Taxonomic review of the genus *Stenocaris* Sars (Copepoda: Harpacticoida, Cylindropsyllidae), with (re)descriptions of two *Stenocaris* species from the Far East (#75601)

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Taxonomic review of the genus *Stenocaris* Sars (Copepoda: Harpacticoida, Cylindropsyllidae), with (re)descriptions of two *Stenocaris* species from the Far East

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The taxonomic concept of the genus *Stenocaris* Sars, 1909 is uncertain because none of the synapomorphies for *Stenocaris* species are defined. Detailed comparison of previous records of *Stenocaris minor* (T. Scott, 1892) from different localities reveals that this species represents a species complex composed of two species, *S. minor* s. str. and *S. minor* sensu Cottarelli & Venanzetti, 1989. Because the latter species has fundamental differences in the nature of the fifth leg in females and the sexual dimorphism of the second leg, we newly name it *S. figaroloensis* sp. nov. We also suggest that *S. minor* sensu Apostolov, 1971, *S. minor* sensu Marinov, 1971, and *S. minor* sensu Apostolov & Marinov, 1988 from the Black Sea and *S. minor* sensu Wilson, 1932 from North America should be relegated to *species inquirenda* in the genus. Taxonomic review of the morphology of all *Stenocaris* species indicated that the generic concept must be restricted to accommodate *S. minor* s. str., *S. gracilis* Sars, 1909, *S. intermedia* Itô, 1972, and the South Korean new species, *S. marcida* sp. nov. based on a significant synapomorphy that is a confluent condition of the fifth leg in males. As a result of our analysis, two *Stenocaris* species, *S. baltica* Arlt, 1983 and *S. pygmaea* Noodt, 1955, are transferred to the genus *Vermicaris* Kornev & Chertoprud, 2008 as *V. baltica* (Arlt, 1983) comb. nov. and *V. pygmaea* (Noodt, 1955) comb. nov. based on the affinities in a reduced condition of the second and fifth legs. Additionally, *S. arenicola* Wilson, 1932 and *S. kliei* (Kunz, 1938) are allocated to a new genus, *Huysicaris* gen. nov., mainly characterized by distinct caudal rami with a recurved dorsal spinous process and convex inner margins, as *H. arenicola* (Wilson, 1932) comb. nov. and *H. kliei* (Kunz, 1938) comb. nov. A marine interstitial harpacticoid collected from the subtidal substrate off Dok-do Island in the East Sea of South Korea is proposed as *S. marcida* sp. nov. and the distribution of *S. intermedia* originally known from Japanese waters is newly reported in this area based on the Korean and Russian specimens. We provide their detailed descriptions and illustrations and discuss the morphological characters supporting their identities.

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Abstract

The taxonomic concept of the genus *Stenocaris* Sars, 1909 is uncertain because none of the synapomorphies for *Stenocaris* species are defined. Detailed comparison of previous records of *Stenocaris minor* (T. Scott, 1892) from different localities reveals that this species represents a species complex composed of two species, *S. minor* s. str. and *S. minor* sensu Cottarelli & Venanzetti, 1989. Because the latter species has fundamental differences in the nature of the fifth leg in females and the sexual dimorphism of the second leg, we newly name it *S. figaroloensis* sp. nov. We also suggest that *S. minor* sensu Apostolov, 1971, *S. minor* sensu Marinov, 1971, and *S. minor* sensu Apostolov & Marinov, 1988 from the Black Sea and *S. minor* sensu Wilson, 1932 from North America should be relegated to *species inquirenda* in the genus. Taxonomic review of the morphology of all *Stenocaris* species indicated that the generic concept must be restricted to accommodate *S. minor* s. str., *S. gracilis* Sars, 1909, *S. intermedia* Itô, 1972, and the South Korean new species, *S. marcida* sp. nov. based on a significant synapomorphy that is a confluent condition of the fifth leg in males. As a result of our analysis, two *Stenocaris* species, *S. baltica* Arlt, 1983 and *S. pygmaea* Noodt, 1955, are transferred to the genus *Vermicaris* Kornev & Chertoprud, 2008 as *V. baltica* (Arlt, 1983) comb. nov. and *V. pygmaea* (Noodt, 1955) comb. nov. based on the affinities in a reduced condition of the second and fifth legs. Additionally, *S. arenicola* Wilson, 1932 and *S. kliei* (Kunz, 1938) are allocated to a new genus, *Huysicaris* gen. nov., mainly characterized by distinct caudal rami with a recurved dorsal spinous process and convex inner margins, as *H. arenicola* (Wilson, 1932) comb. nov. and *H. kliei* (Kunz, 1938) comb. nov. A marine interstitial harpacticoid collected from the subtidal substrate off Dok-do Island in the East Sea of South Korea is proposed as *S. marcida* sp. nov. and the distribution of *S. intermedia* originally known from Japanese waters is newly reported in this area based on the Korean and Russian specimens. We provide their detailed descriptions and illustrations and discuss the morphological characters supporting their identities.

Keywords. *Huysicaris* gen. nov., *Huysicaris arenicola* (Wilson, 1932) comb. nov., *Huysicaris kliei* (Kunz, 1938) comb. nov., interstitial meiofauna, Korean waters, Russian waters, *Stenocaris figaroloensis* sp. nov., *Stenocaris marcida* sp. nov.

Introduction

Harpacticoids are the second-most species-rich and abundant group in the meiofaunal community after nematodes (*Hicks & Coull, 1983*). They exhibit diverse morphological adaptations for being colonized in benthic habitats, e.g., endobenthic species have specialized thoracic appendages or a well-developed rostrum to facilitate burrowing (*Gee & Huys, 1996*; *Corgosinho, 2012*; *Kim & Lee, 2020*), and interstitial species ~~have evolved with~~ three morphological trends to swim or crawl within the lacunae between sediment particles: miniaturization of body size, elongation along the body axis, and reduction of the setal armature ~~in~~ the thoracic legs (*Noodt, 1971*; *Martínez Arbizu & Moura, 1994*; *Huys & Conroy-Dalton, 2006a*; *Corgosinho, 2012*).

The family Cylindropsyllidae Sars, 1909, currently comprising 39 species in 13 genera, is a representative of mesopsammic harpacticoids (*Richer, 2019*). Members of this family have an interstitial lifestyle and exhibit the above morphological trends except for miniaturization, ~~as~~ a cylindrical or vermiform habitus without a distinct ~~contraction~~ between the prosome and urosome, and slender swimming legs with reduced segmentation and setal armature (*Huys & Conroy-Dalton, 2006a*; *Richter, 2019*). These morphological features likely enhance their flexibility and ability to wriggle ~~from~~ sand grains ~~to~~ shell gravel in shallow coastal and sublittoral environments (*Huys, 1988*; *Huys & Conroy-Dalton, 1993, 2006a*; *Huys & Lee, 2018*), but some species have been documented in deep-sea mud (*Becker et al., 1979*; *Moura & Pottek, 1998*; *Richter, 2019*). *Huys (1992)* reported a strong correlation between the distribution of cylindropsyllid species and sediment conditions. ~~The cylindropsyllid copepods~~ are also morphologically characterized by sexual dimorphism of the second and third swimming legs in the male and the fifth leg forming a single plate in both sexes (*Huys, 1988*).

Since *Lang*'s *(1948)* familial concept of the Cylindropsyllidae (~~as~~ a subfamily at that time), the genus *Stenocaris* Sars, 1909 had until the 1970s served as a repository to accommodate more advanced cylindropsyllid harpacticoids (*i.e.*, retaining a slender-type maxilliped with a geniculate claw, a non-prehensile endopod of the first leg, the second and third legs with reduced endopod segmentation), ~~and~~ without ~~a~~ morphologic or phylogenetic inference. Therefore, the monophyly of this genus is questionable (*Huys, 1988*; *Huys & Conroy-Dalton, 1993, 2006b*) and apomorphies ~~are not~~ defined (*Richter, 2019*). These taxonomical problems were partially resolved by the following contributions. *Apostolov (1982)* established a new genus *Stenocaropsis* Apostolov, 1982 to accommodate *Stenocaris pristina* Wells, 1968 and *Stenocaris valkanovi* Marinov, 1974 ~~having~~ a two-segmented endopod on the second and third legs against *Sars*'s *(1909)* generic diagnosis ~~representing~~ the one-segmented ~~conditions~~. However, he questionably retained two deep-sea species, *Stenocaris abyssalis* Becker, Noodt & Schriever, 1979 and *Stenocaris profundus* Becker, Noodt & Schriever, 1979, which have the same endopodal segmentation as *Stenocaropsis*~~, in *Stenocaris*~~. Although *Kunz (1994)* assigned the latter two deep-sea species to *Stenocaropsis*, *Moura & Pottek (1998)* established a new genus *Selenopsyllus* Moura & Pottek, 1998 for *Becker et al.*'s *(1979)* two deep-sea species and two new Antarctic species, *Selenopsyllus dahmsi* Moura & Pottek, 1998 and *Selenopsyllus* *antarcticus* Moura & Pottek, 1998. The latter were characterized by a six-segmented female antennule~~,~~ at most, with an aesthetasc on the third segment (*Moura & Pottek*, *1998*). *Huys & Conroy-Dalton (1993)* transferred *Stenocaris kerguelenensis* Bodiou, 1977 to a new monophyletic genus *Navalonia* Huys & Conroy-Dalton, 1993. *Kornev & Chertoprud (2008)* removed *Stenocaris minuta* Nicholls, 1935 and *Stenocaris pontica* Chappuis & Serban, 1953, and placed them in a new genus *Vermicaris* Kornev & Chertoprud, 2008. As a result of these efforts, *Stenocaris* currently comprises seven valid species: *Stenocaris minor* (T. Scott, 1892), *S. gracilis* Sars, 1909 (type species; *cf*. *Huys*, *2009*: 98), *S. arenicola* Wilson, 1932, *S. kliei* Kunz, 1938, *S. pygmaea* Noodt, 1955 [*Apostolov (1972)* and *Apostolov & Marinov (1988)* considered it a junior synonym of *V. pontica* (Chappuis & Serban, 1953), but it was reinstated as a valid species of *Stenocaris* by *Huys & Conroy-Dalton (1993*: 295*)*], *S. intermedia* Itô, 1972, and *S. baltica* Arlt, 1983. However, their phylogenetic relationship is still unclear.

~~In South Korean waters, research focusing~~ on the marine harpacticoid family Cylindropsyllidae has been limited ~~in terms of ecological work~~. *Back et al*. *(2009)* reported the family in a sublittoral environment off Sungap-do Island in the Yellow Sea during a survey of the meiofaunal community in a sand-mining area. The following sections provide a taxonomical report of the family in this area based on the specimens identified as *S. intermedia* and a new *Stenocaris* species from the subtidal sediments of the East Sea (including Russian waters), describe the morphological characteristics supporting their identities, and review the phylogenetic relationships among *Stenocaris* species to resolve ~~a taxonomic problem regarding~~ the polyphyly of the genus.

Material & Methods

Sediment samples were collected from the sublittoral ~~substrata~~ off Ulleung-do and Dok-do Islands (South Korean~~ waters~~) and the coast of Primorsky (Russian~~ waters~~) in the East Sea (Sea of Japan) via scuba diving (depths of 8.0–30.5 m) or a Smith-McIntyre grab (depth of 73.3 m) (Fig. 1). These field samplings were approved by the National Marine Biodiversity Institute of Korea (MABIK) and the National Institute of Biological Resources (NIBR). Samples were immediately preserved in 95% ethanol or 10% formalin solution ~~in the field~~. In the laboratory, they were filtered through a 50-μm sieve under tap water. Harpacticoid copepods were removed using a Pasteur pipette under a Leica M165 C stereomicroscope. Specimens of two *Stenocaris* species were prepared and mounted in lactic acid on a temporary reverse slide (*Humes & Gooding*, *1964*). Line drawings of the whole specimen and its dissected appendages were ~~created~~ using a camera lucida on an Olympus BX53 compound microscope equipped with a differential interference contrast objective. Total body length was measured from the anterior tip of the rostrum to the posterior end of the caudal rami ~~on a~~ lateral view using an Olympus DP28 microscope camera. After morphological examination, the dissected parts were transferred to and permanently mounted in glycerin on Higgins-Shirayama (H-S) slides comprising two coverslips (*Shirayama et al*., *1993*). The slides were deposited in MABIK or NIBR in South Korea. Maps of sampling stations and the distribution of *Stenocaris* species were generated using Ocean Data View ver. 5.6.1 (*Schlitzer*, *2022*).

We follow *Huys et al. (1996)* for the morphological terminology of the body and appendages, and the setal armature formulae of swimming legs. Abbreviations used in the text and figure captions are as follows: acro, acrotheck composed of one aesthetasc and two setae (fused basally); ae, aesthetasc; EXP(ENP)1(2, 3), first (second, third) exopodal (endopodal) segment; P1–P6, first to sixth thoracic legs. We also follow *Huys & Conroy-Dalton (2006b)*'s designations for armature elements on the fifth leg (innermost = seta *a*, second innermost = seta *b* … outermost = seta *h* in females and seta *f* in males) to compare their positions and modifications in other genera or species.

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Results

Taxonomy

Phylum Arthropoda von Siebold, 1848
Subphylum Crustacea Brünnich, 1772
Subclass Copepoda Milne-Edwards, 1840
Order Harpacticoida Sars, 1903
Family Cylindropsyllidae Sars, 1909
Genus *Stenocaris* Sars, 1909

Amended diagnosis.—Cylindropsyllidae. Habitus slender, cylindrical. Rostrum triangular, as long as first antennular segment, defined at base. Genital double-somite in ♀ completely fused. Anal somite as long as penultimate somite. Caudal rami elongate, at least 2.5 times as long as wide; seta I diminutive, principal seta V styliform or composite in ♀. Antennule six- or seven-segmented, with aesthetasc on fourth and terminal segments in ♀, haplocer and nine- or ten-segmented in ♂; second segment distinctly elongated in both sexes. Antenna with allobasis; exopod one-segmented, bearing 2 terminal setae. Mandibular palp two-segmented, uniramous, with one seta on basis, and one lateral and three or four distal setae on endopod. Maxillule with two setae on coxal endite; exopod and endopod represented by two setae and three or four setae, respectively. Maxilla with two syncoxal endites and one-segmented endopod. Maxilliped well-developed, with geniculate endopodal claw. P1 endopod non-prehensile; ENP2 with one small and two long setae. P2–P4 exopods three-segmented; P2–P3 EXP3 with two outer spines and P4 EXP3 with one or two outer spines; P2 EXP3 without and P3–P4 EXP3 with one inner seta; P2 EXP3 in ♂ strongly modified, as long as EXP1 and EXP2 combined, with wavy inner margin, and one stout and distally recurved apical spine, and lacking inner element; P4 exopod longer than those of P2–P3. Endopods in ♀ one-segmented in P2–P3 and two-segmented in P4. P2 in ♂ with spinous anterior process on basis and two-segmented endopod. P3 in ♂ with two-segmented endopod; ENP1 with apophysis in *S. minor* and *S. figaroloensis* sp. nov., but without in others; ENP2 modified ~~as~~ stout apophysis in *S. gracilis* and *S. intermedia*, subovate in *S. minor* and *S. figaroloensis* sp. nov., and with spinose projection in *S. marcida* sp. nov. Setal armature of P1–P4 as follows:

	exopod	endopod
P1	0.0.112	1.120
P2	0.0.022 [0.0.022 in ♂]	11–20 [1.010 in ♂]
P3	0.0.122	01–20 [0.apo10 or apo.010 in ♂]
P4	0.0.121–2	0.0–110

P5 forms a single plate in both sexes, with seven distal elements in ♀, of which innermost one spine-like (fused basally in *S. gracilis*, *S. intermedia* and *S. marcida* sp. nov.) and second innermost one spine-like (seta-like in *S. minor* and *S. figaroloensis* sp. nov.), and five distal setae in ♂; baseoendopods separate in ♀, but fused medially in ♂.

P6 with two or three setae in ♀ and three setae in ♂.

Type species.—*Stenocaris gracilis* Sars, 1909

Other species.—*S. minor* (T. Scott, 1892), *S. intermedia* Itô, 1972, *S. figaroloensis* sp. nov., and *S. marcida* sp. nov.

Remarks.—See the discussion (below) on a *Stenocaris minor* species complex, and taxonomic positions of *S. arenicola*, *S. baltica*, *S. kliei*, and *S. pygmaea*.

Stenocaris marcida sp. nov.

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Figs. 2–7

Type locality.—Sublittoral sandy sediments ~~(37°14'5.63"N 131°51'43.19"E)~~ off Dok-do Island ~~of~~ Korea~~, water depth~~ 73.3 m).

Type material.—Holotype: ♀ dissected on 11 slides (MABIK CR 00001) collected from the type locality, ~~J.G. Kim leg.,~~ November 2, 2018. Allotype: ♂ dissected on eight slides (MABIK CR 00002), collection data as a holotype. Paratypes: 3♀♀, 2♂♂ (MABIK CR 00003) preserved together in a vial with 99% ethanol, collection data as a holotype.

Description of female (based on the holotype MABIK CR 00001).—Total body length about 736.0 µm (length range = 736.0–842.8 µm; mean = 786.7 µm, n =4); habitus (Fig. 2A, B) slender, cylindrical, without distinct separation between prosome and urosome. Integument of cephalothorax, all somites and caudal rami pitted, with several sensilla and pores except for penultimate somite. Posterior border~~s~~ of cephalothorax and all somites with smooth hyaline frill. Cephalothorax occupying 25% of body length, slightly tapering anteriorly in dorsal aspect. P5-bearing somite longer than third free pedigerous somite. Genital double-somite completely fused, longer than preceding somite; genital pores (Fig. 4G) separate, each covered by small plate bearing two setae (representing P6); mid-ventral copulatory pore located at same level of genital pores, probably covered by membrane with opening (Fig. 4G). Two free urosomites and anal somite slightly tapering posteriorly. Anal somite elongate, as long as penultimate somite, with one pair of dorsal sensilla and three pairs of ventrolateral pores; operculum wide, with smooth posterior margin.

Rostrum (Figs. 2A, 3A) prominent, triangular, defined at base, not exceeding first ~~antennary~~ segment, slightly longer than maximum width; with one pair of subapical sensilla.

Caudal rami (Fig. 2A–D) slightly divergent, as long as anal somite, about 3.1 times as long as maximum width; medial margin slightly concave in dorsal view; dorsal surface with one pore subdistally, and ventral surface with one pore proximally and one pore subdistally; with seven setae: setae I and II inserted in distal fifth of lateral margin at same level; seta I diminutive, noticeable at high magnification; seta II as long as caudal ramus; seta III arising from dorsal surface subdistally, about 1.3 times longer than caudal ramus; terminal setae IV and V fused basally; seta IV slender, about 1.5 times as long as caudal ramus; principal seta V composite, ~~composed of styliform, which~~ slightly shorter than seta IV, ~~in proximal part,~~ and long slender ~~seta in~~ distal part; seta VI short, ventrally inserted in distal margin; seta VII tri-articulate basally, arising ~~from half~~ of caudal rami on dorsal surface, slightly shorter than caudal ~~rami~~.

Antennule (Fig. 3A) slender, longer than cephalothorax, seven-segmented. First segment small, with one small seta ventrally. Second segment elongated, about 5.9 times as long as preceding one, with two bi-articulate and six slender setae, and one tube pore. Third segment small, twice as long as wide, with four bi-articulate setae. Fourth segment smaller than preceding one, with one seta and one distal peduncle bearing one aesthetasc and one small seta. Fifth segment smaller than preceding one, with one seta. Sixth segment smallest, with one seta. Terminal segment slightly longer than two preceding ones combined, tapering distally, with one seta, six bi-articulate setae, and one acrothek. Setal formula: 1-[1], 2-[8], 3-[4], 4-[1 + (1 + ae)], 5-[1], 6-[1], 7-[7 + acro].

Antenna (Fig. 4A). Coxa small, unornamented. Allobasis elongate, 3.8 times as long as maximum width. Exopod arising ~~from~~ proximal third of allobasis, one-segmented, slender, with two long setae distally. Free endopodal segment elongate; ~~abexopodal~~ margin with two unipinnate spines, one spinule, and one group of spinules; distal margin oblique, with one delicate seta, two pinnate spines, and three geniculate setae, of which outermost one spinulose and fused to one delicate seta; with ~~two~~ hyaline frill~~s~~ distally ~~or~~ subdistally.

Mandible (Fig. 4B). Coxa well-developed, transversely elongate, with one medial bulge; gnathobase with one bicuspidate and three multicuspidate teeth, and one unipinnate seta ~~which~~ fused to one stout spine. Palp uniramous, two-segmented; basis elongate, about 4.6 times as long as wide, with one subdistal seta; endopod elongate, twice as long as wide, with one lateral seta, and two distal sets of two setae basally fused.

Maxillule (Fig. 4C). Praecoxa with one row of posterior spinules; arthrite well-developed, with seven spines distally and two pinnate setae subdistally, and one long and one small seta anteriorly. Coxa small, unornamented; cylindrical endite with one spinulose and one bare seta. Basis with one row of spinules both posteriorly and anteriorly; distal margin with one spinulose and three bare setae; subdistal endite with two bare setae. Exopod and endopod represented by two and three bare setae, respectively.

Maxilla (Fig. 4D). Syncoxa unornamented, with two endites: proximal endite with one unipennate spine, and one bare and one unipinnate seta distally; distal endite with three unipinnate setae. Allobasis drawn out into stout claw, with spinules subdistally and two setae proximally. Endopod one-segmented, with four distal setae.

Maxilliped (Fig. 4E). Syncoxa elongate, 2.7 times as long as wide, subdistally with one unispinulose seta. Basis longer than preceding ~~one~~, 2.8 times longer than maximum width, with one outer spinule subdistally. Endopod small, with one unipinnate and geniculate claw.

P1 (Fig. 3B). Praecoxa large, triangular, unornamented. Coxa rectangular, about 0.6 times as long as broad, pitted, with one row of anterior setules; posterior surface with three rows of spinules. Basis smaller than preceding ~~one~~, with one row of antero-distal spinules, one anterior pore, and one long inner seta (uniplumose distally); outer seta absent. Exopod three-segmented, slightly longer than endopod, with spinular ornamentation along outer margins; length ratio of EXP1–EXP3 1: 0.81 : 0.78; EXP1 and EXP2 with one small unipinnate outer spine~~, respectively~~; EXP3 with four unispinulose spines, of which distal and inner ones geniculate. Endopod reaching ~~mid-length~~ of EXP3, two-segmented, with outer spinular ornamentation; ENP1 elongate, slightly exceeding distal end of EXP1, with one unipinnate seta posteriorly; ENP2 slender, as long as preceding ~~one~~, distally with one unipinnate ~~and~~ geniculate spine and one long geniculate seta (uniplumose proximally), and posteriorly with one small bare seta.

P2 (Fig. 5A). Praecoxa small, unornamented. Intercoxal sclerite subrectangular, distal margin concave. Coxa rectangular, pitted, unornamented. Basis smaller than preceding ~~one~~, with one bare outer seta and one anterior pore. Exopod three-segmented, much longer than endopod; length ratio of EXP1–EXP3 1: 0.66: 1.05; EXP1 and EXP2 with spinular ornamentation along outer margin subdistally and surface frill ~~on inner margin~~, spinous process bearing anterior spinules distally, and unipinnate outer spine, respectively; EXP3 with spinular ornamentation along outer and distal margins, two unipinnate outer spines, and two pinnate distal spines, of which inner one ornamented with more distinct spinules. Endopod one-segmented, reaching distal fourth of EXP1, 3.6 times as long as broad, with one pinnate spine distally, one small bare posterior seta subdistally, and one long serrate posterior seta proximally.

P3 (Fig. 5B). ~~Protopod~~ and intercoxal sclerite as in P2, but ~~reduced in size~~ than in P2; ~~length of~~ outer seta ~~on~~ basis longer than those of P2 and P4. Ornamentation and segmentation of both rami ~~similar~~ in P2. Length ratio of EXP1–EXP3 1: 0.66: 1.19; exopodal armature as in P2 except for presence of one uniserrate inner seta in EXP3. ENP1 not exceeding ~~mid-length~~ of EXP1, with one stout pinnate spine distally and one small posterior seta subdistally.

P4 (Fig. 5C). ~~Protopod~~ and intercoxal sclerite ~~similar~~ in P2 and P3, but ~~reduced in size~~ than in P2 and P3. Exopod longer than in P2 and P3; length ratio of EXP1–EXP3 1: 0.97: 0.65; EXP1 with three groups of outer spinules, outer distal corner not produced, with one row of stout spinules, and distal hyaline frill expanded roundly; ornamentation of EXP2 as in EXP1 except for presence of only one group of outer spinules; EXP1 and EXP2 with one pinnate outer ~~spine, respectively~~; EXP3 with distal hyaline frill, two pinnate outer spines, two pinnate distal spines, and one uniserrate inner seta.

P5 (Fig. 4F). Exopod ~~fused into~~ baseoendopod forming a single plate; with eight elements: seta *a* spiniform, fused to baseoendopod, serrate subdistally; other setae setiform, setae *b*, *d*, *e* longer than others, and seta *c* half length of seta *b*, and seta *f* ~~smallest~~; seta *h* ~~(derived from baseoendopod)~~ very long, bi-articulate basally, ~~and~~ uniplumose distally.

Description of male (based on allotype MABIK CR 00002). ~~Total body length~~ slightly ~~smaller~~ than females, about 702.0 µm (range = 698.5–744.1 µm; mean = 714.9 µm, n = 3); habitus (Fig. 6A) as in females, ~~but show differences in~~ the following characters.

Cephalothorax (Fig. 6A) with mid-dorsal integumental window.

Urosome (Figs. 6A, 7A) six-segmented, genital somite and ~~second~~ urosomite separated; spermatophore elongate, about 1/5 of body length.

Caudal rami (Figs. 6A, 7A). Seta III 1.8 times as long as caudal ramus. Seta V composite composed of slender and elongate spine proximally and flagellate distally.

Antennule (Fig. 6B) haplocer, ten-segmented, with geniculation between seventh and eighth segments. First segment small, posteriorly with one patch of minute spinules, one row of spinules, and one bare seta. Second segment longest, with one tube pore, one uniplumose, one bi-articulate, and seven bare setae. Third segment small, with one bi-articulate and six bare setae; outer margin concave. Fourth segment smaller than preceding one, with two setae. Fifth segment swollen, with one uniplumose, one bi-articulate and three setae, and one distal peduncle bearing one long aesthetasc and one bare seta (fused basally). Sixth segment small, with one long and one small uniplumose seta. Seventh segment elongate, slightly curved inwardly, with one uniplumose and two bare setae. Eighth segment slightly shorter than preceding one, with one minute seta. Ninth segment smallest, unarmed. Terminal ~~one~~ as long as seventh segment, tapering distally, with one bare and six bi-articulate setae, and ~~one~~ acrothek. Setal formula: 1-[1], 2-[9], 3-[7], 4-[2], 5-[5 + (1 + ae)], 6-[2], 7-[3], 8-[1], 9-[0], 10-[7 + acro].

P2 (Fig. 7B). Basis with spinose inner process anteriorly. EXP3 elongate, 0.85 times as long as EXP1 and EXP2 combined, uneven along inner margin, with three pinnate outer spines and one modified distal seta~~; distal seta stout,~~ recurved distally, ~~bearing~~ one row of ~~oblique~~ minute spinules. Endopod two-segmented, not exceeding ~~mid-length~~ of EXP2; ENP1 with convex inner margin and one distally serrate seta posteriorly; ENP2 1.7 times as long as preceding ~~one~~, with one small ~~and~~ distally recurved seta ~~on distal margin~~.

P3 (Fig. 7C). Basis with one row of anterior spinules proximally and distally. Endopod two-segmented, not ~~exceeding~~ distal end of EXP1; ENP1 small, slightly longer than ~~width~~, unarmed; ENP2 about 1.5 times as long as preceding ~~one~~, with one small and stout distal seta, and one spinose projection on inner margin.

P5 (Fig. 5D). Baseoendopods of right and left legs fused medially; each with one lateral and three anterior pores. Exopod ~~fused to~~ baseoendopod forming a single plate, tapering distally, with truncate distal end; with six elements: seta *a* smallest, seta b twice as long as rami length, seta c slightly shorter than seta b, setae d and e slightly longer than seta *a*, and seta *f* ~~(derived from baseoendopod)~~ three times as long as ramus ~~length~~, bi-articulate basally, ~~and~~ uniplumose distally.

P6 (Fig. 7A) asymmetrical, each represented by small plate, with one bi-articulate and two bare setae, of which middle one longest.

Variability.—Several female specimens have styliform caudal seta V by being broken off the distal part (~~flagellate seta;~~ see Fig. 2D). This could lead to the misconception that the female's caudal seta V ~~are~~ styliform.

Etymology.—The specific name is derived from the Latin adjective *marcidus*, meaning withered, and alludes to the relatively short seta on the male P3 ENP2. It is nominative singular, ~~and of feminine gender~~.

Remarks.—*Stenocaris marcida* sp. nov. resembles *S. minor* s. str. in ~~that it shares the significant characteristics of a~~ seven-segmented female antennule ~~segmentation~~ and armature of swimming legs, and the ~~presence of~~ setiform seta *b* (= second innermost seta) on female P5. However, the new species is characterized by the following structures: (1) seta *a* (= innermost spine) on female P5 is fused to segment, and distally serrate and blunt (~~whereas~~ *S. minor* s. str. ~~is defined and pinnate~~); (2) a distal spine, which is stout and distally recurved, on male P2 EXP3 is slightly shorter than P2 EXP1 (~~which is~~ very long, distinctly longer than P2 EXP1 and EXP2 combined in *S. minor* s. str.); (3) male P2 EXP3 ~~is~~ approximately twice as long as EXP2 (~~and~~ slightly longer than ~~the latter segment~~ in *S. minor* s. str.); (4) male P2 ENP2 ~~is~~ approximately twice as long as ENP1, bearing a small distal spine, which is setule-like in the distal part (~~and~~ slightly longer than ~~the preceding one~~, ~~bearing~~ a long and pinnate seta in *S. minor* s. str.); (5) the sexual dimorphism of male P3 ~~differs between them~~ in that~~, in~~ *S. marcida* sp. nov.~~, male P3 ENP2~~ exhibits an apophysis of a small spinose process and has a spine-like seta shorter than the distal segment, while, in *S. minor* s. str., a stout apophysis appears in P3 ENP1, and subovate ENP2 has a long and slender distal seta; (6) caudal seta V is ~~a~~ composite composed of a styliform ~~in the~~ proximal part and a slender ~~seta in the~~ distal part (~~whereas~~ it is ~~likely~~ non-composite~~,~~ in both sexes~~,~~ in *S. minor* s. str.). In addition, ~~*S. minor* s. str. has very small and bulbous~~ caudal seta VI in both sexes~~,~~ whereas it is ~~nominal~~ in the new species.

The new species shares sexual dimorphism ~~features on~~ P3 with *S. gracilis* and *S. intermedia*, suggesting a close relationship. However, *S. marcida* sp. nov. is readily distinguishable from them by ~~a~~ combination of the female seven-segmented antennule (*vs.* six-segmented), male P3 ENP2 with a small spinous process (*vs.* absent, but the segment drawn out into an apophysis), and the setiform seta *b* on the female P5 (*vs.* spiniform).

Stenocaris intermedia Itô, 1972

Figs. 8–12.

Stenocaris intermedia Itô, *1972*: p. 323, Figs. 13–16; *Kornev & Chertoprud*, *2008*: p. 280, Fig. 146E.

Material examined: 2♀♀, 1♂ (NIBR IV 00001, NIBR IV 00002, NIBR IV 00003) each dissected on a slide, 5♀♀, 4♂♂ (NIBR IV 00004) persevered together in a vial with 99% ethanol, sublittoral sediments ~~(37˚33'02.60"N 130˚54'26.50"E)~~ at Gwaneum-do Islet off Ulleung-do Island in the East Sea of Korea, T.W. Jung leg., September 16, 2016, ~~water depth~~ 30.5 m; 1♀, 1♂ (NIBR IV 00005, NIBR IV 00006) each dissected on a slide, 6♀♀, 4♂♂ (NIBR IV 00007) preserved together in a vial with 99% ethanol, sublittoral sediments ~~(42˚37'20.00"N 131˚07'41.40"E)~~ at the coast of Primorsky in the East Sea of Russia, S.H Kim, J.W Kang legs., October 9, 2019, water depth 8 m.

Description of female (based on NIBR IV 00001).—Total body length ranged 966.1–1087.3 µm (mean = 1016.1 µm, n = 7; Korean population); body (Fig. 8A) slender, cylindrical, without clear distinction between prosome and urosome; integuments pitted and covered with sensilla and pores except for penultimate somite; smooth hyaline frill present in all somites. Cephalothorax representing 18% of body length. Free pedigerous somites slightly narrower than cephalothorax. First urosomite (P5-bearing somite) slightly tapering towards anterior end and other urosomites slightly tapering towards posterior end. Genital double-somite completely fused (Fig. 8A); genital slits separate, each covered by small plate with three small setae (representing P6) and copulatory pore covered by oval-shaped bulb (Fig. 10G, H). Anal somite 1.4 times as long as wide, with one pair of lateral secretory pores subdistally (Fig. 8B) and one pair of dorsal sensilla; anal operculum wide, moderately rounded, unarmed (Fig. 8A).

Rostrum (Fig. 8A) triangular, defined at base, with one pair of subapical sensilla; slightly shorter than maximum width.

Caudal rami (Fig. 8A, B) slightly divergent, cylindrical, about three times as long as maximum width, with one dorsal ~~pore~~ and two lateral pores; with seven setae: position of each seta as in *S. marcida* sp. nov.; seta I diminutive, shortest; setae II short, about 1/3 of ramus length; seta III as long as seta II; seta IV slightly shorter than setae II and III, fused to seta V basally; principal seta V conical-shaped, spiniform, about 1/3 of ramus length; seta VI short, as long as setae II and III; seta VII tri-articulate at base, as long as setae II and III.

Antennule six-segmented (Fig. 9A). First segment small, with one small seta, and ornamented with one row of outer spinules and two rows of minute posterior spinules. Second segment longest, about 3.4 times as long as maximum width, with one secretory pore and eight setae. Third segment 0.4 times shorter than preceding one, with four setae. Fourth segment smaller then preceding one, about 1.7 times as long as wide, with one long seta and one distal peduncle bearing one seta and one aesthetasc (basally fused). Fifth segment shortest, about 1.8 times as long as wide, with one seta bearing fracture plane basally. Sixth segment slightly tapering towards apical end, about 5.5 times as long as maximum width, with one seta bearing fracture plan, two bare setae, six bi-articulate setae, and one acrothek. Armature formula: 1-[1], 2-[8], 3-[4], 4-[1 + (1 + ae)], 5-[1], 6-[8 + acro].

Antenna (Fig. 9B). Coxa small, with one row of minute spinules. Allobasis elongate, about four times as long as wide, with two rows of spinules near abexopodal margin. Exopod slender, one-segmented, with one pinnate and one plumose seta. Free endopodal segment, with one row of inner spinules, one row of anterior spinules, one row of posterior spinules, and one distal hyaline frill; lateral armature composed of two uniserrate spines; distal armature comprised of one minute bare seta, two serrate spines, three unipinnate, geniculate setae, of which outermost one bearing row of stout spinules and basally fused to adjacent small seta.

Mandible (Fig. 10A, B) with well-developed coxa bearing one medial bulge and one row of spinules; gnathobase well-developed, with one bi-cuspidate and three multicuspidate teeth, one unipinnate seta fused to small spine, and one row of minute spinules. Uniramous palp consisting of basis and one-segmented endopod; basis elongate, about 3.7 times as long as maximum width, with one subdistal seta; endopod small, about 2.3 times as long as wide, with one lateral and four apical setae (two sets of setae merged basally).

Maxillule (Fig. 10C). Praecoxa large, with one row of posterior spinules; well-developed arthrite with seven spines distally, of which two anterior ones ornamented with one large spinule subdistally and one anterior one ornamented with few long spinules proximally, two plumose setae laterally, and one long and one small bare setae anteriorly; posterior surface with two rows of minute spinules, and lateral margin with one spinule. Coxal endite reaching mid-length of praecoxal arthrite, with one pinnate spine and one bare seta. Basis with one row of spinules anteriorly, and one pinnate and three bare setae distally; subdistal endite rudimentary, represented by two bare setae. Both exopod and endopod incorporated into basis, each represented by three and two setae, respectively.

Maxilla (Fig. 10D). Syncoxa large, with two endites: proximal endite distally with one unipinnate spine (fused to endite basally) and two unipinnate setae; distal endite with one spine (bearing few spinules) and two setae (bearing several spinules medially). Allobasis drawn out into a stout claw (bearing few spinules subdistally) accompanying three setae proximally. Endopod represented by four setae fused together basally.

Maxilliped (Fig. 10E) prehensile, three-segmented. Syncoxa elongate, about 3.2 times as long as wide, with one plumose seta subdistally. Basis elongate, 3.4 times as long as maximum width, unarmed. Endopod small, one-segmented, with one curved, geniculate claw bearing spinular row.

P1 (Fig. 10F). Coxa wide, unornamented. Intercoxal sclerite wide. Basis smaller than ~~preceding one~~, with one large anterior pore, and one long plumose inner seta. Segmentation, setation, and ornamentation of both rami as in *S. marcida* sp. nov. Length ratio of EXP1–EXP3 1: 0.84 : 0.84; outer spines on EXP3 unipinnate or pinnate, and distal setae unipinnate medially and uniplumose subdistally. Endopod not exceeding distal end of EXP3; ENP1 reaching ~~mid-length~~ of ~~ENP~~2, with one uniserrate inner seta; inner margin ~~of ENP1~~ convex medially; ENP2 narrower and 0.9 times longer than ~~that of~~ preceding ~~one~~; distal setae ~~unipinnate and geniculate~~, of which inner one uniplumose.

Segmentation and setation of P2–P4 as in *S. marcida* sp. nov.

P2 (Fig. 11A). Praecoxa small, triangular. Coxa large, unornamented. Basis with one bare outer seta; anterior surface with one pore and one row of spinules. Length ratio of EXP1–EXP3 1: 0.66 : 1.05; two distal setae on EXP3 bipinnate (ornamented with more distinct spinules than those of outer spines), and inner seta 1.5 times longer than distal one. Endopod one-segmented, reaching distal fourth of EXP1, with one outer row of fine spinules; ~~one~~ uniserrate inner seta more deeply serrate than that of *S. marcida* sp. nov.

P3 (Fig. 11B). Praecoxa unornamented. Coxa with two rows of minute anterior spinules. Basis with ~~one~~ long plumose outer seta exceeding distal end of EXP1; ornamentation as in P2. Length ratio of EXP1–EXP3 1: 0.66 : 1.10; two distal setae on EXP3 bipinnate (ornamented with more distinct spinules than those of outer spines), and inner seta subdistally uniserrate. ENP1 reaching distal fourth of EXP1, with distal hyaline.

P4 (Fig. 11C). Praecoxa and coxa larger than those of P2 and P3; coxa with two rows of posterior spinules. Basis with one bare outer seta; ornamentation as in P2 and P3. Length ratio of EXP1–EXP3 1: 1 : 0.76; EXP3, two outer spines stouter than those of *S. marcida* sp. nov., inner distal seta 1.3 times longer than outer distal one. Endopod as long as EXP1; ENP1 and ENP2 each with hyaline frill distally.

P5 (Fig. 11D). Baseoendopod and exopod fused into a robust plate, with three anterior secretory pores proximally; with eight elements: seta *a* spiniform, stout spur-like, fused to segment basally, reaching proximal quarter of next strong spine (seta *b*), with strongly serrate tip; seta *b* also spiniform, 1.5 times as long as length of plate; setae *c*–*g* setiform, seta *c* shorter than seta *b*, and seta *d* 1.8 times as long as length of plate; setae *e* and *f* pinnate subdistally, seta *e* exceeding tip of seta *b*, twice as long as seta *f*; seta *g* bare, slightly exceeding ~~to~~ tip of seta *a*; seta *h* longest, bi-articulate basally, and uniplumose subdistally.

Description of male (based on NIBR IV 00002). Body length 912.9 µm (range = 859.9–978.3 µm; mean = 934.6 µm; n = 5; Korean population); habitus (Fig. 8C) as in female~~s~~, but ~~representing~~ sexual dimorphism~~s in following features~~.

Urosome (Figs. 8C, 12A) six-segmented; genital and first abdominal ~~somite~~ separate.

Caudal rami (Fig. 12A, B) about 2.5 times longer than maximum width, tapering towards posterior end. Caudal seta II slightly longer than ramus; seta III 1.3 times as long as ramus; seta IV slightly shorter than seta II; principal seta V elongate, composite composed of slender spiniform proximal part and flagellate distal part, ~~and~~ as long as urosomites 1–4 combined.

Antennule (Fig. 9C) haplocer, ten-segmented, with geniculation between seventh and eighth segments. First segment small, with one bare seta and two rows of posterior spinules. Second segment longest, about 3.6 times as long as maximum width, with two plumose and seven bare setae, and one ~~secrete~~ pore. Third segment tapering distally, with seven setae. Fourth segment minute, with two setae distally. Fifth segment swollen, with seven setae, one cylindrical process bearing one slender seta and one long aesthetasc (fused basally). Sixth segment small, with one small and one long seta. Seventh segment elongate, about twice as long as wide, with two setae. Eight segment shorter than preceding one, with one small seta. Ninth segment 0.36 times as long as preceding one, ~~lacking setae~~. Terminal segment 3.5 times as long as preceding one, tapering distally, with one bare and six bi-articulate setae, and one acrothek. Armature formula: 1-[1], 2-[9], 3-[7], 4-[2], 5-[5 + (1 + ae)], 6-[2], 7-[2], 8-[1], 9-[0], 10-[7 + acro].

P2 (Fig. 12C). Inner distal corner of basis forming a distinct spinous process anteriorly. EXP2 with few inner setules. EXP3 longer than in females, as long as EXP1 and EXP2 combined; inner margin wavy, with two groups of setules; distal element modified ~~as~~ strong spine~~, which~~ recurved distally and ~~has~~ one row of spinules medially and one minute setule apically; with three pinnate outer spines. Endopod two-segmented, as long as EXP1; ENP1 with one serrated seta posteriorly; ENP2 slightly shorter than preceding ~~one~~, with one apical seta curved outwardly.

P3 (Fig. 12D). Endopod two-segmented; ENP1 small, unarmed; ENP2 strongly modified ~~as~~ recurved apophysis, about 3.9 times as long as preceding ~~one~~, with one unipinnate distal seta.

P5 (Fig. 12A, E) as in *S. marcida* sp. nov.; with two anterior pores and six setae: seta *a* ~~smallest~~; seta *b* twice as long as ~~plate~~; seta *c* 0.6 times as long as seta *b*; seta *d* ~~small~~, twice as long as seta *a*; seta *e* slightly shorter than seta *d*; and seta *g* longest, uniplumose subdistally.

P6 (Fig. 12A, F) as in *S. marcida* sp. nov.; asymmetrical plates, each with three setae, of which outer one about two times longer than others.

Variability.—Morphology of female P5 is variable among the geographical populations in the length of seta *b* to the single plate. ~~Korean population length ratio (1.6 times) is much longer than those of~~ Japanese (see *Itô, 1972*: ~~Fig. 15, 5 and 6~~) and Russian (see Fig. 11E) populations (about 0.9 times). It is likely that this morphological variability ~~is depending~~ on the body size of ~~populations~~; Korean population (966.1–1087.3 µm) ~~is~~ smaller than the two others (1200.0 µm in Japanese populations; 1077.3−1245.5 µm in Russian population).

Remarks.—This marine harpacticoid was originally described by *Itô (1972)* based on both sexes living on an intertidal sandy beach at Akkeshi, Hokkaido, Japan, and subsequently recorded in sublittoral environments in the White Sea (Russia) by *Kornev & Chertoprud (2008)*. The latter authors provided a brief description of the body and caudal rami, the armature of P2–P4, and a drawing of female's caudal rami, recognizing only ~~a~~ difference in ~~female body length~~ (1200 µm in Japanese specimens *vs.* 923 µm in the Russian specimen). However, *Kornev & Chertoprud's (2008)* setal armature differs from the original description. *Itô (1972)* considered a setule-like element near the inner subdistal margin in P2–P3 ENP1 and P4 ENP2 as a setule. However, based on both the illustrations of Itô (1972: Fig. 15) and our observation of specimens from the East Sea (arrowheads in Fig. 11), this element can be interpreted as ~~an armature,~~ indicating that the armature patterns of P2–P4 endopods are '210', '110', and '0.110', respectively. The fact that *Kornev & Chertoprud (2008)* provided the armature formula of P4 endopod as '0.010' conceivably implies either that their report is an observational error ~~in P4 ENP2~~ or that specimens from the White Sea ~~can be recognized as a~~ distinct species with close affinity to *S. intermedia*. Without ~~a~~ re-examination of Kornev & Chertoprud's specimens, the latter decision might be premature because several older records of *Stenocaris* species do not mention these elements (*cf. Scott*, *1892*, *1900*; *Sars*, *1909*).

Stenocaris intermedia displays certain features in common with *S. gracilis*, *i.e.*, the sexual dimorphic condition of male P3 endopod consisting of ENP1 without any apophysis and ENP2 modified ~~as~~ a long apophysis, the female six-segmented antennule, and female P5 with a spur-like seta *a* (fused to ~~segment basally~~) and a spiniform seta *b*. However, these two species can be distinguished based on three features: the relative length of the terminal to the penultimate segments in the female antennule (at least threefold in *S. intermedia vs.* twofold in *S. gracilis*); the elements on male P3 ENP2 (one delicate apical seta in *S. intermedia vs.* one outer (?) spine and one delicate apical seta in *S. gracilis*); and the structure of female caudal seta V (distinctly small and stout, approximately one-third of the caudal ramus ~~length~~ in *S. intermedia vs.* non-composite in *S. gracilis*). The latter characteristic is the most conspicuous feature of *S. intermedia*.

Our *S. intermedia* ~~specimens~~ from the East Sea (South Korean and Russian waters) ~~generally~~ correspond to the original description ~~of the characters mentioned above~~. However, we observed several minor differences that can be considered ~~a part of~~ intraspecific variability: the mandibular palp ~~of the specimens~~ is more elongated; the two outer elements on P4 EXP3 are more developed in our specimens; ~~and the~~ seta *b* on female P5 is distinctly longer than that of *Itô*'s *(1972)* specimen (about threefold as long as seta *a* in our specimen *vs.* twofold in the Japanese specimen). When *Itô (1972)* described this species, he presented two morphological variations in female P5 in the length-to-width ratio of a single segment and the thickness and length of setae/spines. We observed similar variations between specimens from the same locality or geographical population (South Korean *vs.* Russian specimens). Thus, we assumed that *S. intermedia* has high intra-population variability in this leg, although the details of P5 are important for separating harpacticoid species (*e.g.*, *Kim et al*., 2021; *Yeom et al*., *2021*). Additionally, the absence of the outer element of P1 could be attributed to an observational error of *Itô (1972)*, because we detected a very delicate outer seta in our specimens.

Discussion

On the taxonomic status of the *Stenocaris minor* complex

Based on only female specimens, *Scott (1892)* originally described this species (as *Cylindropsyllidae minor* at that time) from the Firth of Forth, Scotland, with a brief description and illustrations of ~~a~~ body, antennule, maxilliped, and P1–P5 (his figures of P2 and P3 were erroneously labeled P3 and P2, respectively; see *Scott*, *1892*: Plate XL, Figs. 21, 22). Subsequently, he revised the previous description of the female specimen (in particular, the relative length ratio of antennular segments, and setation of P1 ~~of both rami~~) and provided information on males including the sexual dimorphic features of P2 and P3, based on specimens from the type locality (see *Scott*, *1900*: Plate XIV, Figs. 23–32). Since this correction, *S. minor* has been reported from a variety of coastal regions: Korshamn, Norway (*Sars*, *1911*)~~,~~ Helgoland Island, Germany (*Kunz*, *1938*)~~,~~ Roscoff, France (*Monard*, *1935*)~~,~~ Naushon Island, and Massachusetts (*Wilson*, *1932*); the Bulgarian coast of the Black Sea (*Apostolov*, *1971*; *Marinov*, *1971*; *Apostolov & Marinov*, *1988*); and Figarolo Island (Olbia, Italy) in the Mediterranean Sea (*Cottarelli & Venanzetti*, *1989*).

The description of *Sars (1911)* has been accepted as an appropriate standard for *Stenocaris minor* (*Kunz*, *1938*; *Lang*, *1948*). However, the fact that most of ~~these~~ subsequent records include insufficient descriptions and illustrations, or are occasionally known from only one sex, may have hampered comprehensive comparisons, possibly broadening the taxonomic concept of *S. minor*. Because harpacticoid species complexes can be divided into several cryptic species (*e.g.*, *Fiers & Kotwicki*, *2013*; *Huys & Mu*, *2021*; *Karaytuğ et al.*, *2021*), some of these records might be ~~a~~ *Stenocaris minor* complex. *Monard (1935)* and *Kunz (1938)* reported the characteristics of males of this species from European waters near the type locality. Despite discrepancies in details of P2 (length ratio~~s~~ of ~~segmentations~~ and setal armature~~s~~), they were ~~likely~~ considered identical to *Stenocaris minor* due to their geographical proximity. Several authors have documented the sympatric occurrence of *Stenocaris minor* from the Black Sea, but the descriptions given by *Apostolov (1971)*, *Marinov (1971)*, and *Apostolov & Marinov (1988)* deviate from *S. minor* s. str. in several respects. *Apostolov*'s *(1971)* specimen has only one outer spine on P3–P4 EXP3, no inner seta on P4 EXP3, and female P5 ~~that~~ is broad and has a distinct notch on the distal margin, reminiscent of the legs of immature copepodid stages or different species (see *Apostolov*, *1971*: Figs. 29–31). Except for observable errors in male P2 ENP2 without a distal element and the reduced setation of male P5, the Bulgarian specimen of *Marinov (1971)* differs from Scottish specimens described by *Scott (1900)* in the sexual dimorphism of male P3 endopod (one-segmented in Bulgarian *vs.* two-segmented in the Scottish and other records), raising doubts about its actual condition. The caudal rami of *S. minor* sensu Apostolov & Marinov, 1988 were illustrated as possessing a composite terminal seta V (with the ~~flagellum~~ part distally), at least 1.5-fold as long as the caudal ramus (*vs.* slightly longer). Despite these differences, limited information and inaccuracy have hampered determination of the Black Sea specimens' taxonomic identities. Pending collection of *Stenocaris* species from the Black Sea, *S.*

minor sensu Apostolov, 1971, *S. minor* sensu Marinov, 1971, and *S. minor* sensu Apostolov & Marinov (1988) are here classified as *species inquirenda* of *Stenocaris*.

Wilson (1932) reported the first occurrence of *S. minor* in North America based on females collected from freshwater of Naushon Island, Massachusetts. His insufficient description and figures of the caudal ramus and female P5 hamper morphological comparison between American specimens and the reports of *Scott (1900)* and *Sars (1911)*. Re-description of the species is essential to rule its identity and would facilitate the discovery of a new species given the wide geographical area. Therefore, the American population is also regarded as a *species inquirenda* of the genus.

Stenocaris figaroloensis sp. nov.
urn:lsid:zoobank.org:act: AE4F4E54-05E9-4F05-8AD6-55E8CE752934

Stenocaris minor (T. Scott, 1892) *sensu* Cottarelli & Venanzetti (1989)

Original description.—Cottarelli & Venanzetti (1989—as *Stenocaris minor*): 202–204; Fig. 10.
Type locality — Italy, Figarolo Island (the Tyrrhenian Sea); sandy sediments at a depth of 1 m.
Type material.—The female and male specimens illustrated *by Cottarelli & Venanzetti (1989)* in his figure 10 are here fixed as the holotype and paratype of *S. figaroloensis* sp. nov. in accordance with *ICZN (1999)* Arts. 16.4 and 72.5.6.
Etymology.—The specie name is named after the type locality of the new species

Remarks.—*Cottarelli & Venanzetti (1989)* recorded both sexes of *Stenocaris* species under the name *S. minor* from the Tyrrhenian Sea, the Mediterranean Sea (Italy), providing details of the mandible, P2–P5, and male P6. Although their description contained some uncertain characteristics, such as the absence of a setule-like element on P2 ENP1 and P4 ENP2, only one outer spine on P4 EXP3, and male P3 endopod comprising only one segment, the Italian population differs significantly from the re-descriptions of *S. minor* by *Scott (1900)* and *Sars (1911)*. (1) The mandibular endopod has only one lateral and three apical setae (*vs.* four apical setae). (2) Male P2 ENP1 lacks a long seta posteriorly (*vs.* present). (3) The relative length and nature of elements on female P5, *i.e*., the stout seta *a* is remarkably uniserrate medially and flagellate distally (this form is not known from other congeners), and setae *c*, *f*, and *g* are markedly shorter than other elements. Based on these differences, we attribute *Cottarelli & Venanzetti*'s *(1989)* specimens to a distinct species named *S. figaroloensis* sp. nov.

On the polyphyletic status of *Stenocaris*

The monophyly of the genus *Stenocaris* have been suspected by many previous works (*Apostolov*, *1982*; *Huys & Conroy-Dalton*, *1993*; *Kunz*, *1994*; *Moura & Pottek*, *1998*; *Kornev & Chertoprud*, *2008*). This taxonomic confusion might have been resulted from the long-accepted simple criteria used to distinguish cylindropsyllid genera, such as segmentation of the thoracic legs and the degree of development of the maxilliped. However, recent researches have clarified the characteristics of the body and caudal rami, the nature of the mouth appendages, the sexually dimorphic structures of P2–P3, and the setation pattern of the swimming legs as well as P5 in both sexes to (re-)define the general classification of the family Cylindropsyllidae (*Huys & Conroy-Dalton*, *1993*; *Moura & Pottek*, *1998*; *Huys & Conroy-Dalton*, *2006a*, *b*; *Kornev & Chertoprud*, *2008*; *Richter*, *2019*). In addition, *Richter (2019)* noted that apomorphies for the genus defined. Following these approaches, a reevaluation of the morphological features of *Stenocaris* species for the monophyly of the genus is needed.

Arlt (1983) originally described *Stenocaris baltica* based on only one male specimen collected from a fine sandy substrate at a 13-m depth in the Baltic Sea. Although he claimed that a relationship of this species with *Stenocaris* is supported by the well-developed maxilliped (being not reduced as in *Cylindropsyllus*) and six-segmented antennule, his illustrations of the antenna and swimming legs (*Arlt*, *1983*: Fig. 14) raised doubts that *S. baltica* could be attributed to *Vermicaris*. The following characteristics of this species appear to be strongly related to the latter genus: the total body length (440 µm in the male) is distinctly smaller than other *Stenocaris* species (about 1000 µm); the antennary exopod is extremely reduced and expressed as a small seta (*vs*. one-segmented, with two apical setae in *Stenocaris*), P1 ENP2 has only two apical setae (*vs*. three setae in *Stenocaris*), male P2 ENP2 is a semicircular process lacking a distal element (*vs*. oblong, bearing one distal seta in *Stenocaris*), and male P3 ENP2 is one-segmented (*vs.* two-segmented in *Stenocaris*). In Cylindropsyllidae, the structure of P5 in both sexes is generally a single plate, but *Arlt (1983)* questionably mentioned that the exopod is separated from the baseoendopod. Note that *Arlt*'s *(1983*: Fig. 14*)* illustration of P5 bearing a single apical seta is probably reminiscent of male P6, and he stated that the baseoendopod was damaged during preparation. This is undoubtedly based on an observational error. Given these morphological features, this species should be reinstated in *Vermicaris* as *V. baltica* (Arlt, 1983) comb. nov.

Noodt (1955) described *Stenocaris pygmaea* from the Bay of Biscay in the Atlantic Ocean based on one female specimen (body length 370 µm), stating its close affinity with both *S. minuta* (= *V. minuta*) and *S. pontica* (= *V. pontica*). Based on the morphology of the Bulgarian species identified as *S. pontica*, Marinov (1971) presumed this species to be identical to *S. pontica* described from the Romanian coast of the Black Sea, and subsequent authors (*Apostolov*, *1972*; *Apostolov & Marinov*, *1988*) considered it a junior synonym of the latter. However, *S. pygmaea* was reinstated as a valid species by *Huys & Conroy-Dalton (1993)*, who pointed out a significant difference in the segmentation of P2 endopod between the two species, supporting the removal of its synonym from *S. pontica*. Although this unusual condition of *S. pygmaea* deviates from the generic boundary of *Vermicaris*, this species can be allocated to the latter as *V. pygmaea* (Noodt, 1955) comb. nov. rather than being placed in *Stenocaris*. This is based on the observations that female P3 endopod is one-segmented, semicircular apically, and lacking any elements, and that female P5, which is more smaller than those of other genera, has a reduced armature with 2–3 setae. We here suggest that these two characters could be potential autapomorphies for *Vermicaris*.

Within the family, the morphology of caudal rami in *S. arenicola* and *S. kliei* displays a reduced ramal length and a dorsal spinous process. Members of the family except for *Monsmeteoris* Richter, 2019 have elongated caudal rami that are at least twice as long as broad. In the *Navalonia* clade comprising the genera *Bolbotelos*, *Boreovermis*, *Willemsia*, and *Navalonia*, it is modified to bulbous appendages (*Huys & Conroy-Dalton*, *1993*). However, in *S. arenicola* and *S. kliei*, the shape of these rami is strongly reduced: they are as long as broad and have a convex inner margin. *Huys & Conroy-Dalton (1993)* proposed phylogenetic relationships among *Boreopontia heipi* Willems, 1981, *S. arenicola*, and *S. kliei* based on the presence of a dorsal spinous process on the caudal rami; they also re-examined Wilson's collection of *S. arenicola*, which was provided with only a brief drawing of habitus by *Wilson (1932)*. Although four *Stenocaropsis* species have a process similar to the above three species, it involves fundamental differences (*Huys & Conroy-Dalton*, *1993*: 293). They suggested that this recurved process is derived from a dorsal integumental extension, which can be interpreted as convergent evolution in *B. heipi* and the *S. arenicola*/*S. kliei* group based on the significant differences in the sexual dimorphism of P2 and P5. Indeed, several fundamental discrepancies between them can be readily noticed. In the male P2–P3, the exopodal segments are strongly modified in the *S. arenicola*/*S. kliei* group as in other congenic genera (see the remarks on *Huysicaris* gen. nov.), whereas *B. heipi* does not exhibit such sexual dimorphism. Male P5 of *B. heipi* is characterized by the modification of seta *a* or *b* into a spine bearing a crenate tip and a distal setule, of seta *c* or *d* into a stout spine bearing a distal setule in females, and of seta *b* or *c* (second innermost) into a stout spine in males (see *Huys & Conroy-Dalton*, *2006b*: Figs. 36–37). In the insufficient original illustration of *S. arenicola* by *Wilson (1932)*, male P5 exhibits seven setae, which is the maximum number of setae and known only in *Evansula* T. Scott, 1906, and seta *a* (innermost) is modified into a stout spine. A similar modification in the male P5 was present in the original description of *S. kliei*, although seta *a* is fused to the segment basally (see *Kunz*, *1938*: Abb. 12, Fig. 8). Indeed, two different types of modified spine are present in the same genus, *i.e.*, it is defined in the female of *S. minor* s. str. and *S. figaroloensis* sp. nov. *vs.* fused in *S. gracilis*, *S. intermedia*, and *S. marcida* sp. nov. The homologous position of the spine in *S. arenicola* and *S. kliei* could support *Huys & Conroy-Dalton*'s *(1993)* review and their isolated taxonomic position within *Stenocaris*. Both species can be distinguished from *Stenocaris* in the extreme elongation of the penultimate somite as in *Boreopontia* and the *Navalonia* clade; the lack of caudal seta I; the second antennary segment being not elongated in both sexes; P1 ENP2 with only two (sub)distal setae; and male P5 being separate (*vs.* medially confluent in *Stenocaris*; see below). Considering these characteristics and the generic discriminant, we propose a new genus *Huysicaris* gen. nov. to accommodate *H. arenicola* (Wilson, 1932) comb. nov. and *H. kliei* (Kunz, 1938) comb. nov. to move toward monophyly of *Stenocaris*.

Genus *Huysicaris* gen. nov.
urn:lsid:zoobank.org:act:18ADF050-EF12-4198-86EA-1DE3C2BA1C83

Type species.—*Huysicaris kliei* (Kunz, 1938) comb. nov. [by original designation]

Other species.—*H. arenicola* (Wilson, 1932) comb. nov.

Diagnosis.—Cylindropsyllidae. Body vermiform, without separation between prosome and urosome; penultimate somite extremely elongated; anal operculum wide. Rostrum triangular, defined at base. Caudal rami as long as broad or slightly longer, with a recurved spinous process on dorsal margin; inner margin bulbous; with six setae, ~~lacking seta I~~. Antennule elongate, 7-segmented in ♀, with aesthetasc on segments 4 and 7; haplocer and 8(?)-segmented in ♂. Antenna with allobasis; exopod small, 1-segmented, with 2 distal setae. Information on mouth appendages lacking except for maxilliped. Maxillipedal syncoxa with 1 subdistal seta; endopod represented by claw ~~accompanying~~ a seta or lacking. P1 exopod 3-segmented; EXP2 and EXP3 lacking inner element. P1 endopod 2-segmented; ENP1 with 1 inner seta, ENP2 with 2 distal setae. P2 basis with hook-like process anteriorly. P2–P4 exopods 3-segmented; ~~length of~~ P4 exopod extremely elongated ~~and~~ P4 EXP3 shortest; P2–P3 exopods strongly modified (stout and bending inwardly) in ♂; inner distal seta on P2 EXP3 modified ~~as~~ claw in ♂. P2–P3 endopods 1-segmented and P4 endopod 2-segmented; P3 ENP1 with long and stout apophysis in ♂. Setal armature formula of P1–P4 as follows:

	exopod	endopod
P1	0.0.021–2	1.011
P2	0.0.022 [0.0.011–2 in ♂]	110 [01–20 in ♂]
P3	0.0.122 [0.0.012 in ♂]	0.010 [apo.?]
P4	0.0.0–121–2	0.0–110

P5 forming single plate, with 1 spinose process and 6(?) setae in ♀; in ♂ with very long basal seta and 5–6 setae, ~~among them~~ the innermost seta modified into stout spine (fused to plate basally in *H. kliei* comb. nov.).

P6 ♀ unknown; in ♂, represented by opercula each bearing 1 short and 2 long setae.

Etymology.—The generic name is dedicated to Dr. Rony Huys (National History Museum, London), in recognition of his numerous contributions to harpacticoid diversity and taxonomy including the family Cylindropsyllidae.

Notes.—Due to incomplete original descriptions of *H. arenicola* comb. nov. and *H. kliei* comb. nov. and the restriction of their type series, some characters of the generic diagnosis remain undefined.

Remarks.—*Huys & Conroy-Dalton (1993)* pointed out the different sexual dimorphism in P2 and P3 of *H. arenicola* comb. nov. and *H. kliei* comb. nov. Incomplete descriptions and vague illustrations by *Wilson (1932)* and *Kunz (1938)* hamper detection of (aut)apomorphies for this new genus and determination of ~~the~~ taxonomic position ~~of the genus~~. However, in accordance with *Kunz*'s *(1938)* figures, male P3 of *H. kliei* comb. nov. displays two uncommon characteristics: (1) EXP3 is recurved subdistally and inwardly and has only one distal and two outer elements; and (2) the endopod is probably three-segmented, with a stout recurved apophysis on ENP2 reaching the distal end of EXP3. The ~~first sexual dimorphism in P3 EXP3~~ is regarded here as an autapomorphy for ~~this new genus~~ because it is not expressed in any cylindropsyliid genera; unfortunately, *Wilson (1932)* did not provide information on male P3 of *H. arenicola* comb. nov. In the family, the three-segmented condition of male P3 is retained in *Evansula*, which occupies ~~the~~ basal position in the family (*cf. Huys & Conroy-Dalton*, *2006b*). However, both members of ~~this new genus~~ exhibit an unusual spinous process on male P2 basis, which supports the monophyly of all genera except for *Evansula*. Therefore, ~~this new genus~~ is assumed to ~~be the~~ basal node within the monophyletic group based on retention of the plesiomorphic condition in the endopodal ramus.

Another taxonomic problem with *Stenocaris* is that autapomorphies have not been defined. Removal of four species—*H. arenicola* comb. nov., *H. kliei* comb. nov., *V. baltica* comb. nov., *V. pygmaea* comb. nov.—from *Stenocaris* might justify its generic concept and determine its autapomorphies within the Cylindropsyllidae. The sexual dimorphic features of male P2 and P3 are the primary characters used to reconstruct phylogenetic relationships among cylindropsyllid genera, *i.e.*, the presence of a minute or recurved apophysis on P2 basis, a modified distal spine on P2 EXP3, fusion of P2 EXP2 and EXP3, and a recurved or minute apophysis on male P3 endopod (*Moura & Pottek*, *1998*; *Huys & Conroy-Dalton*, *2006b*). Based on the latter feature and the one-segmented endopods in female P2–P3, *Moura & Potteck (1998)* presumed that *Stenocaris* is nested in the *Navalonia* clade. However, *Huys & Conroy-Dalton (2006a)* demonstrated that the *Navalonia* clade can be characterized by allometric growth of male P3 endopod. Within the genus, males of *S. gracilis*, *S. intermedia*, and *S. marcida* sp. nov. lack an apophysis on male P3 ENP1, although it is present in both *S. minor* s. str. and *S. figaroloensis* sp. nov. Despite this discrepancy, ~~these five *Stenocaris* species have male P5 that is confluent medially~~ (*vs*. separated in all other genera; *cf. Huys & Conroy-Dalton*, *2006b*: Fig. 37)~~.~~ ~~Therefore, this~~ could be considered the most distinct autapomorphy for *Stenocaris*.

Conclusions

We describe a new marine harpacticoid, *Stenocaris marcida* sp. nov., from the subtidal ~~substrate~~ off Dok-do Island in the East Sea of South Korea, and report the occurrence of *S. intermedia* Itô, 1972 based on specimens collected from subtidal sediments of Ulleung-do Island in South Korean waters and the coast of Primorsky in Russian waters. Our detailed morphological comparison of all *Stenocaris* species and their taxonomic records provides insight into the generic concept and confirms that the nature of the fifth leg, caudal rami, and sexual dimorphic features of the second and third legs can be used to define the generic boundary. The monophyly of the genus is supported by a significant synapomorphy ~~that is~~ the confluent condition of ~~a pair of~~ the fifth legs in males, ~~comprising only~~ *S. gracilis* Sars, 1909, *S. minor* (T. Scott, 1892), *S. intermedia*, *S. figaroloensis* sp. nov., and *S. marcida* sp. nov. Based on this taxonomic review, other *Stenocaris* species ~~must be~~ transferred to the genus *Vermicaris* Kornev & Chertoprud, 2008 or the new genus *Huysicaris* gen. nov. as *V. baltica* (Arlt, 1983) comb. nov., *V. pygmaea* (Noodt, 1955) comb. nov., *H. arenicola* (Wilson, 1932) comb. nov., and *H. kliei* (Kunz, 1938) comb. nov. Further studies on the *S. minor* species complex will enhance understanding of the diversity of cryptic species and the phylogenic relationships among cylindropsyllid harpacticoids.

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Figure legends

Figure 1. Map of the sampling stations of *Stenocaris marcida* sp. nov. (filled triangle, ▲) and *S. intermedia* Itô, 1972 (filled circle, ●).

Figure 2. *Stenocaris marcida* sp. nov., female, holotype (A–C) and paratype 1 (D). (A) Habitus, dorsal; (B) Habitus, lateral; (C) Urosome, ventral; (D) Caudal ramus, lateral. Scale bars are given in µm.

Figure 3. *Stenocaris marcida* sp. nov., female, holotype (A, B). (A) Rostrum and antennule; (B) P1. Scale bars are given in µm.

Figure 4. *Stenocaris marcida* sp. nov., female, holotype (A–F) and paratype 1 (G). (A) Antenna; (B) Mandible; (C) Maxillule; (D) Maxilla; (E) Maxilliped; (F) P5; (G) Genital field. Scale bars are given in µm.

Figure 5. *Stenocaris marcida* sp. nov., female, holotype (A–C), male, allotype (D). (A) P2; (B) P3; (C) P4; (D) P5. Scale bars are given in µm.

Figure 6. *Stenocaris marcida* sp. nov., male, allotype. (A) Habitus, dorsal; (B) Antennule. Scale bars are given in µm.

Figure 7. *Stenocaris marcida* sp. nov., male, allotype. (A) Urosome, ventral; (B) P2; (C) P3. Scale bars are given in µm.

Figure 8. *Stenocaris intermedia* Itô, 1972, female (A, B) and male (C) from Korean waters. (A) Habitus, dorsal; (B) Urosome, ventral; (C) Habitus, dorsal. Scale bars are given in µm.

Figure 9. *Stenocaris intermedia* Itô, 1972, female (A, B) and male (C) from Korean waters. (A) Antennule; (B) Antenna; (C) Antennule. Scale bars are given in µm.

Figure 10. *Stenocaris intermedia* Itô, 1972, female from Korean waters. (A) Mandible; (B) Mandibular ganathobase; (C) Maxillule; (D) Maxilla; (E) Maxilliped; (F) P5; (G) Genital field, ventral; (H) Genital field, lateral. Scale bars are given in µm.

Figure 11. *Stenocaris intermedia* Itô, 1972, females from Korean (A–D) and Russian (E) waters. (A) P2; (B) P3; (C) P4; (D) P5; (E) P5. Arrowheads indicate delicate and setule-like elements. Scale bars are given in µm.

Figure 12. *Stenocaris intermedia* Itô, 1972, male from Korean waters. (A) Urosome, ventral; (B) Caudal ramus, lateral; (C) P2; (D) P3; (E) P5; (F) P6. Scale bars are given in µm.

Figure 1

Map of the sampling stations of *Stenocaris marcida* sp. nov. (filled triangle, ▲) and *S. intermedia* Itô, 1972 (filled circle, ●).

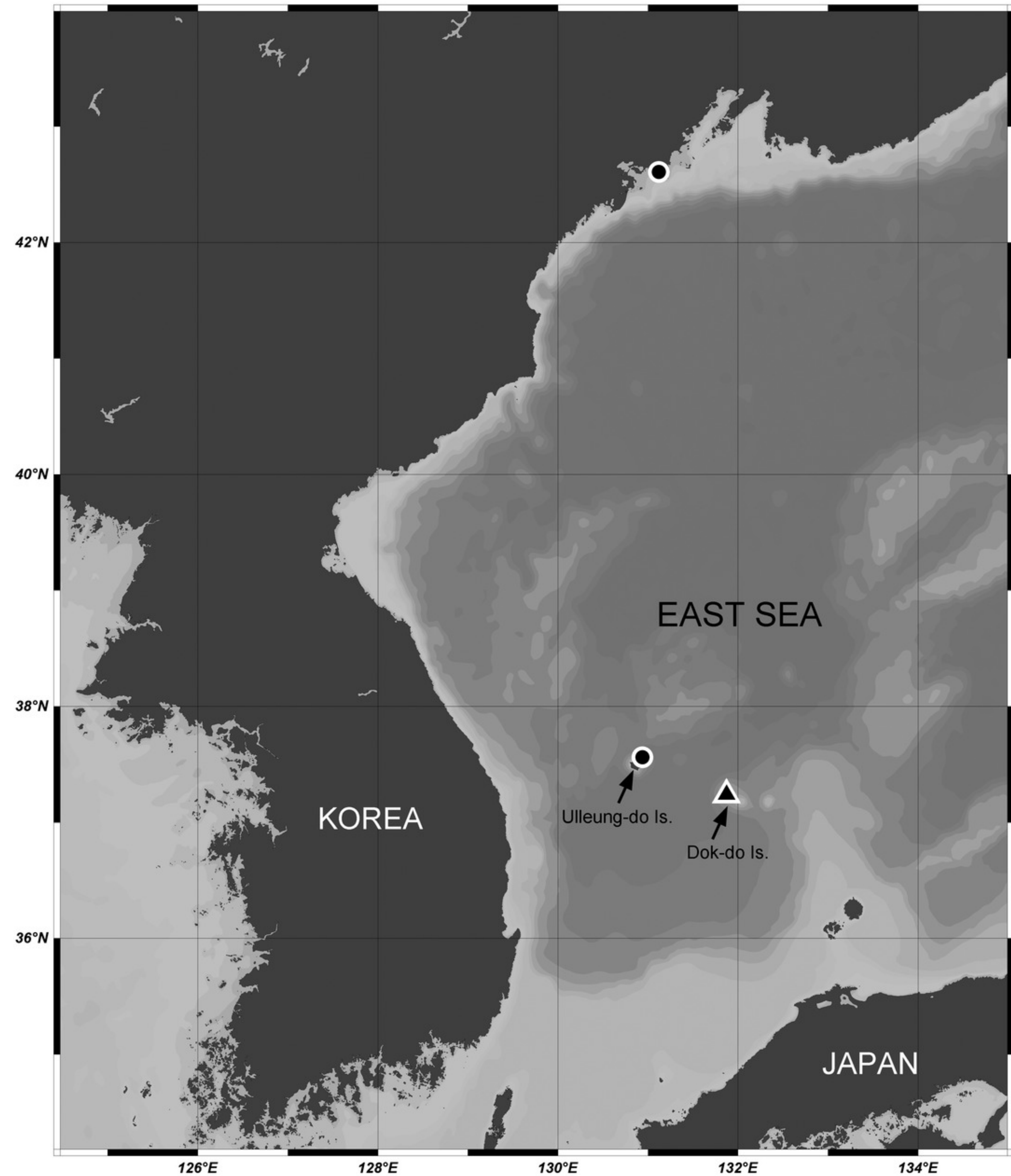

42°N
40°N
38°N
36°N
126°E
128°E
130°E
132°E
134°E
EAST SEA
KOREA
JAPAN
Ulleung-do Is.
Dok-do Is.
Ocean Data View

Figure 2

Stenocaris marcida sp. nov., female, holotype (A–C) and paratype 1 (D).

(A) Habitus, dorsal; (B) Habitus, lateral; (C) Urosome, ventral; (D) Caudal ramus, lateral. Scale bars are given in µm.

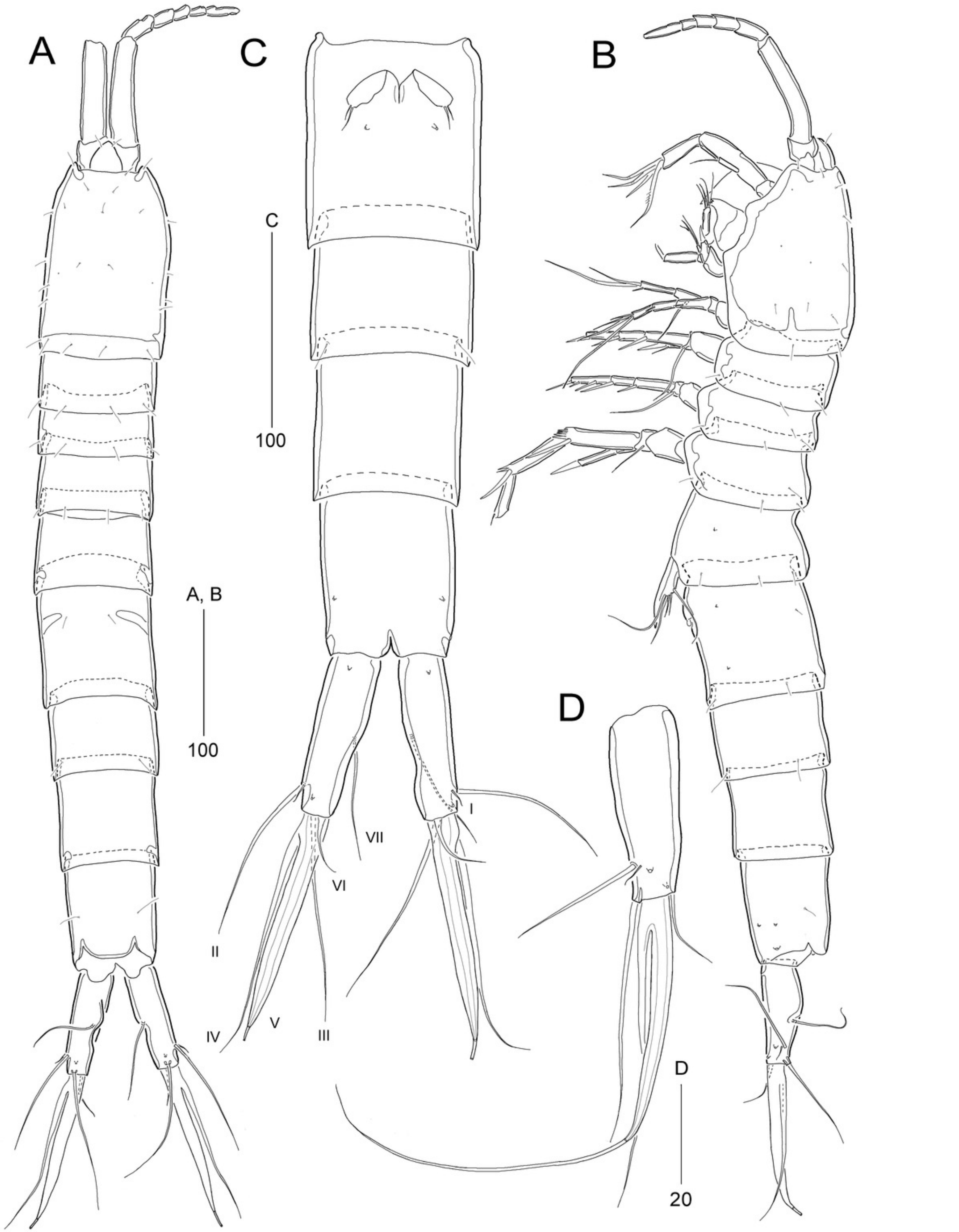

A
C
B
D
C
100
A, B
100
I
II
III
IV
V
VI
VII
D
20

Figure 3

Stenocaris marcida sp. nov., female, holotype (A, B).

(A) Rostrum and antennule; (B) P1. Scale bars are given in µm.

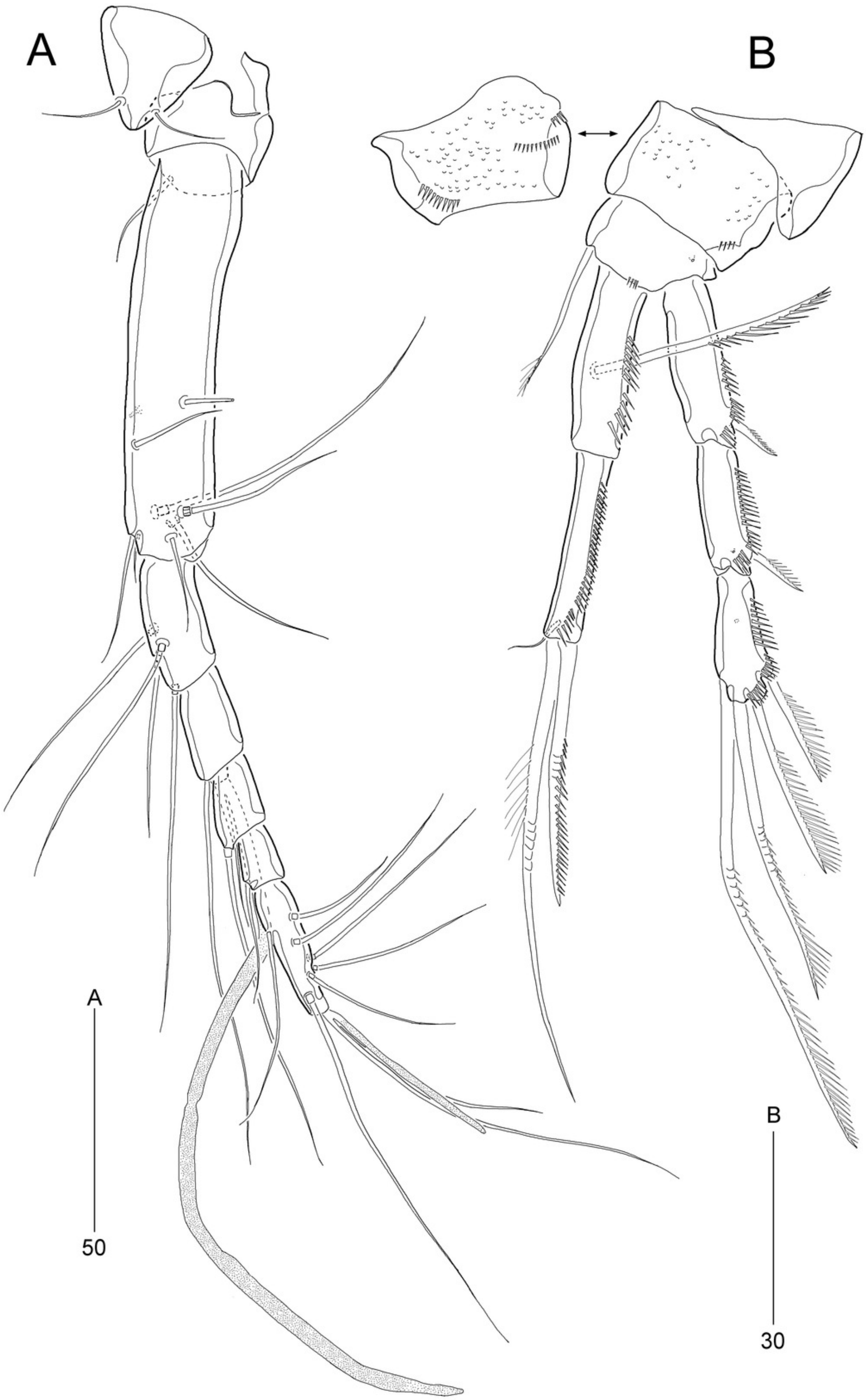

A
B
A
50
B
30

Figure 4

Stenocaris marcida sp. nov., female, holotype (A–F) and paratype 1 (G).

(A) Antenna; (B) Mandible; (C) Maxillule; (D) Maxilla; (E) Maxilliped; (F) P5; (G) Genital field. Scale bars are given in µm.

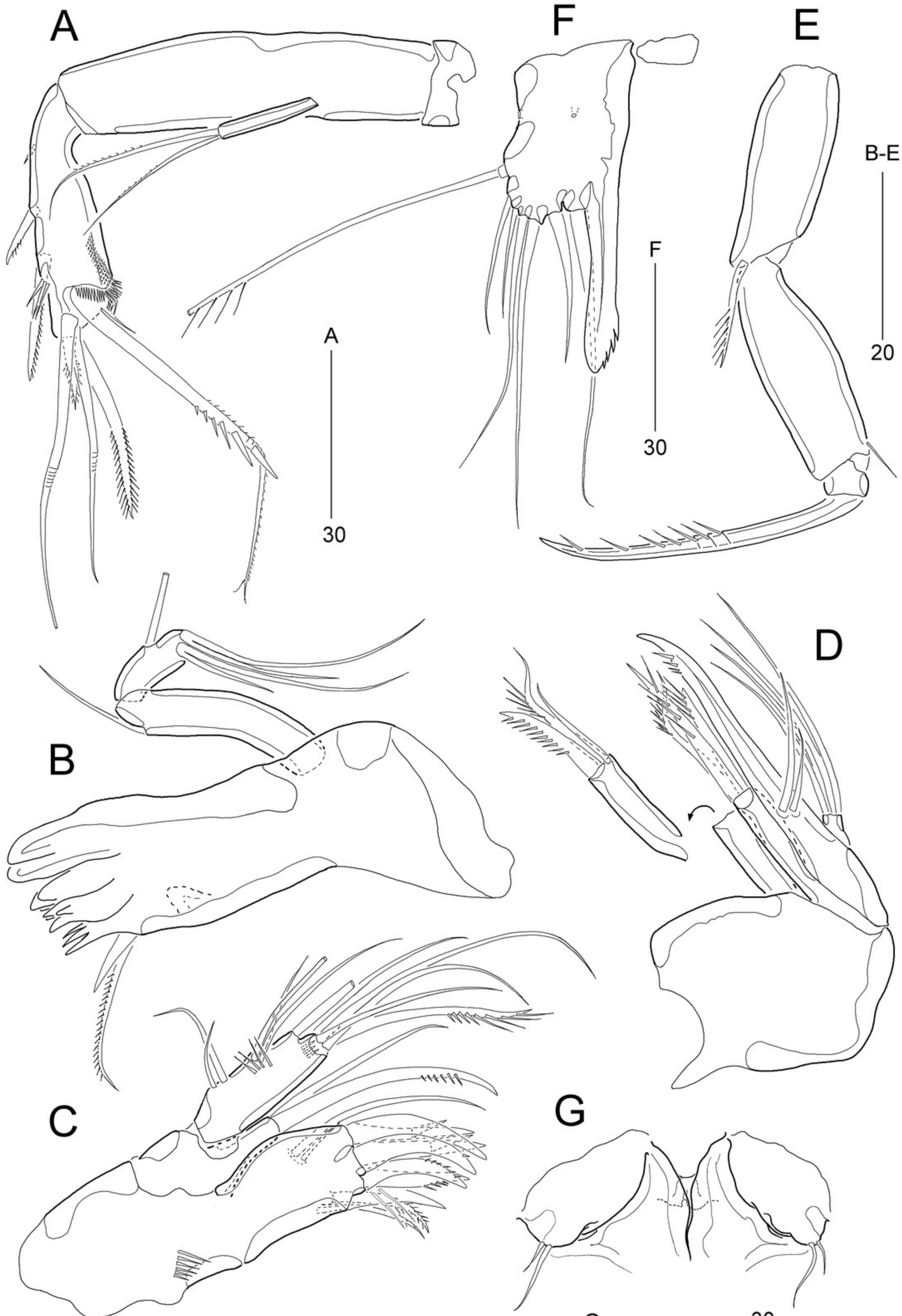

A
F
E
B-E
20
F
30
A
30
D
B
C
G
G 30

Figure 5

Stenocaris marcida sp. nov., female, holotype (A–C), male, allotype (D).

(A) P2; (B) P3; (C) P4; (D) P5. Scale bars are given in µm.

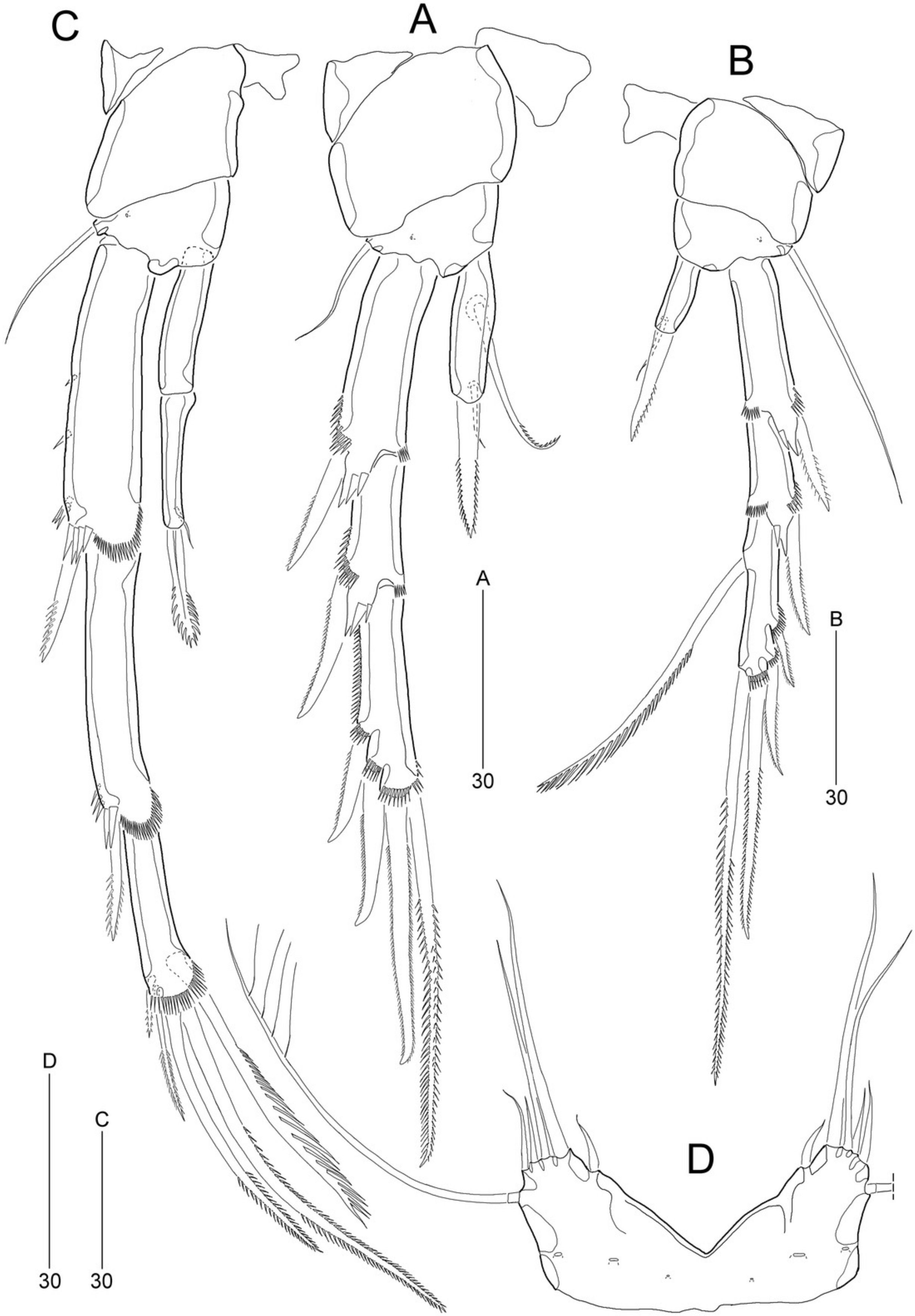

C
A
B
A
30
B
30
D
D
30
C
30

Figure 6

Stenocaris marcida sp. nov., male, allotype.

(A) Habitus, dorsal; (B) Antennule. Scale bars are given in µm.

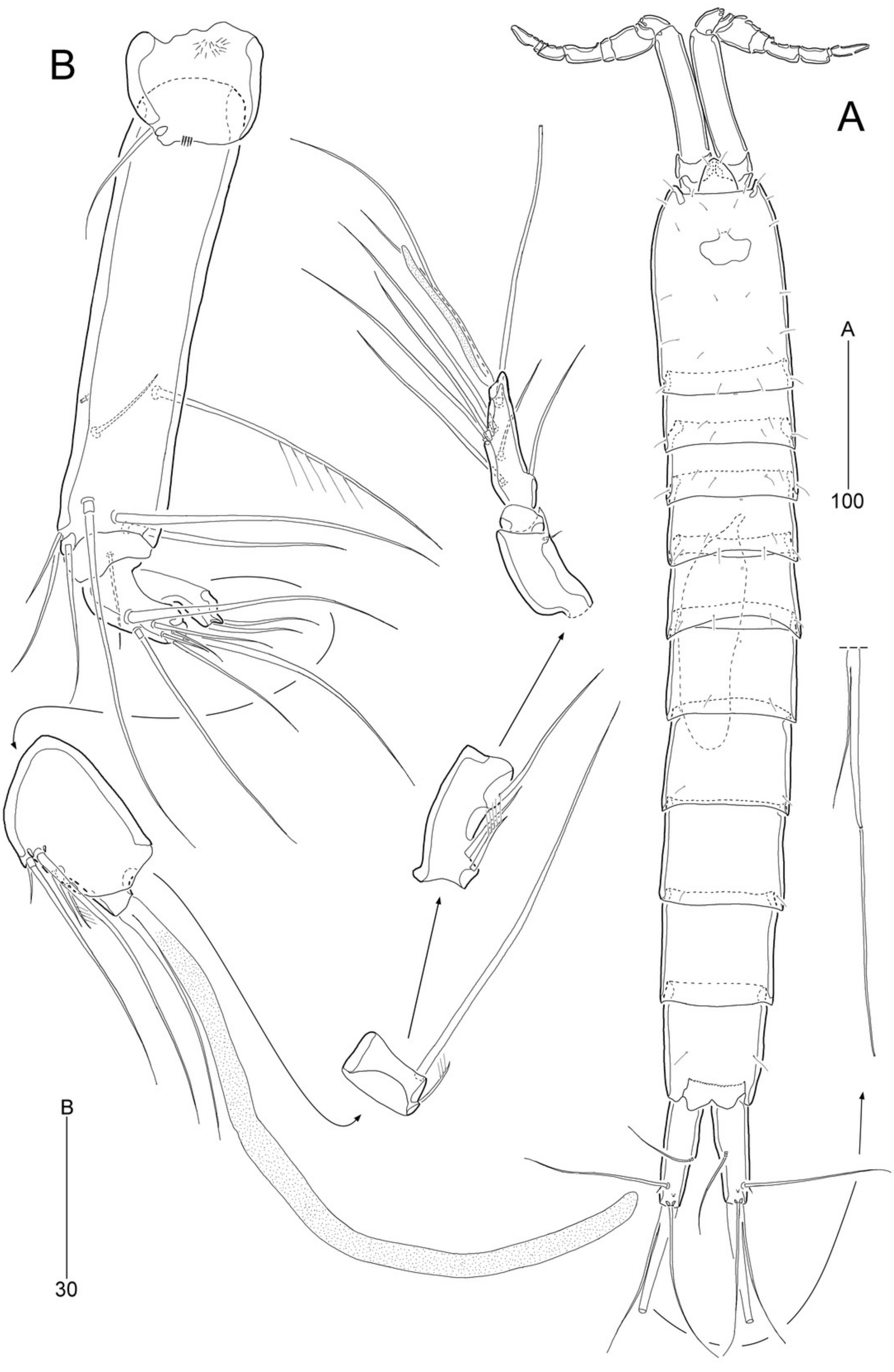

B
A
A
100
B
30

Figure 7

Stenocaris marcida sp. nov., male, allotype.

(A) Urosome, ventral; (B) P2; (C) P3. Scale bars are given in µm.

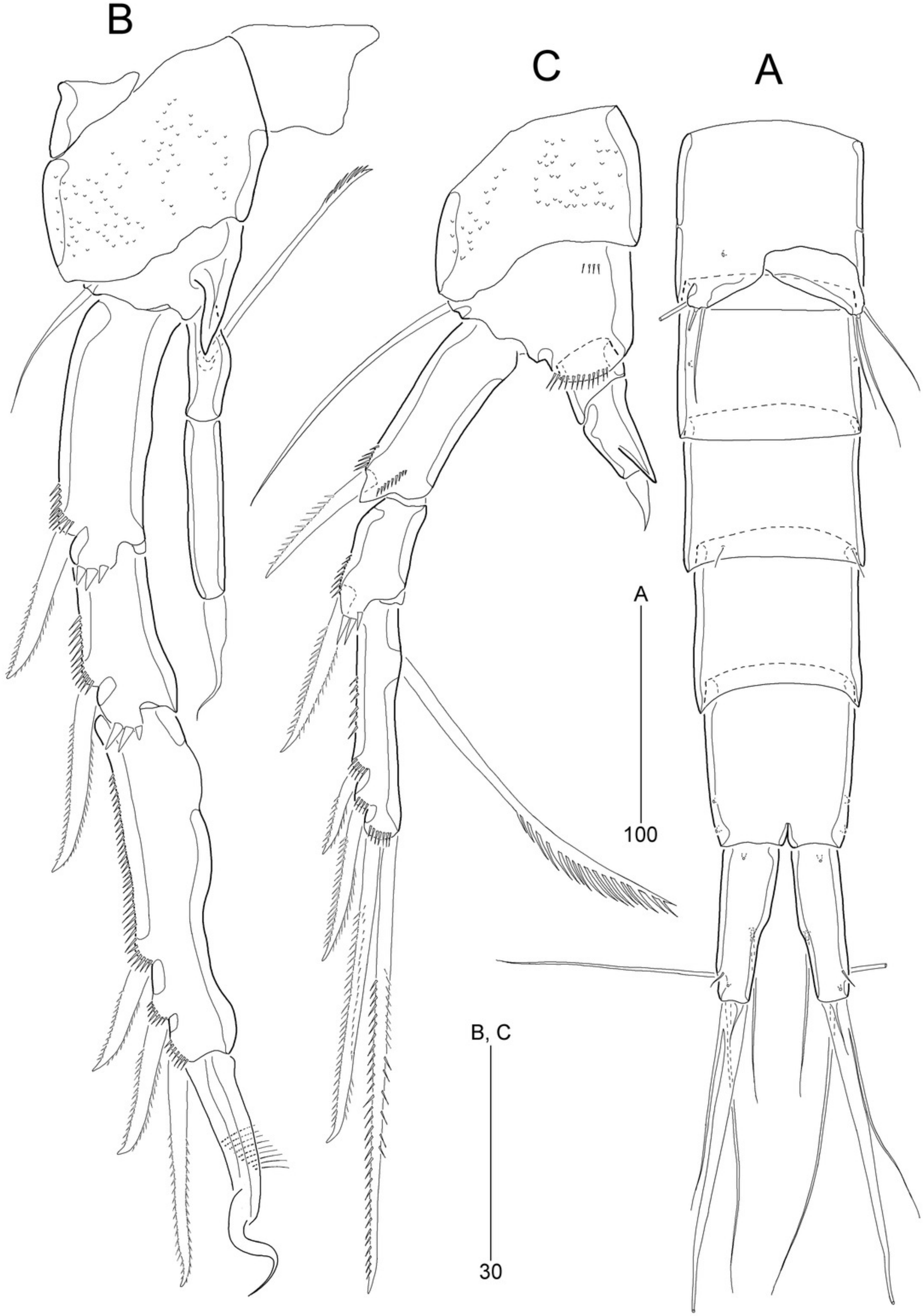

B
C
A
A
100
B, C
30

Figure 8

Stenocaris intermedia Itô, 1972, female (A, B) and male (C) from Korean waters.

(A) Habitus, dorsal; (B) Urosome, ventral; (C) Habitus, dorsal. Scale bars are given in µm.

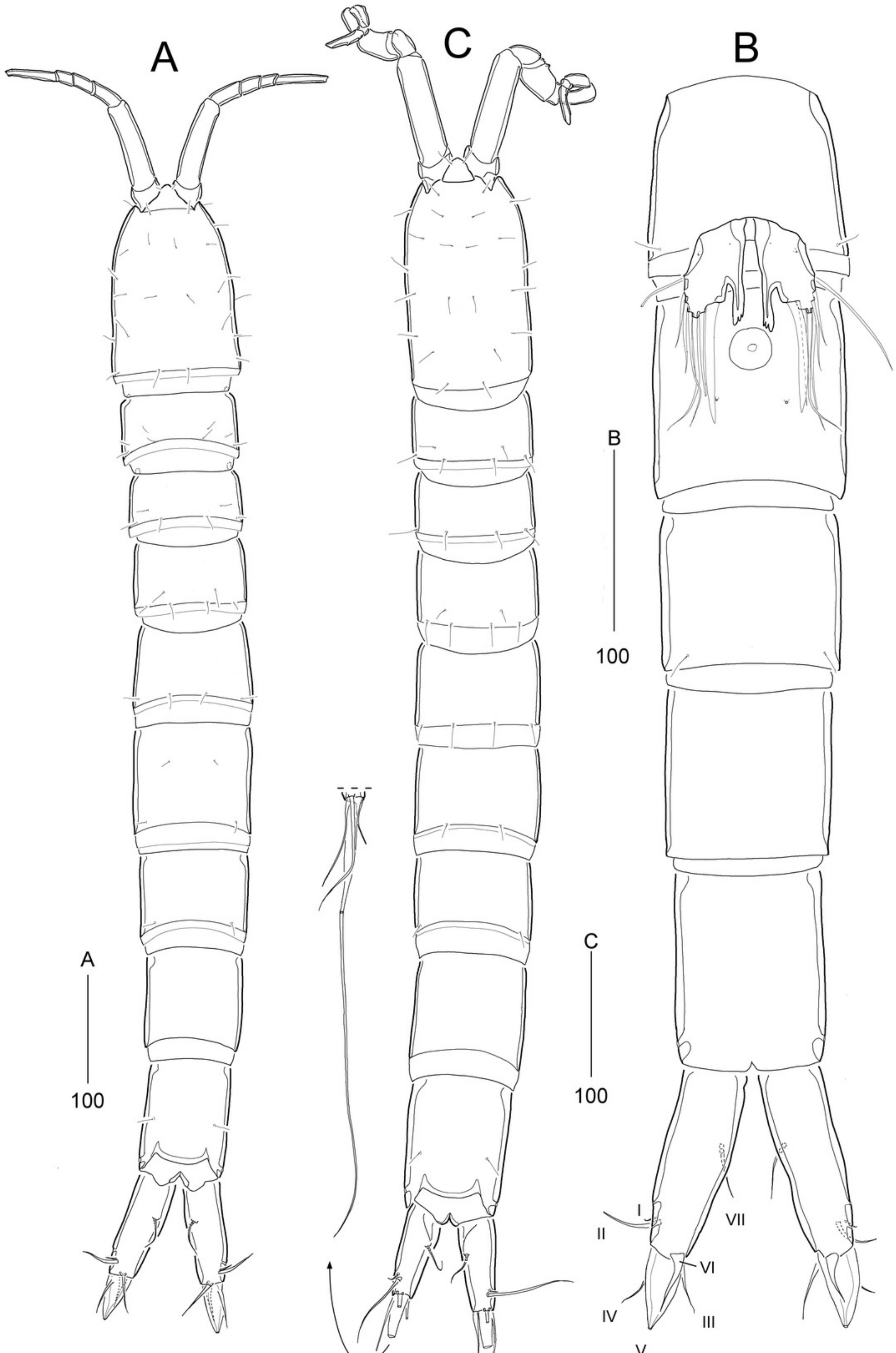

A
C
B
B
100
A
100
C
100
I
II
VII
VI
IV
III
V

Figure 9

Stenocaris intermedia Itô, 1972, female (A, B) and male (C) from Korean waters.

(A) Antennule; (B) Antenna; (C) Antennule. Scale bars are given in µm.

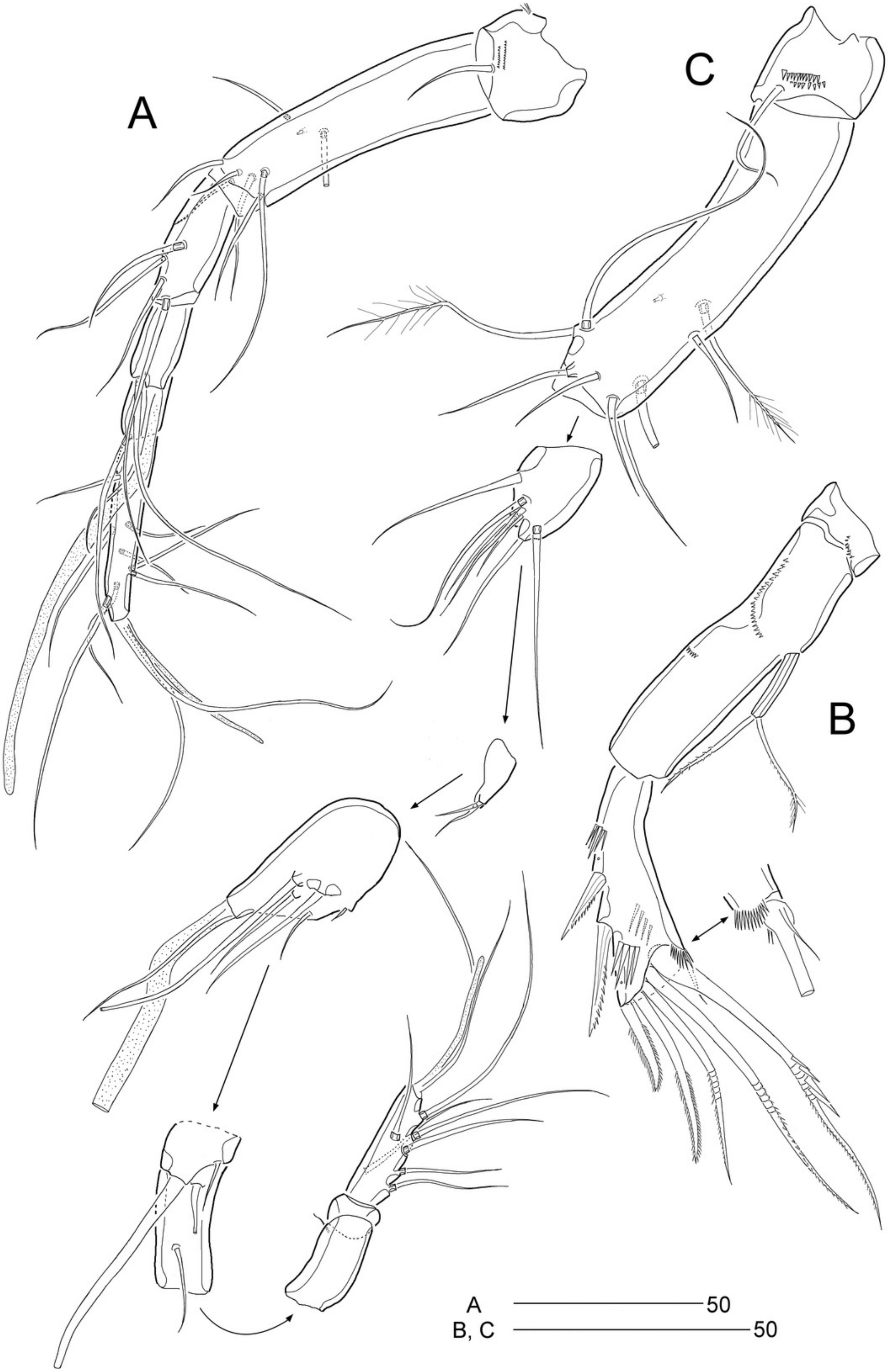

A
C
B
A 50
B, C 50

Figure 10

Stenocaris intermedia Itô, 1972, female from Korean waters.

(A) Mandible; (B) Mandibular ganathobase; (C) Maxillule; (D) Maxilla; (E) Maxilliped; (F) P5; (G) Genital field, ventral; (H) Genital field, lateral. Scale bars are given in μm.

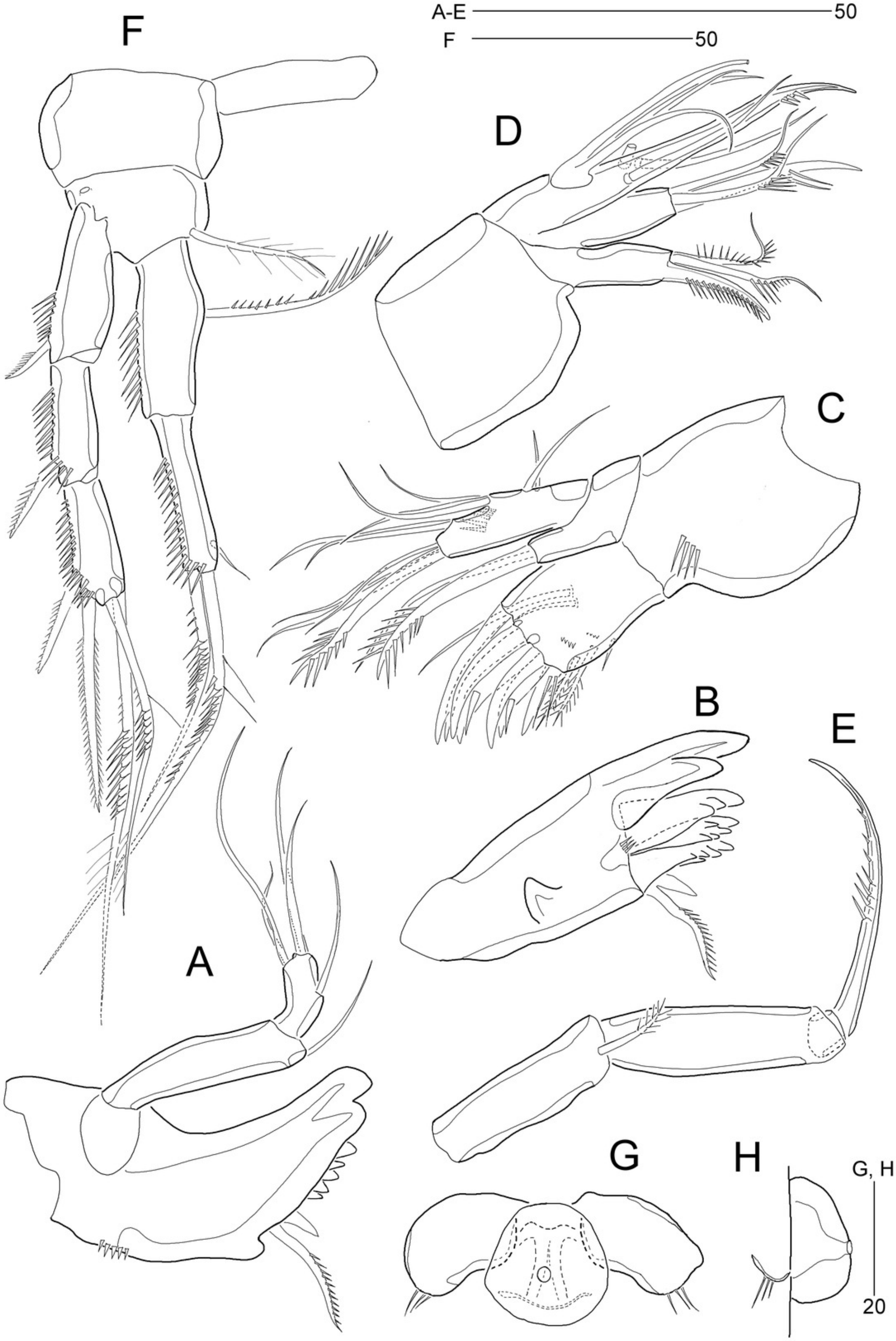

A-E 50
F 50
F
D
C
B
E
A
G
H
G, H
20

Figure 11

Stenocaris intermedia Itô, 1972, females from Korean (A–D) and Russian (E) waters.

(A) P2; (B) P3; (C) P4; (D) P5; (E) P5. Arrowheads indicate delicate and setule-like elements. Scale bars are given in µm.

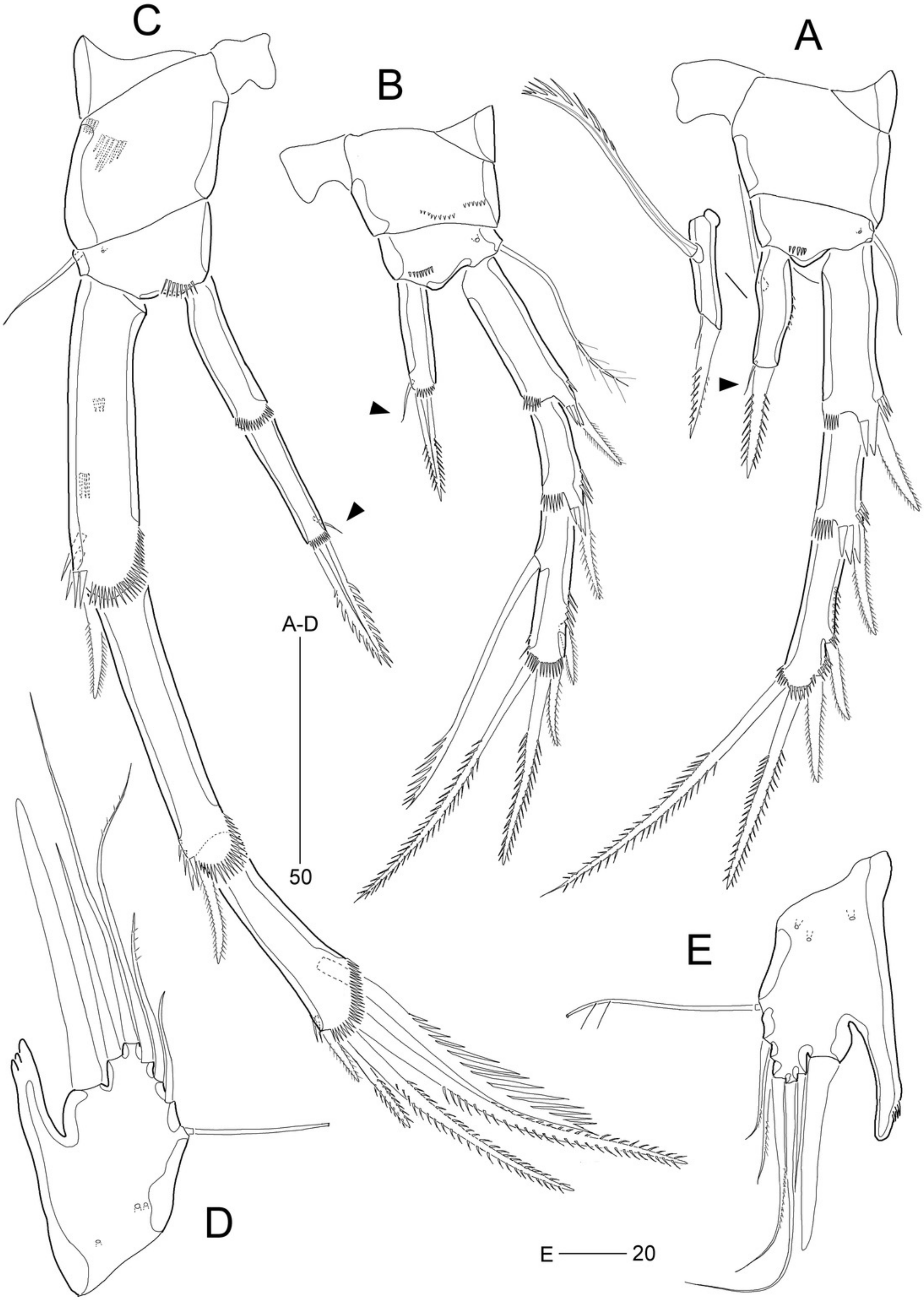
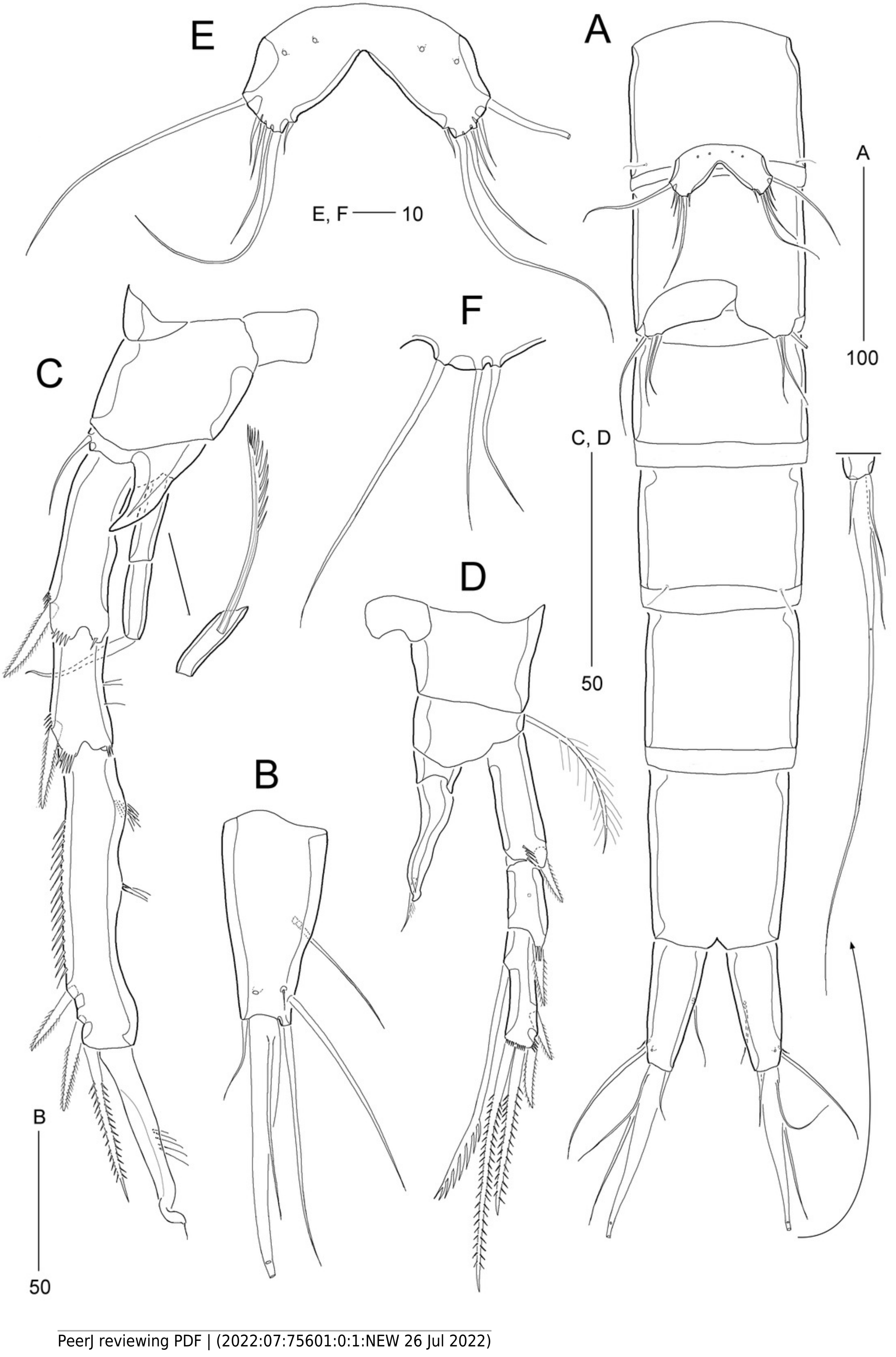

C
B
A
A-D
50
E
D
E
20

Figure 12

Stenocaris intermedia Itô, 1972, male from Korean waters.

(A) Urosome, ventral; (B) Caudal ramus, lateral; (C) P2; (D) P3; (E) P5; (F) P6. Scale bars are given in µm.


E
A
E, F 10
A
100
C
F
C, D
50
D
B
50
B
50