishery Bulletin, United States National Marine Fisheries Service*, 71, 965–1010.
- Folk, R.L. (1974) *Petrology of sedimentary rocks*. Hemphill Publishing Company, Austin, Texas, USA, 184 pp.
- Galassi, D.M.P., De Laurentiis, P. & Giammateo, M. (1998) Integumental morphology in copepods: assessment by confocal laser scanning microscopy (CLSM) (Crustacea, Copepoda). *Fragmenta Entomologica*, 30, 79–92.
- Gurney, R. (1927) Report on the Crustacea. Copepoda (littoral and semiparasitic); Zoological Results of the Cambridge Expedition to the Suez Canal, 1924, no. 33. *Transactions of the Zoological Society of London*, 22, 451–577.
<http://dx.doi.org/10.1111/j.1096-3642.1927.tb00207.x>
- Hamrova, E., Krajčec, M., Karanovic, T., Cerny, M. & Petrussek, A. (2012) Congruent patterns of lineage diversity in two species complexes of planktonic crustaceans, *Daphnia longispina* (Cladocera) and *Eucyclops serrulatus* (Copepoda), in East European mountain lakes. *Zoological Journal of the Linnean Society*, 166, 754–767.
<http://dx.doi.org/10.1111/j.1096-3642.2012.00864.x>
- Hebert, P.D.N., Cywinska, A., Ball, S.L. & deWaard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London*, 270, 313–321.
<http://dx.doi.org/10.1098/rspb.2002.2218>
- Hicks, R.F. (1988) Harpacticoid copepods from biogenic substrata in offshore waters of New Zealand, I. New species of *Paradactylopodia*, *Stenhelia* (*St.*) and *Laophonte*. *Journal of the Royal Society of New Zealand*, 18, 437–452.
<http://dx.doi.org/10.1080/03036758.1988.10426467>
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468 pp.
<http://dx.doi.org/10.1163/193724092x00193>
- Huys, R., Fatih, F., Ohtsuka, S. & Llewellyn-Hughes, J. (2012) Evolution of the bomolochiform superfamily complex (Copepoda: Cyclopoida): New insights from ssrDNA and morphology, and origin of umazuracolidids from polychaete-infesting ancestors rejected. *International Journal of Parasitology*, 42, 71–92.
<http://dx.doi.org/10.1016/j.ijpara.2011.10.009>
- Huys, R., Llewellyn-Hughes, J., Conroy-Dalton, S., Olson, P.D., Spinks, J. & Johnston, D.A. (2007) Extraordinary host switching in siphonostomatoid copepods and the demise of the Monstrilloida: integrating molecular data, ontogeny and antennular morphology. *Molecular Phylogenetics and Evolution*, 43, 368–378.
<http://dx.doi.org/10.1016/j.ympev.2007.02.004>
- Huys, R., Llewellyn-Hughes, J., Olson, P.D. & Nagasawa, K. (2006) Small subunit rDNA and Bayesian inference reveal *Pectenophilus ornatus* (Copepoda *incertae sedis*) as highly transformed Mytilicolidae, and support assignment of Chondracanthidae and Xarifiidae to Lichomolgoidea (Cyclopoida). *Biological Journal of the Linnean Society*, 87, 403–425.
- Huys, R., MacKenzie-Dodds, J. & Llewellyn-Hughes, J. (2009) Cancrincolidae (Copepoda, Harpacticoida) associated with

- land crabs: a semiterrestrial leaf of the ameirid tree. *Molecular Phylogenetics and Evolution*, 51, 143–156. <http://dx.doi.org/10.1016/j.ympev.2008.12.007>
- Huys, R. & Mu, F.-H. (2008) Description of a new species of *Onychostenhelia* Itô (Copepoda, Harpacticoida, Miraciidae) from the Bohai Sea, China. *Zootaxa*, 1706, 51–68.
- Itô, T. (1979) Descriptions and records of marine harpacticoid copepods from Hokkaido, VII. *Journal of the Faculty of Science Hokkaido University, Zoology*, 22, 42–68.
- Itô, T. (1981) Descriptions and records of marine harpacticoid copepods from Hokkaido, VIII. *Journal of the Faculty of Science Hokkaido University, Zoology*, 22, 422–450.
- Karanovic, T. (2010) First record of the harpacticoid genus *Nitocrellopsis* (Copepoda, Ameiridae) in Australia, with descriptions of three new species. *International Journal of Limnology*, 46, 249–280. <http://dx.doi.org/10.1051/limn/2010021>
- Karanovic, T. & Cho, J.-L. (2012) Three new ameirid harpacticoids from Korea and first record of *Proameira simplex* (Crustacea: Copepoda: Ameiridae). *Zootaxa*, 3368, 91–127.
- Karanovic, T., Cho, J.-L. & Lee, W. (2012) Redefinition of the parastenocaridid genus *Proserpinicaris* (Copepoda:Harpacticoida), with description of three new species from Korea. *Journal of Natural History*, 46, 1573–1613. <http://dx.doi.org/10.1080/00222933.2012.681316>
- Karanovic, T. & Cooper, S.J.B. (2011a) Molecular and morphological evidence for short range endemism in the *Kinnecaris solitaria* complex (Copepoda: Parastenocarididae), with descriptions of seven new species. *Zootaxa*, 3026: 1–64.
- Karanovic, T. & Cooper, S.J.B. (2011b) Third genus of paratenocaridid copepods from Australia supported by molecular evidence (Copepoda, Harpacticoida). In: Defaye, D., Suárez-Morales, E & von Vaupel Klein, J.C. (Eds.), *Crustaceana Monographs, Studies on Freshwater Copepoda: a Volume in Honour of Bernard Dussart*, Brill, 293–337. <http://dx.doi.org/10.1163/ej.9789004181380.i-566.116>
- Karanovic, T. & Cooper, S.J.B. (2012) Explosive radiation of the genus *Schizopera* on a small subterranean island in Western Australia (Copepoda : Harpacticoida): unravelling the cases of cryptic speciation, size differentiation and multiple invasions. *Invertebrate Systematics*, 26, 115–192. <http://dx.doi.org/10.1071/is11027>
- Karanovic, T., Grygier, M. & Lee, W. (2013) Endemism of subterranean *Diacyclops* in Korea and Japan, with descriptions of seven new species of the *languidoides*-group and redescriptions of *D. brevifurcus* Ishida, 2006 and *D. suoensis* Itô, 1954 (Crustacea, Copepoda, Cyclopoida). *Zookeys*, 267, 1–76. <http://dx.doi.org/10.3897/zookeys.267.3935>
- Karanovic, T. & Hancock, P. (2009) On the diagnostic characters of the genus *Stygonitocrella* (Copepoda, Harpacticoida), with descriptions of seven new species from Australian subterranean waters. *Zootaxa*, 2324, 1–85.
- Karanovic, T. & Krajicek, M. (2012a) When anthropogenic translocation meets cryptic speciation globalised bouillon originates; molecular variability of the cosmopolitan freshwater cyclopoid *Macrocyclus albidus* (Crustacea: Copepoda). *International Journal of Limnology*, 48, 63–80. <http://dx.doi.org/10.1051/limn/2011061>
- Karanovic, T. & Krajicek, M. (2012b) First molecular data on the Western Australian *Diacyclops* (Copepoda, Cyclopoida) confirm morpho-species but question size differentiation and monophyly of the *alticola*-group. *Crustaceana*, 85, 1549–1569. <http://dx.doi.org/10.1163/156854012x651709>
- Karanovic, T. & Lee, W. (2012) A new species of *Parastenocaris* from Korea, with a redescription of the closely related *P. biwae* from Japan (Copepoda: Harpacticoida: Parastenocarididae). *Journal of Species Research*, 1, 4–34.
- Kim, K., Park, E. & Lee, W. (2011) First record of *Onychostenhelia bispinosa* (Copepoda: Harpacticoida: Miraciidae) from Korea. *Bulletin of the National Institute of Biological Resources*, 2, 55–65.
- Koomen, P. (1992) The integumental perforation pattern of the *Euchirella messinensis* female (Copepoda, Calanoida): Corrections, additions, intraspecific variation, and a checklist of pore sites. *Crustaceana*, 63, 113–159. <http://dx.doi.org/10.1163/156854092x00532>
- Kornev, P.N. & Chertoprud, E.C. (2008) *Copepod Crustaceans of the Order Harpacticoida of the White Sea: Morphology, Systematics, Ecology*. Biology Faculty, Moscow State University, Tovarishestvo Nauchnikh Izdaniy KMK, Moscow, 379 pp. [in Russian]
- Lang, K. (1948) *Monographie der Harpacticiden, 1-2*. Nordiska Bokhandeln, Lund, 1682 pp.
- Lang, K. (1965) Copepoda Harpacticoida from the Californian Pacific coast. *Kungl. Svenska Vetenskapsakademiens Handlingar*, 10, 1–560.
- Lee, C.E., Remfert, J.L. & Chang, Y.-M. (2007) Response to selection and evolvability of invasive populations. *Genetica*, 129, 179–192. <http://dx.doi.org/10.1007/s10709-006-9013-9>
- Lee, C.E., Remfert, J.L. & Gelembiuk, G.W. (2003) Evolution of physiological tolerance and performance during freshwater invasions. *Integrative and Comparative Biology*, 43, 439–449.
- Lee, W. & Karanovic, T. (2012) Editorial: Biodiversity of invertebrates in Korea. *Zootaxa*, 3368, 5–6.
- Lee, W., Park, E. & Song, S.J. (2012) *Invertebrate Fauna of Korea, 21 (11), Marine Harpacticoida*. National Institute of Biological Resources, Ministry of Environment, South Korea, 276 pp.
- Lefébure, T., Douady, C.J., Gouy, M. & Gibert, J. (2006) Relationship between morphological taxonomy and molecular

- divergence within Crustacea: Proposal of a molecular threshold to help species delimitation. *Molecular Phylogeny and Evolution*, 40, 435–447.
<http://dx.doi.org/10.1016/j.ympev.2006.03.014>
- Ma, L. & Li, X.-Z. (2011) *Delavalia qingdaoensis* sp. nov. (Harpacticoida, Miraciidae), a new copepod species from Jiaozhou Bay, Yellow Sea. *Crustaceana*, 84, 1085–1097.
<http://dx.doi.org/10.1163/001121611x584334>
- Malt, S.J. (1983) Polymorphism and pore signature patterns in the copepod genus *Oncaea* Philippi, 1843. *Journal of the Marine Biological Association of the United Kingdom*, 63, 449–466.
<http://dx.doi.org/10.1017/s002531540007079x>
- Marinov, T.M. & Apostolov, A.M. (1981) Contribution à l'étude des Copépodes Harpacticoides de la mer Adriatique (côte yougoslave), I. Le genre *Stenhelia* Boeck. *Acta Zoologica Bulgarica*, 17, 66–72.
- Mauchline, J. (1977) The integumental sensilla and glands of pelagic Crustacea. *Journal of the Marine Biological Association of the United Kingdom*, 57, 973–994.
<http://dx.doi.org/10.1017/s0025315400026060>
- Mu, F.-H. & Huys, R. (2002) New species of *Stenhelia* (Copepoda, Harpacticoida, Diosaccidae) from the Bohai Sea (China) with notes on subgeneric division and phylogenetic relationships. *Cahiers de Biologie Marine*, 43, 179–206.
- Por, F. (1964) Littorale Harpacticoiden der Norwest-Küsten des Schwarzen Meeres. *Travaux du Muséum d'Histoire Naturelle "Gr. Antipa"*, 2, 97–143.
- Por, F.D. (1964) A study of the Levantine and Pontic Harpacticoida (Crustacea, Copepoda). *Zoologische Verhandlungen*, 64, 1–128.
- Sakaguchi, S.O. & Ueda, H. (2010) A new species of *Pseudodiaptomus* (Copepoda: Calanoida) from Japan, with notes on the closely related *P. inopinus* Burckhardt, 1913 from Kyushu Island. *Zootaxa*, 2612, 52–68.
- Scott, A. (1902) On some Red Sea and Indian Ocean Copepoda. *Proceedings and Transactions of the Liverpool Biological Society*, 16, 397–428.
- Soyer, J. (1971) Contribution à l'étude des Copépodes Harpacticoides de Méditerranée occidentale, 5. *Stenhelia* (*Delavalia*) *coineauae* n. sp. *Stenhelia* (*D.*) *bocqueti* n. sp. et *Typhlamphiascus bouligandi* n. sp. (Diosaccidae, Sars). *Vie et Milieu*, 22, 263–280.
- Stock, J.K. & von Vaupel Klein, J.C. (1996) Mounting media revisited: the suitability of Reyne's fluid for small crustaceans. *Crustaceana*, 69, 749–798.
<http://dx.doi.org/10.1163/156854096x00826>
- Strickler, R. (1975) Intra- and interspecific information flow among planktonic copepods: Receptors. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 19, 2951–2958.
- Walter, T.C. & Boxshall, G. (2013) World Copepoda database. Available from: <http://www.marinespecies.org/copepoda/aphia.php?p=taxdetails&id=115135> (accessed 21 March 2011)
- Wells, J.B.J. (1967) The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Transactions of the Royal Society of Edinburgh*, 67, 189–358.
- Wells, J.B.J. (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida. *Zootaxa*, 1568, 1–872.
- Wells, J.B.J. & Chandrasekhara Rao, G. (1987) Littoral Harpacticoida (Crustacea: Copepoda) from Andaman and Nicobar Islands. *Memoirs of the Zoological Survey of India*, 16 (4), 1–385.
- Willen, E. (2000) *Phylogeny of the Thalestridimorpha Lang, 1944 (Crustacea, Copepoda)*. Cuvillier Verlag, Goettingen, 233 pp.
- Willen, E. (2002) Notes on the systematic position of the Stenheliinae (Copepoda, Harpacticoida) within the Thalestridimorpha and description of two new species from Motupore Island, Papua New Guinea. *Cahiers de Biologie Marine*, 43, 27–42.
- Willen, E. (2003) A new species of *Stenhelia* (Copepoda, Harpacticoida) from a hydrothermal, active, submarine volcano in the New Ireland Fore-Arc system (Papua New Guinea) with notes on deep sea colonization within the Stenheliinae. *Journal of Natural History*, 37, 1691–1711.
<http://dx.doi.org/10.1080/00222930110114437>
- Wilson, M.S. (1965) North American harpacticoid copepods, 7. A new species of *Stenhelia* from Nuwuk Lake on the Arctic Coast of Alaska. *Proceedings of the Biological Society of Washington*, 78, 179–188.
- Winkler, G., Dodson, J.J. & Lee, C.E. (2008) Heterogeneity within the native range: population genetic analyses of sympatric invasive and noninvasive clades of the freshwater invading copepod *Eurytemora affinis*. *Molecular Ecology*, 17, 415–430.
<http://dx.doi.org/10.1111/j.1365-294x.2007.03480.x>
- Wyngaard, G.A., Holynska, M. & Schulte, J.A. II (2010) Phylogeny of the freshwater copepod *Mesocyclops* (Crustacea: Cyclopidae) based on combined molecular and morphological data, with notes on biogeography. *Molecular Phylogenetics and Evolution*, 55, 753–764.
<http://dx.doi.org/10.1016/j.ympev.2010.02.029>