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Article in *Proceedings of the Biological Society of Washington* · July 2014

DOI: 10.2988/0006-324X-127.1.248

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**A new species of *Enhydrosoma* (Copepoda: Harpacticoida: Cletodidae)
from Korea, with redescription of *E. intermedia* and establishment of a new
genus**

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A new species of *Enhydrosoma* (Copepoda: Harpacticoida: Cletodidae) from Korea, with redescription of *E. intermedia* and establishment of a new genus

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Abstract.—Two species of *Enhydrosoma* Boeck, 1873, found in muddy sediments in the sublittoral zone of Gwangyang Bay, represent the first record of this genus in Korea. *Enhydrosoma coreana*, new species, shares a number of rare morphological features with the type species, *E. curticauda* Boeck, 1872, such as a bifid rostrum with centrally inserted sensilla, endopodal lobe of P5 with a peduncle, and a characteristic shape of the female genital field. They differ in the armature formula of the mandible, P1 endopod, and P5 exopod, size of the P5 peduncle, and minor details in the ornamentation of several somites. *Enhydrosoma intermedia* Chislenko, 1978 is redescribed from its holotype, freshly collected Korean material, and freshly collected material from and near its type locality in the Russian Far East. Its male is described for the first time. Minor morphological differences are observed between these two disjunct populations, such as longer caudal rami and sparse hair-like spinules on somites in Korean specimens. However, molecular data from the mtCOI gene suggest them to be conspecific. Detailed morphological comparisons between *E. coreana* and *E. intermedia* reveal a number of important differences, and molecular phylogenies suggest only a remote relationship. Their average pairwise maximum likelihood distances are very similar to those between other well-established genera of harpacticoid copepods. *Geehydrosoma*, new genus, is erected to accommodate *E. intermedia*, together with *E. brevipodum* Gómez, 2004, from the Pacific coast of Mexico.

Keywords: East Asia, *Geehydrosoma*, mtCOI, phylogeny, sublittoral, taxonomy

The family Cletodidae T. Scott, 1905 mostly includes active mud burrowers from shallow and sublittoral marine habitats, with some species in the deep sea and brackish waters (Boxshall & Halsey 2004).

It is a medium size harpacticoid family with about 115 valid species, classified into 23 genera, and a near global distribution (Wells 2007). The genus *Enhydrosoma* Boeck, 1873 is the largest group in the family, with more than 60 species described so far (Boxshall & Huys 2013), although

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many have subsequently been synonymized (Sars 1909, Lang 1948, Por 1986, Fiers 1996) or transferred to other known or newly established genera (Lang 1936, 1948, 1965; Gee 1994, 2001; Gee & Huys 1996). The genus currently harbors 34 valid species (Wells 2007) but is still not considered a monophyletic group (Gee 1994).

As with many other copepod genera, with the addition of new species the generic diagnosis has been expanded continually to accommodate newly discovered morphological features, with the end result being an extremely heterogeneous group (Fiers 1987, Mielke 1990, Gee & Huys 1996). However, several researchers made notable efforts to redefine this group of species (Sars 1909, Lang 1936, 1948, 1965; Gee 1994, 2001), often as a part of a broader *Enhydrosoma/Cletodes* "clade" of the family, although we are still awaiting a phylogenetic analysis of any sort. One of the main difficulties all researchers face, which remains true to this day, is that many of the species are known from a very limited set of morphological characters, often with the type material lost or impossible to trace. Gee (1994) re-described the type species, *E. curticauda* Boeck, 1872 and provided a very comprehensive overview of major morphological characters in the entire family. Gee, however, noted that the type species has a very isolated position in the genus, and that proper revision may eventually result in *Enhydrosoma* becoming a very small, or even monospecific genus.

We report here on two species of *Enhydrosoma* from muddy sediments in the sublittoral zone of Gwangyang Bay, which represent the first record of this genus in Korea. One of them is interesting because it is the first congener that shares a number of rare morphological features with the type species. The other one is morphologically very similar to *Enhydrosoma intermedia* Chislenko, 1978, described originally from a single female from Posyet Bay in the Russian Far East (Chislenko 1978), but with several minor

morphological differences. To determine the nature of these differences, we borrowed the holotype of this species from the Zoological Museum in St. Petersburg. We also collected several specimens from and near its type locality in Russia for both morphological and molecular analyses.

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, Hamrová et al. 2012, Karanovic & Krajcicek 2012a), invasions of new habitats and colonization pathways (Lee et al. 2003, 2007; Winkler et al. 2008, Karanovic & Cooper 2011a, 2012), anthropogenic translocation (Karanovic & Krajcicek 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 & Krajcicek 2012b, Karanovic & Kim 2014).

Materials and Methods

Korean specimens were collected from the sublittoral zone of Gwangyang Bay,

Korea, sampling stations 3, 5, 7, 10, 13, 14, and 16 on 25 Jan 2006, 18 Feb 2012, and 30 Jul 2012 for morphological and molecular analyses. Details of the sampling stations are provided by Karanovic & Kim (2014). Water depth ranged from 4 to 11 m, always with muddy sediment. Primary sediment samples were collected with a van Veen grab with a surface area of 0.1 m^{-2} on board the R/V *Hansan*. Secondary sediment samples were collected with an acrylic corer with a surface area of 10 cm^{-2} for quantitative analysis, and the surface layer of sediment was collected with a rice paddle for qualitative analysis. Each sediment sample was fixed in 70% ethanol for morphological analysis and in 99.9% ethanol for molecular analysis. Harpacticoids were extracted from sediment samples using a $38 \mu\text{m}$ sieve and the Ludox method (Burgess 2001) and preserved in 70% or 99.9% ethanol. Russian specimens were collected from Posyet Bay (Minonosok Inlet) and Russky Island (Rynda bay), using hand-nets (100 μm mesh size) during scuba dives. Water depths ranged from 4 to 7 m, with sandy sediment. Data for sampling stations and number of specimens are provided in the Material examined section.

Before dissection, the habitus was drawn, and the body length was measured from whole specimens mounted temporarily in lactophenol. Specimens were dissected in lactophenol, and the dissected parts were mounted on slides, using lactophenol or CMC-10 mounting medium. The coverslips were sealed with transparent nail varnish. All drawings were prepared using a drawing tube on Olympus BX51 and Leica DM2500 differential interference contrast microscopes. Some specimens were examined with a Hitachi S-4700 scanning electron microscope (SEM) at Eulji University, Seoul, Korea. Specimens were prepared for SEM by dehydration through graded ethanol, critical-point dried, mounted on stubs and sputter-coated with gold. Scale bars in all illustra-

tions and SEM micrographs are in μm . Digital photographs were processed and combined into plates using Adobe Photoshop CS4.

The holotype female of *E. intermedia* Chislenko, 1978, dissected on one slide, was borrowed from St. Petersburg to check the original description from Russia.

The descriptive terminology follows Huys et al. (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; enp, endopod; exp, exopod; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. The type series is deposited in the collections of the National Institute of Biological Resources (NIBR), Incheon, South Korea. Specimens prepared for SEM are deposited in the collection of one of the authors (WL) in the Laboratory of Biodiversity, Department of Life Science, Hanyang University, Seoul.

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 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 omitted, and 60 μl (instead of 200 μl) of Buffer AE was added in the final step, to increase the density of DNA. The mitochondrial cytochrome oxidase subunit I (mtCOI) gene was amplified through polymerase chain reaction (PCR) using PCR premix (BiONEER Co.) in a TaKaRa PCR thermal cycler (Takara Bio Inc., Otsu, Shiga, Japan). The amplification primers used were the 'universal' primers LCOI490 and HCO2198 (Folmer

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

| Code | Species | Sex | Country | Station | Coordinates | Date | Bases | GenBank |
|------|-------------------------------|-----|---------|------------|-----------------------------|-------------|-------|----------|
| KC16 | <i>Enhydrosoma coreana</i> | ♀ | Korea | St. 10 | 34°55'15.4"N, 127°47'07.9"E | 30 Jul 2012 | 660 | KJ572386 |
| KC17 | <i>Enhydrosoma coreana</i> | ♀ | Korea | St. 10 | 34°55'15.4"N, 127°47'07.9"E | 30 Jul 2012 | 660 | KJ572387 |
| KC18 | <i>Enhydrosoma coreana</i> | ♂ | Korea | St. 10 | 34°55'15.4"N, 127°47'07.9"E | 30 Jul 2012 | 679 | KJ572388 |
| KC35 | <i>Enhydrosoma intermedia</i> | ♀ | Korea | St. 13 | 34°51'09.9"N, 127°47'27.6"E | 18 Feb 2012 | 567 | KJ572389 |
| KC36 | <i>Enhydrosoma intermedia</i> | ♂ | Korea | St. 13 | 34°51'09.9"N, 127°47'27.6"E | 30 Jul 2012 | 663 | KJ527390 |
| KC37 | <i>Enhydrosoma intermedia</i> | ♂ | Korea | St. 13 | 34°51'09.9"N, 127°47'27.6"E | 30 Jul 2012 | 663 | KJ527391 |
| KC39 | <i>Enhydrosoma intermedia</i> | ♀ | Russia | Posyet Bay | 42°36'33.2"N, 130°51'42.1"E | 06 May 2012 | 669 | KJ527392 |
| KC40 | <i>Stylicletodes</i> sp. | ♀ | Korea | St. 3 | 34°53'03.9"N, 127°39'50.5"E | 30 Jul 2012 | 660 | KJ527393 |
| KC41 | <i>Stylicletodes</i> sp. | ♀ | Korea | St. 3 | 34°53'03.9"N, 127°39'50.5"E | 30 Jul 2012 | 660 | KJ527394 |

et al. 1994). The amplification protocol was: initial denaturation at 94°C for 300 sec, 40 cycles of denaturation at 94°C for 30 sec, annealing at 42°C for 120 sec, extension at 72°C for 60 sec, and final extension at 72°C for 600 sec; the 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 nine cletodid 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 & Crandall 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. Neighbor-joining (NJ) analysis used the Tamura-Nei model (Tamura & Nei 1993) with uniform rates (TN). All phylogenetic and molecular evolutionary analyses were conducted using MEGA version 5.2.2 (Tamura et al. 2011). Five hundred bootstrap replicates were performed to obtain a relative measure of node support for the resulting trees. Average pairwise ML distances for each dataset were also computed in MEGA version 5.2.2, using the Tamura-Nei model. All trees were rooted with *Coullana* sp., its mtCOI sequences available from GenBank prior to this study [AF315015], which belongs to the supposedly primitive harpacticoid family Canuellidae Lang, 1944 (see Lang 1948, Seifried 2003).

Systematics

Family Cletodidae T. Scott, 1905 sensu Por (1986)
Genus *Enhydrosoma* Boeck, 1873 sensu Gee (1994)

Enhydrosoma coreana, new species
Figs. 1–8

Type locality.—South Korea, South Sea, Gwangyang Bay, sampling station

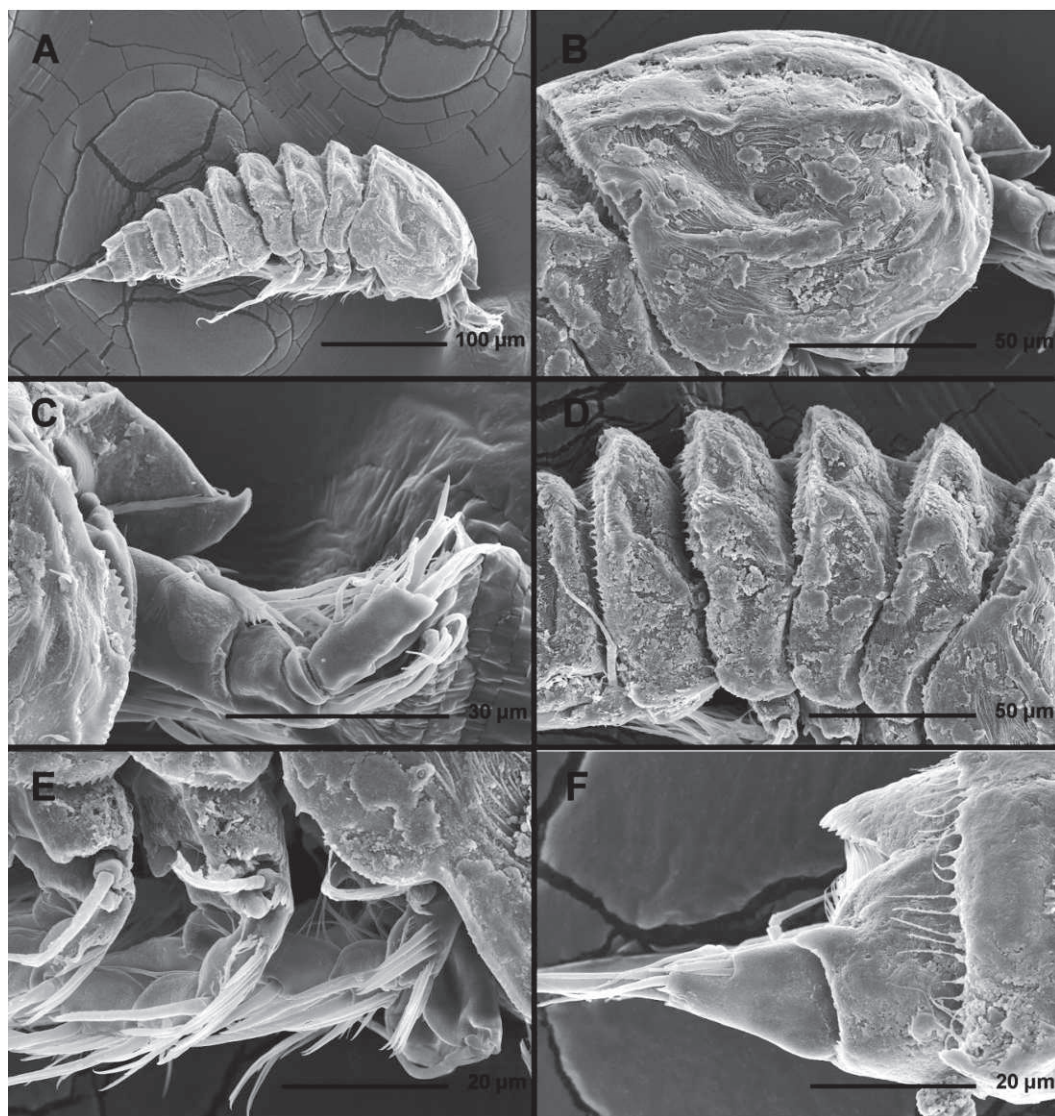


Fig. 1. *Enhydrosoma coreana* (♀), SEM micrographs. A, habitus, lateral; B, cephalic shield, lateral; C, rostrum and antennule, lateral; D, free prosomites, lateral; E, P1–P3, lateral; F, anal somite and caudal ramus, lateral.

10, muddy sediments, 34°55'15.4"N, 127°47'07.9"E.

Material examined.—Holotype ♀ (NIBRIV 0000287189) in 70% ethanol collected from the type locality. Paratypes: 1 ♀ and 2 ♂♂ (NIBRIV 0000287190) in 70% ethanol collected from type locality; 2 ♀♀ (NIBRIV 0000287191) dissected on 9 and 13 slides,

respectively; 1 ♂ (NIBRIV 0000287192) dissected on 9 slides, collected from sampling station 14 (34°49'27.2"N, 127°47'15.9"E); 5 ♀♀ and 1 ♂ (NIBRIV 0000287193) in 70% ethanol, collected from sampling station 14 (34°49'27.2"N, 127°47'15.9"E); 1 ♀ and 1 ♂ (NIBRIV 0000287194) in 70% ethanol, collected from sampling station 16 (34°46'08.0"N,

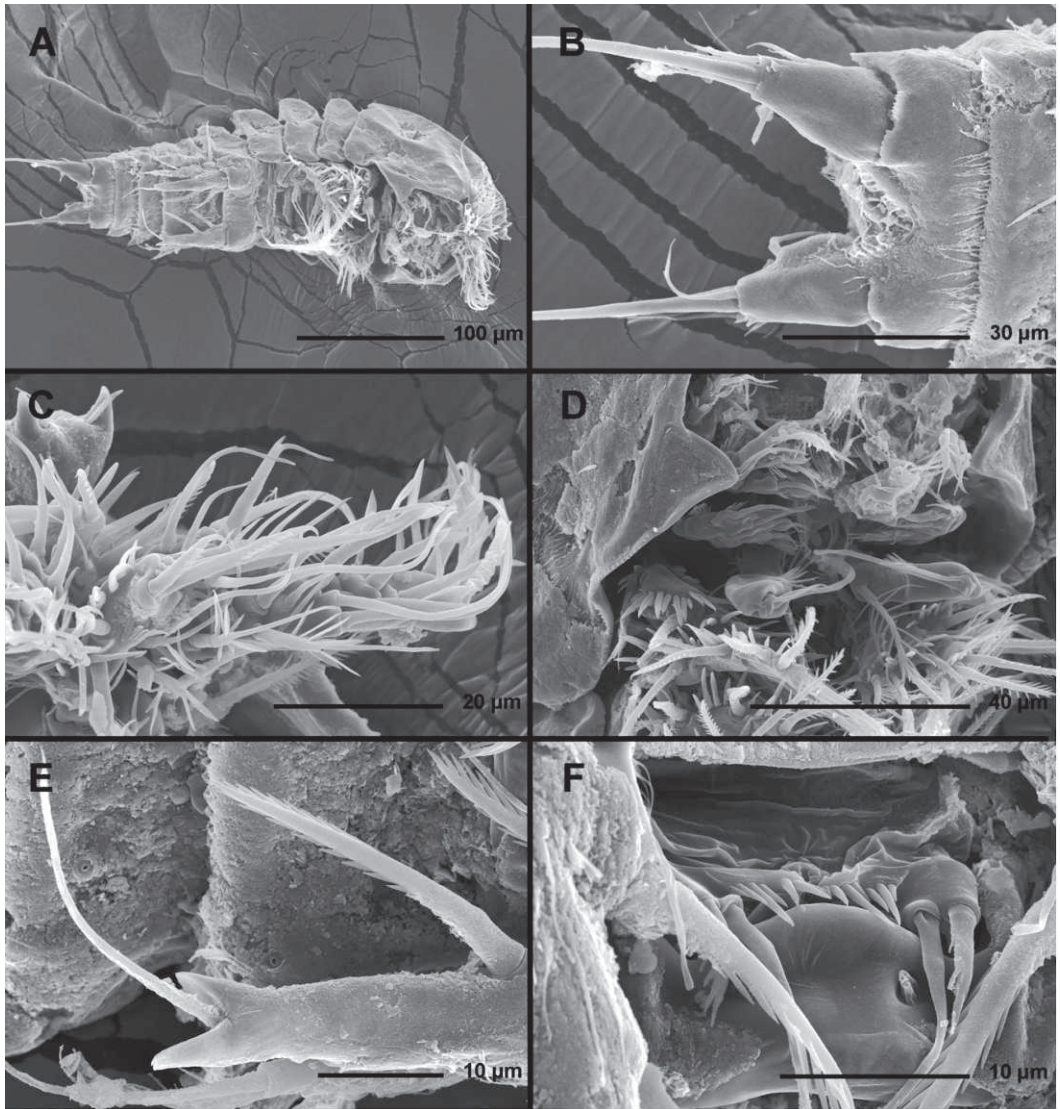


Fig. 2. *Enhydrosoma coreana* (♀), SEM micrographs. A, habitus, ventral; B, anal somite and caudal rami, ventral; C, rostrum and antennule, ventral; D, mouth appendages, ventral; E, P5; F, P6.

127°47'01.7"E). An additional 3 ♀♀ and 1 ♂ were examined with SEM and deposited in the collection of one of us (WL). All type specimens for morphological analysis were collected from the sampling stations in Gwangyang Bay on 25 Jan 2006 by K. Kim. 2 ♀♀ and 1 ♂ used for molecular analyses were collected at the type locality on 30 Jul 2012 by K. Kim.

Etymology.—The specific name refers to the country of the type locality, Gwangyang Bay.

Description of female.—Total body length 306–447 µm (measured from anterior margin of cephalic shield to posterior margin of caudal rami, mean = 363 µm, $n = 6$). Body (Figs. 1A, 2A) tapering from cephalothorax to caudal ramus, curved ventrally in lateral view,

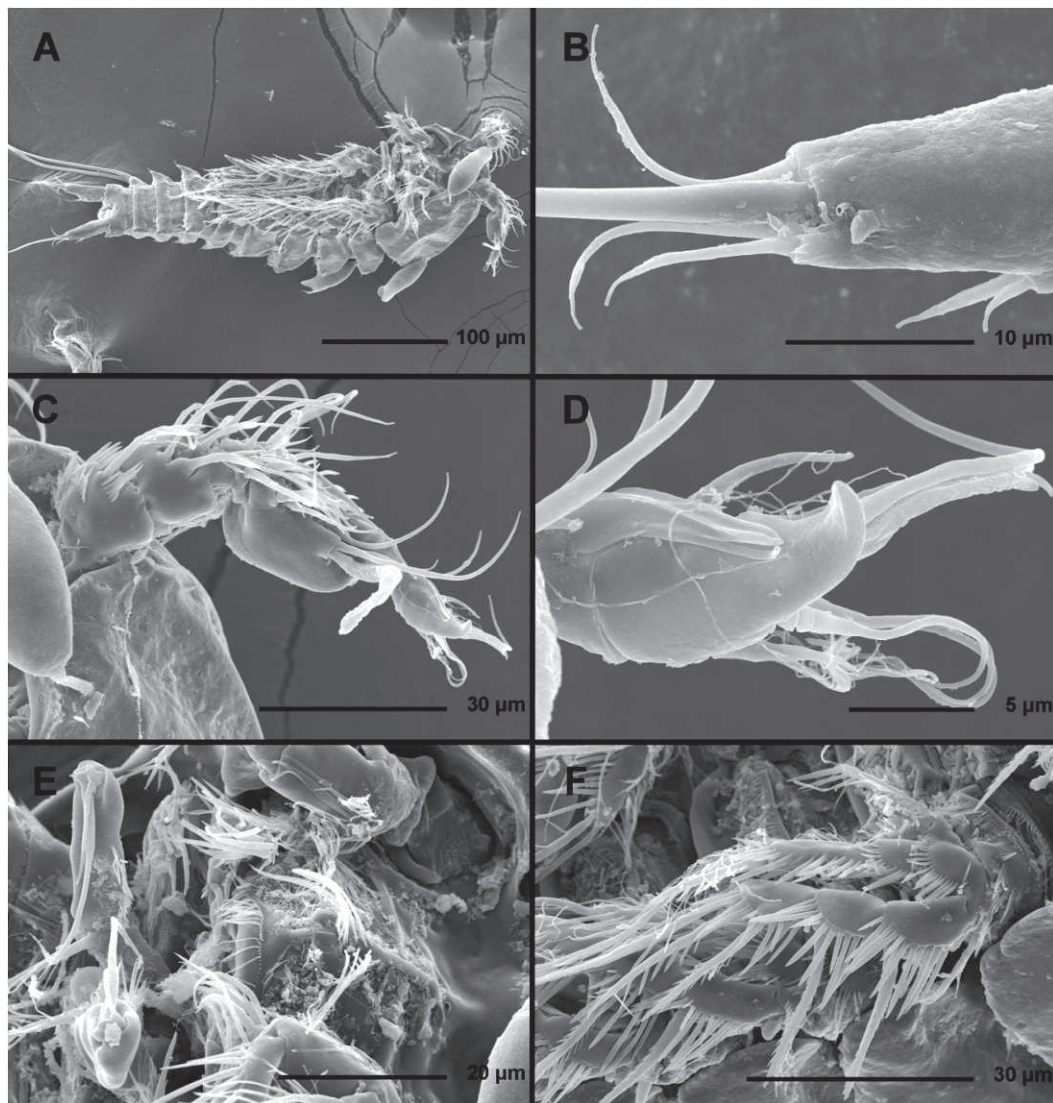


Fig. 3. *Enhydrosoma coreana* (♂), SEM micrographs. A, habitus, ventral; B, caudal ramus, ventral; C, antennule, ventral; D, antennule, distal tip; E, mouth appendages, ventral; F, P1.

without clear distinction between prosome and urosome. All somites with pores and/or sensilla as in SEM photomicrographs in Figures 1 and 2.

Rostrum (Figs. 1C, 2C, 4A) small, fused to cephalic shield, dorsally recurved in lateral view, bifid at tip, bearing two sensilla between bifid structures, pore located on ventral side.

Prosome (Fig. 1B, D) four-segmented, including cephalothorax and three free pedigerous somites. Cephalothorax with dorsal surface with longitudinal ridges and posterior margin ornamented with minute spinules. Free pedigerous somites with short spinules and pair of papillary socles (each bearing sensillum apically) on dorsal posterior margin; two small longitudinal ridges on dorsal surface of each segment.



Fig. 4. *Enhydrosoma coreana* (♀). A, rostrum and antennule, ventral; B-E, segments 2-5, respectively, of antennule, ventral; F, segment 2 of antennule, dorsal; G, antenna; H, labrum; I, mandible; J, maxillule; K, maxilla; L, maxilliped.



Fig. 5. *Enhydrosoma coreana* (♀). A, P1, anterior; B, P2, anterior.



Fig. 6. *Enhydrosoma coreana* (♀). A, P3, anterior; B, P4, anterior.

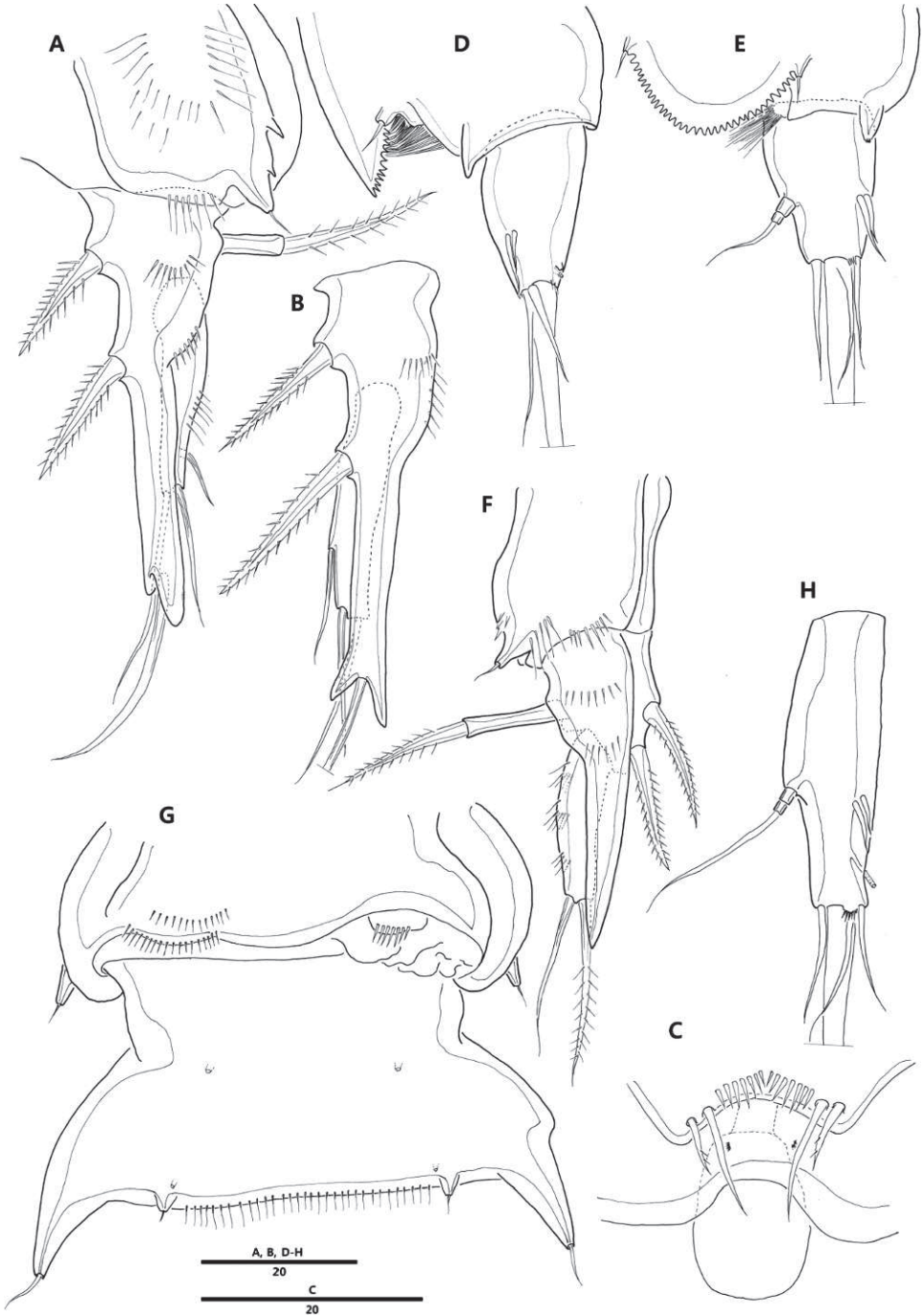


Fig. 7. *Enhydrosoma coreana*. A, P5, ventral (♀); B, P5, inner lateral (♀); C, P6 and genital field, ventral (♀); D, caudal ramus, lateral (♀); E, caudal ramus, dorsal (♀); F, P5, ventral (♂); G, P6 and genital field, ventral (♂); H, caudal ramus, dorsal (♂).

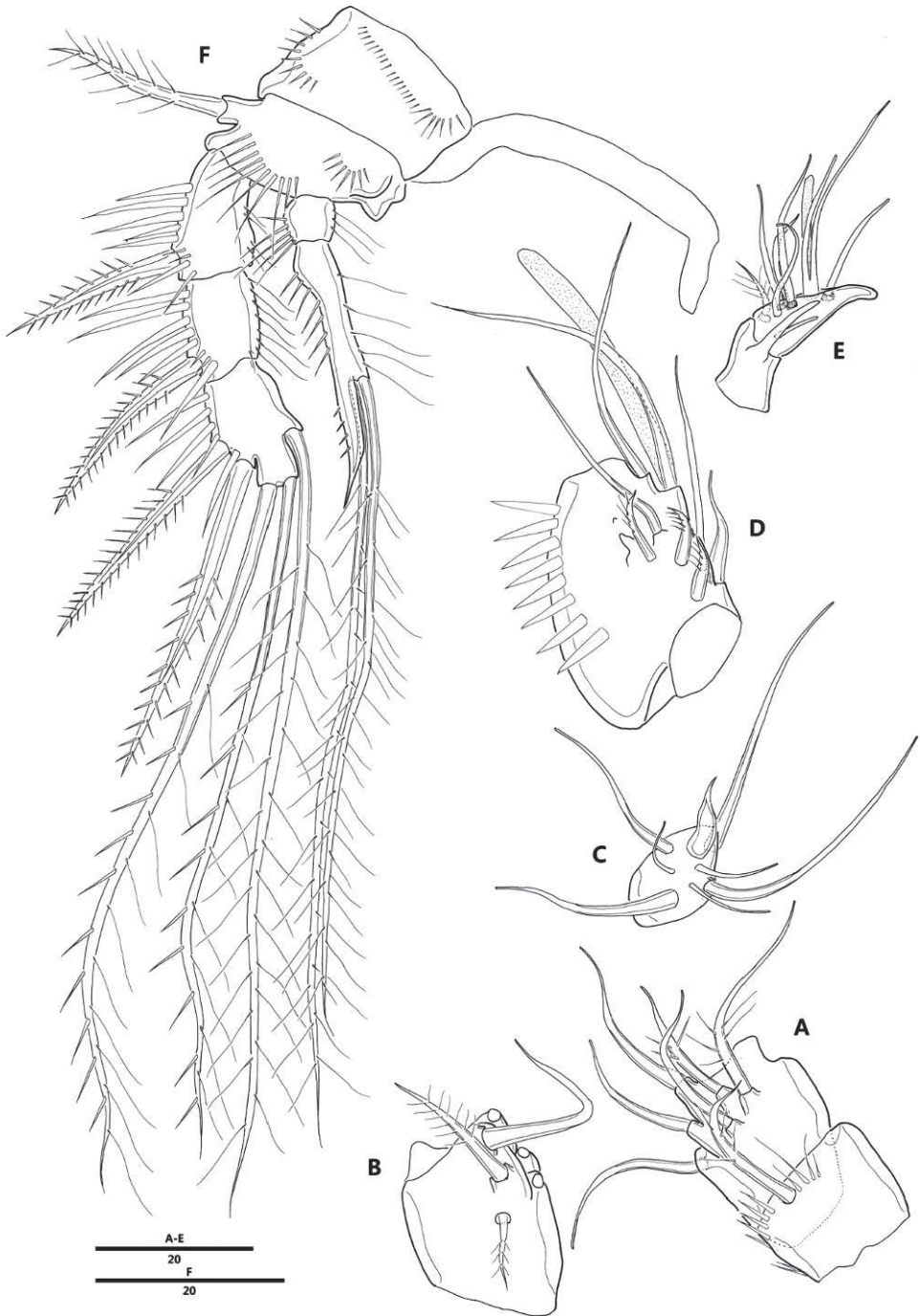


Fig. 8. *Enhydrosoma coreana* (♂). A, segments 1 and 2 of antennule, ventral; B, segment 2 of antennule, dorsal; C, segment 3 of antennule, ventral; D, segment 4 of antennule, ventral; E, segments 5 and 6 of antennule, ventral; F, P3, anterior.

Urosome (Figs. 1A, F, 2A, B) five-segmented, including P5-bearing somite, genital double-somite, and three free abdominal somites. All urosomites, except anal somite, with spinules and pair of papillary socles on dorsal posterior margin, genital double-somite and next two free abdominal somites each with pair of papillary socles ventrolaterally.

Genital double-somite (Figs. 2F, 7C) with dorsal subcuticular ridge indicating line of fusion, but completely fused ventrally. Genital apertures forming common transverse genital slit; covered by vestigial P6, each bearing two setae (one long and naked, one short and pinnate); spinular row developed between P6; midventral copulatory pore moderately large and located at midlength of somite; two groups of three tubular pores located between copulatory pore and genital slit.

Anal somite partially divided medially (Figs. 1F, 2B, 7D, E); dorsolateral socle dentate at tip, without sensillum. Anal operculum dentate, semicircular.

Caudal rami (Figs. 1F, 2B, 7D, E) divergent, vase-shaped, broad at base, tapering posteriorly, 1.5 times longer than wide. All caudal setae bare. Setae I and II located at middle of outer margin, seta II 1.5 times longer than seta I; seta III located on outer distal corner and about two times longer than seta I, origin of seta III dentate; setae IV and V fused at base, seta IV slightly longer than seta III; seta V longest, as long as urosome, broad at base; seta VI located on inner distal corner, as long as seta III; seta VII located dorsolaterally in distal half of inner margin. Small tube pore located on ventral distal corner.

Antennule (Figs. 1C, 2C, 4A–F) short, stout, five-segmented. First segment with spinule rows on ventral surface; second segment with small plumose seta implanted at circular cup-shaped depression on dorsal surface of third segment, with aesthetasc fused basally to seta; last segment with apical acrothek consisting of two setae and aesthetasc. Armature

formula: 1-[1 pinnate], 2-[5 + 5 pinnate], 3-[3 + 2 pinnate + (1 + ae)], 4-[1], 5-[6 + 3 pinnate + acrothek].

Antenna (Fig. 4G). Coxa well developed, ornamented with spinular row on distal margin. Basis and first endopodal segment completely fused, forming allobasis; abexopodal margin with spinular row. Exopod one-segmented with two setae (unipinnate distal seta, and bipinnate subdistal seta) and row of spinules subdistally. Free endopodal segment with spinular rows; stout spinular rows on outer margin and two rows of small spinules subdistally on posterior surface; two stout pinnate spines located on posterior surface medially and five elements distally (two stout unipinnate spines, one geniculate seta, one long naked seta, and one large pectinate spine).

Labrum (Fig. 4H). Coarse and short setules along posterior margin. Chitinous projection located on anterior ventral surface, with long setules.

Mandible (Figs. 2D, 4I). Syncoxa relatively slender, recurved. Gnathobase with several teeth along distal margin and naked seta fused at dorsal corner. Palp one-segmented, with three bipinnate setae and ornamented with three rows of spinules.

Maxillule (Figs. 2D, 4J). Praecoxal arthrite with two large tube setae on anterior surface and six elements distally (three naked spines, one stout claw fused to arthrite, one naked seta, and one small pinnate seta). Coxa with two setae (one pinnate and one naked) distally and spinular row on anterior surface. Exopod and endopod fused to basis, with row of spinules on anterior surface and bearing six elements (one large stout pinnate spine, one short and one long naked seta on distal margin; one subdistal naked seta representing exopod; one seta located on proximal outer margin, and another seta arising from small ridge on posterior surface, representing endopod).

Maxilla (Figs. 2D, 4K). Syncoxa with four spinular rows and single endite. Syncoxal endite (proximal one) with one stout pinnate spine, one slender seta, and one tube seta. Distal endite armed with two pinnate spines and one slender naked seta. Basal endite with smooth spine distinct at base, tube seta on posterior surface and naked seta distally. Endopod represented by two tubular setae fused at their bases.

Maxilliped (Figs. 2D, 4L). Syncoxa with spinular row on posterior surface and bipinnate seta at inner distal corner. Palmar margin of basis with spinular row. Endopod with curved slender claw distinct from endopodal segment, and naked accessory seta fused to endopod at base.

P1 (Figs. 1E, 5A). Praecoxa well developed. Coxa broad; long spinular row toward inside, long setular row toward outside and two minute setular rows on anterior surface. Basis with bipinnate outer seta, pectinate inner spine, and two rows of spinules (one row near base of outer seta and another row along distal margin). Exopod three-segmented, each segment slightly longer than wide; exp-1 with one outer bipinnate spine and spinular row along outer margin; exp-2 with one outer bipinnate spine, spinular row along outer margin, and setular rows on inner margin; exp-3 bearing two outer spines (one bipinnate and another unipinnate) and two distal setae, ornamented with spinular row along outer margin and setular row along inner margin. Endopod two-segmented; enp-1 as long as wide, ornamented with row of slender setules on inner margin and row of spinules along outer margin; enp-2 three times longer than wide, long setules along inner margin and long spinules along outer and distal margin, one bipinnate seta distally and one spine at outer distal corner.

P2 (Figs. 1E, 5B) with thin and wide intercoxal sclerite. Praecoxa with a spinular row. Coxa with long setular row on

outer subdistal corner and three spinular rows on anterior surface. Basis with three spinular rows and bearing outer plumose seta. Exopod three-segmented, each segment slightly longer than wide, all segments with spinular row along outer margin; exp-1 with one bipinnate spine and short spinular row on inner distal corner; exp-2 with one bipinnate outer spine and long setular row along inner margin; exp-3 with two outer spines and two distal setae. Endopod two-segmented, each segment ornamented with spinules along outer margin and setules along inner margin; enp-1 as long as wide; enp-2 3.5 times longer than wide, bearing two setae distally.

P3 (Figs. 1E, 6A) with smooth and wide intercoxal sclerite. Praecoxa with two short spinular rows. Coxa ornamented with three spinular rows on anterior surface and outer distal corner. Basis with three spinular rows near endopod and bearing one outer bipinnate seta, and small rounded projection on inner margin. Exopod three-segmented, each segment longer than broad, all segments with setules on inner margin and spinules along outer margin; exp-1 and exp-2 with bipinnate spine at outer distal corner; exp-3 with two outer spines, two distal setae and one inner seta, all elements bipinnate. Endopod two-segmented, each segment ornamented with setules on inner margin and spinules on outer margin; enp-1 slightly broader than long; enp-2 four times longer than wide, bearing two setae distally.

P4 (Fig. 6B) with smooth and wide intercoxal sclerite. Praecoxa with short spinular row distally. Coxa with three spinular rows. Basis ornamented with three rows of spinules and bearing one outer bipinnate seta, and small rounded projection at middle of inner margin. Exopod three-segmented, each segment slightly longer than wide, all segments ornamented with setules on inner margin and spinules along outer margin; exp-1 and exp-2 with bipinnate spine at outer

distal corner; exp-3 with two outer spines, two distal setae and one inner seta, all elements bipinnate. Endopod two-segmented, each segment ornamented with setules on inner margin and spinules along outer margin; enp-1 wider than long; enp-2 3.5 times longer than wide, bearing two distal bipinnate setae.

Armature of P1–P4 as follows:

| | Exopod | Endopod |
|----|---------|---------|
| P1 | 0.0.022 | 0.011 |
| P2 | 0.0.022 | 0.020 |
| P3 | 0.0.122 | 0.020 |
| P4 | 0.0.122 | 0.020 |

P5 (Figs. 2A, E, 7A, B) biramous, comprising cylindrical exopod and large baseoendopod. Exopod shorter than endopodal lobe; outer margin with one naked seta at proximal fourth and another naked seta subdistally; apex with one naked seta. Baseoendopod ornamented with spinular rows on anterior surface; outer basal seta arising from long slender peduncle. Endopodal lobe elongated and apex splits into two, nearly bifid; inner margin bearing two stout bipinnate spines and one naked seta located between bifid structures.

Description of male.—As in female, except in urosome, genital area, caudal rami, antennule, P3, and P5. Mouth appendages (Fig. 3E) and P1 (Fig. 3F) with no difference from female. Body (Fig. 3A) slightly more slender than female, length 336–373 μm (measured from anterior margin of cephalic shield to posterior margin of caudal rami, mean = 351 μm , $n = 3$). Urosomites-2 and -3 not fused.

Caudal rami (Figs. 3B, 7H), cylindrical, three times longer than wide. Setae I, II, and VII arising at about two-thirds of ramus length. Setal arrangements as in female. Tubepore located subdistally on outer margin.

Antennule (Figs. 3C, D, 8A–E) 6-segmented, short, subchirocer. First segment with two rows of spinules and

bearing one pinnate seta; second segment with small plumose seta implanted at circular depression on dorsal surface, as in female; third segment minute; fourth segment swollen, with spinules on anterior surface; fifth segment with modified spine; apex of seventh segment recurved. Armature formula: 1-[1 pinnate], 2-[5 + 4 pinnate], 3-[8], 4-[4 + 3 pinnate + (1 + ae)], 5-[1], 6-[6 + 1 pinnate + acrothek].

P3 (Fig. 8F). Protopod and exopod as in female. Endopod 2-segmented. Outer distal corner of enp-2 forming spinous process with spinules on outer margin.

P5 (Fig. 7F). Fifth pair of legs not fused medially. Baseoendopod with elongated setophore bearing outer basal seta; endopodal lobe longer than exopod, bearing two bipinnate spines on inner margin, apical seta absent. Exopod cylindrical; ornamented with rows of spinules and bearing two naked apical setae.

P6 (Fig. 7G) asymmetrical; each side represented by small plates with rows of spinules, left plate fused to urosomite and right plate functional, covering gonopore.

Geehydrosoma, new genus

Type species.—*Enhydrosoma intermedia* Chislenko, 1978.

Other species.—*Enhydrosoma brevipodum* Gómez, 2004.

Etymology.—The new genus name is dedicated to Dr. Michael Gee, formerly of the Plymouth Marine Laboratory, United Kingdom, for his contribution to the taxonomy of harpacticoids in general, and revisionary work on cletodids in particular. His last name is prefixed to the neo-Latin noun *Hydrosoma*, commonly used as a stem of cletodid generic names.

Diagnosis.—Habitus robust, spindle-shaped in dorsal view, widest at posterior end of cephalon and slowly tapering toward posterior end of body; podoplean boundary between prosome and urosome not conspicuous. Integument of all somites

relatively strongly sclerotized, generally very strongly sculptured, with very smooth higher areas and depressions of various sizes that are generally filled with hair-like spinules. Hyaline fringe of somites narrow, with posterior row of hair-like spinules and several papillary socles (bearing one sensillum apically). Abdominal somites with uninterrupted posterior rows of large spinules between ventral socles. Rostrum small, triangular, fused to cephalic shield, dorsally recurved in lateral view, apical portion between sensilla convex, ventral surface without pore. Genital double-somite with dorsal subcuticular ridge indicating line of fusion, but fused midventrally; genital apertures forming common transverse genital slit, covered by vestigial P6, represented by one minute seta and small triangular lobe on each side; midventral copulatory pore moderately small and located at midlength of double-somite. Anal somite partially cleft medially; anal operculum dentate or smooth, semicircular. Caudal rami divergent, cylindrical, from 3.5 to 8.3 times as long as wide, broad at base and tapering posteriorly; all caudal setae bare; setae I and II located proximally on outer margin and naked, seta II two times longer than seta I; seta III located at middle of outer margin and three times longer than seta I; setae IV and V fused at base, seta IV similar in length to seta III; seta V longest, as long as caudal ramus; seta VI slightly shorter than seta IV; seta VII as long as seta II, arising from projection located on inner proximal portion of dorsal surface. Female antennule short, stout, five-segmented; first segment with spinular rows; second segment with small plumose seta implanted at circular depression on dorsal surface; fifth segment with three lateral spiniform setae. Male antennule six-segmented, short, subchirocer, without spiniform setae on ultimate segment. Antenna composed of small and unarmed coxa, robust allobasis (unarmed or with very slender seta), one-segmented exopod

armed with two setae, and one-segmented endopod armed with two lateral and five apical elements. Labrum trapezoid. Mandible with very slender syncoxa; palp one-segmented, armed with three setae. Maxillule arthrite with one surface seta and eight distal elements; coxa and basis fused, armed with five setae. Maxilla with two endites on syncoxa, proximal endite armed with three elements, distal with two; distal element on distal endite modified, recurved and fused at base; basal endite with smooth spine fused at base, naked seta on each surface; endopod represented by two setae fused at their bases. Maxilliped with narrow syncoxa without seta at inner distal corner; basis large but also unarmed; endopod with curved slender claw, distinct from endopodal segment, and short naked accessory seta. All swimming legs composed of very short and unarmed praecoxa, unarmed quadriform coxa, short basis with outer spiniform seta (first leg additionally with seta on inner-distal corner), three-segmented exopod, and two-segmented endopod. All exopodal segments of about same length, first endopodal segment shorter than second endopodal segment. No sexual dimorphism in swimming legs, except outer spine on second exopodal segment of third leg larger and recurved in male. Armature formula of swimming legs as follows (P1–P4; Exp/Enp): 0.0.022/0.111; 0.0.022/0.020; 0.0.122/0.021; 0.0.122/0.021. Female P5 biramous, comprising short broad exopod armed with four elements (innermost longest and strongest) and very short endopodal lobe armed with three elements (central longest; outer strongest); exopod partly fused to baseoendopod. Male P5 with much longer exopod, armed with only two elements; endopodal lobe also with only two elements. Male P6 asymmetrical; each side represented by small plate with rows of spinules, left plate fused to urosomite and right plate functionally covering gonopore.

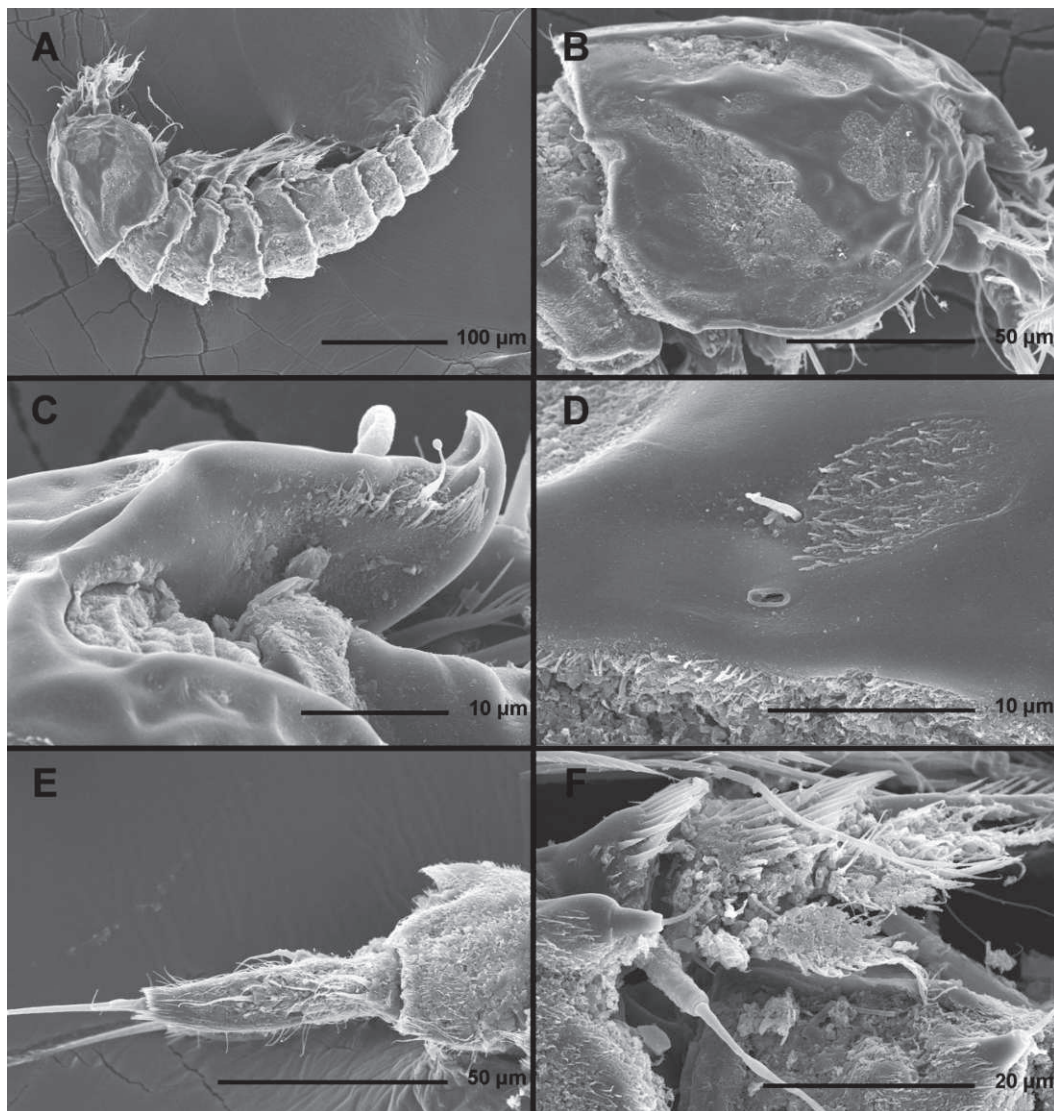


Fig. 9. *Geehydrosoma intermedia* (Chislenko, 1978) (♀) from Russia, SEM micrographs. A, habitus, lateral; B, cephalic shield, lateral; C, rostrum, lateral; D, cephalic shield, detail of ornamentation; E, caudal ramus, lateral; F, P5.

Geehydrosoma intermedia (Chislenko, 1978), new combination
Figs. 9–19

Enhydrosoma intermedia Chislenko, 1978:185, figs. 17, 18

Type locality.—Russia, Primorsky Krai, Posyet Bay, Minonosok inlet, sandy sediments at 3–4 m depth.

Material examined.—Korea: 1 ♀ (NIBRIV 0000287203) dissected on 6 slides, collected from sampling station 5 (34°51'09.0"N, 127°41'05.0"E); 1 ♀ (NIBRIV 0000287204) dissected on 7 slides, collected from sampling station 7 (34°53'49.4"N, 127°45'27.8"E); 1 ♀ (NIBRIV 0000287205) in 70% ethanol, collected from sampling station 8

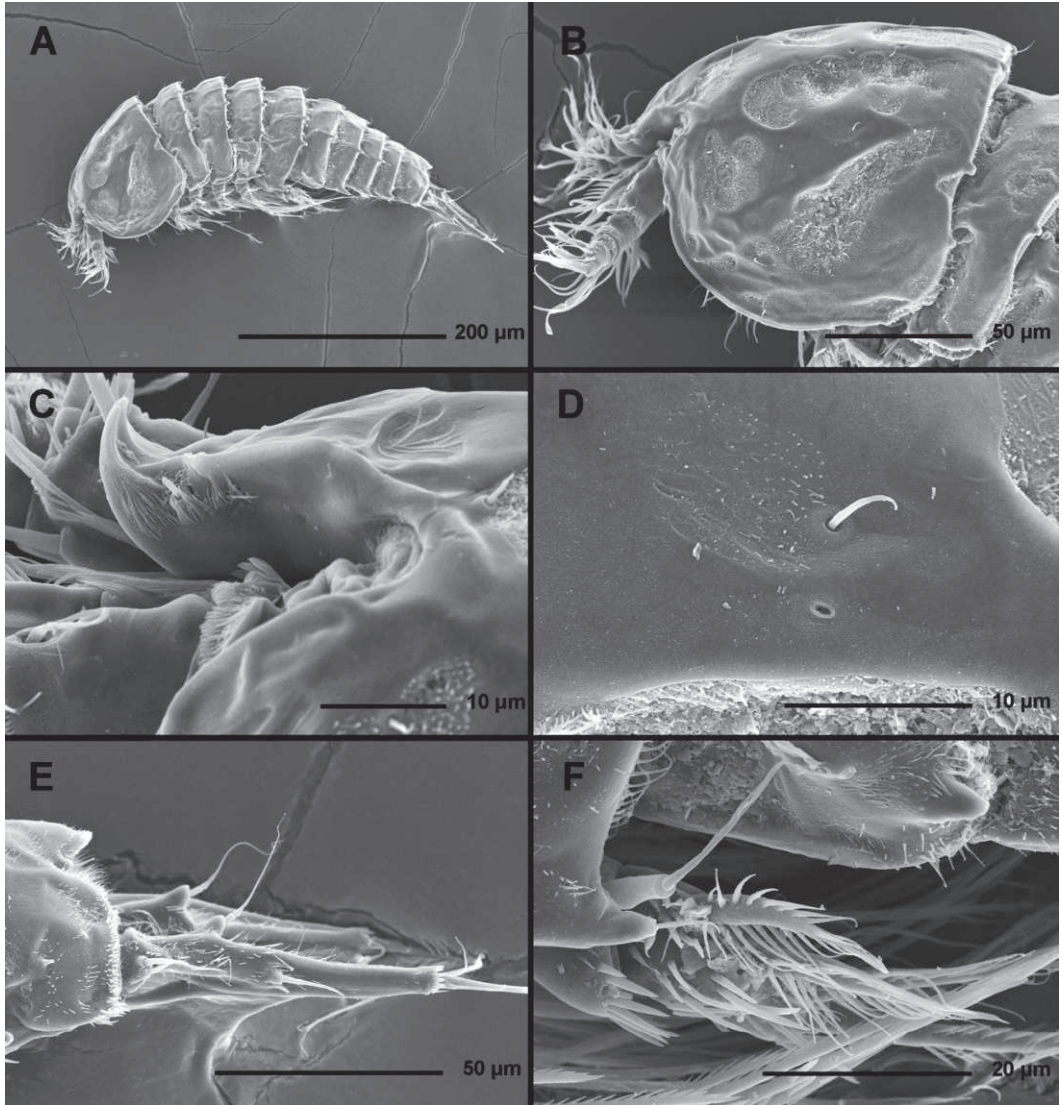


Fig. 10. *Geehydrosoma intermedia* (Chislenko, 1978) (♀) from Korea, SEM micrographs. A, habitus, lateral; B, cephalic shield, lateral; C, rostrum, lateral; D, cephalic shield, detail of ornamentation; E, caudal ramus, lateral; F, P5.

(34°51'55.5"N, 127°46'02.0"E); 1 ♀ (NIBRIV 0000287206) dissected on 12 slides, collected from sampling station 10 (34°55'15.4"N, 127°47'07.9"E); 5 ♀♀ (NIBRIV 0000287207) dissected on 5, 7, 9, 10, and 11 slides, respectively; 3 ♂♂ (NIBRIV 0000287208) dissected on 8, 9, and 13 slides, respectively, collected from sampling station 13 (34°51'09.9"N, 127°47'27.6"E); 3 ♂♂ (NIBRIV

0000287209) in 70% ethanol, collected from sampling station 13 (34°49'27.2"N, 127°47'15.9"E). Additional 3 ♀♀ and 4 ♂♂ were examined with SEM and deposited in the collection of WL. All Korean specimens for morphological analysis were collected from the sampling stations in Gwangyang Bay on 25 Jan 2006 by K. Kim. 1 ♀ and 2 ♂♂ used for molecular analyses were collected from

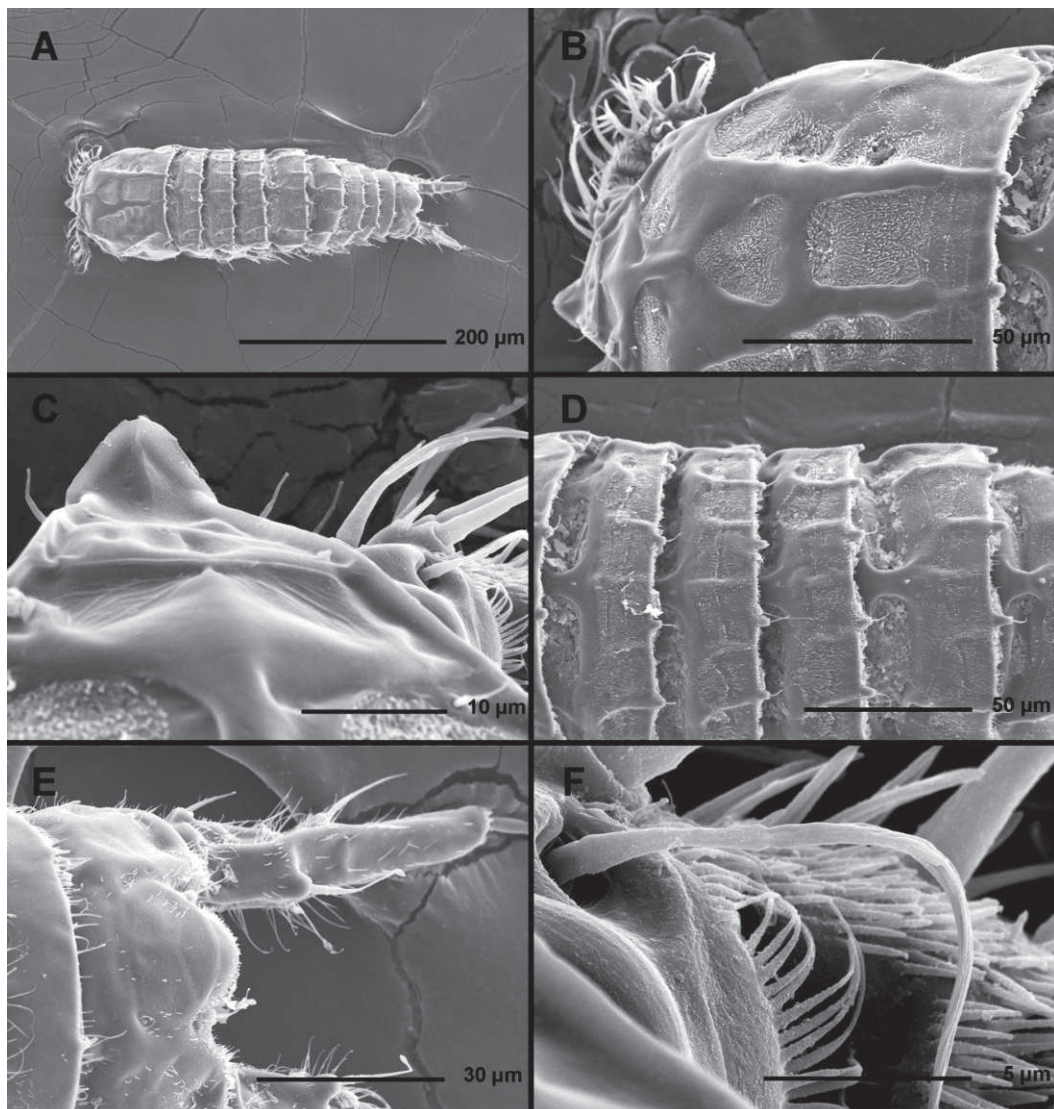


Fig. 11. *Geehydrosoma intermedia* (Chislenko, 1978) (♀) from Korea, SEM micrographs. A, habitus, dorsal; B, cephalic shield, dorsal; C, rostrum, dorsal; D, free prosomites, dorsal; E, anal somite and caudal ramus, dorsal; F, antennule, seta on first segment, dorsal.

sampling station 13 (34°49'27.2"N, 127°47'15.9"E) on 18 Feb and 30 Jul 2012 by K. Kim.

Russia: Holotype ♀ borrowed from the Zoological Museum in St. Petersburg (collection number 61236; Prep. II:13,11), originally dissected on one slide and covered with 9 small pieces of coverslip, collected from Primorsky Krai,

Posyet Bay, Minonosok Inlet, sandy bottoms at 3–4 m depth on 25 Apr 1965 by L. Chislenko. 1 ♀ used for molecular analyses, collected from Primorsky Krai, Posyet Bay, Minonosok Inlet, sandy bottoms at 3–4 m depth (42°36'33 "N, 130°51'42 "E) on 6 May 2012 by Y. Trebukhova. 1 ♀ was examined with SEM and deposited in the collection of WL, collected from

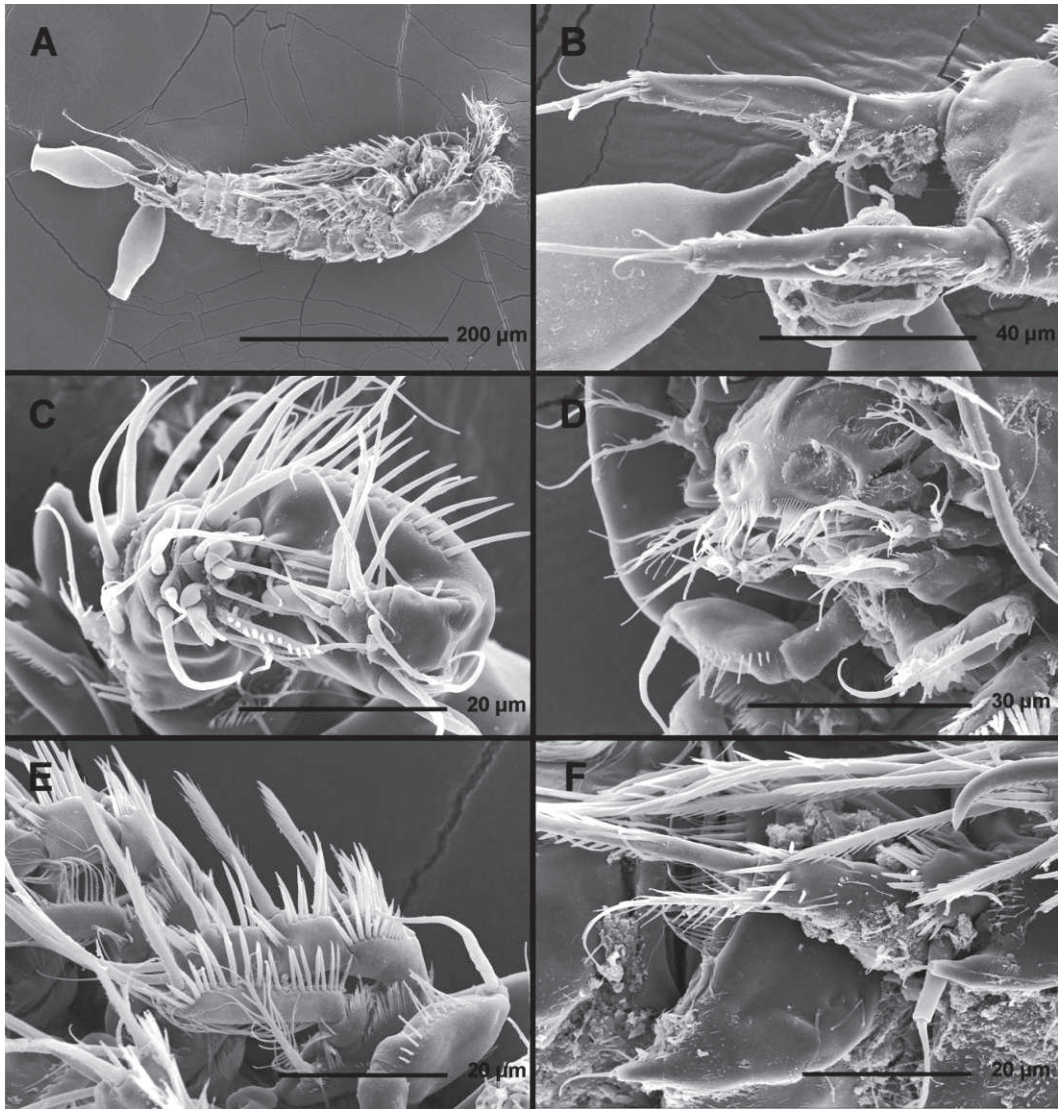


Fig. 12. *Geehydrosoma intermedia* (Chislenko, 1978) (δ) from Korea, SEM micrographs. A, habitus, ventral; B, caudal rami, ventral; C, antennule, ventral; D, mouth appendages, ventral; E, P1; F, P5.

Primorsky Krai, Russky Island, Rynda Bay, sandy bottoms at 3 m depth (43°01'22 "N, 131°48'00 "E) on 19 Apr 2013 by Y. Trebukhova.

Redescription of female.—Total body length 383–498 μm (measured from anterior margin of cephalic shield to posterior margin of caudal rami, mean = 454 μm , $n = 5$). Body (Figs. 9A, 10A, 11A) tapering from cephalothorax to caudal

ramus, curved ventrally in lateral view, without clear distinction between prosome and urosome. All somites (Figs. 9B, D, 10B, D, 11B, D) with pores and/or sensilla as illustrated.

Rostrum (Figs. 9C, 10C, 11C, 13B, 15A, B) small, triangular, fused to cephalic shield, dorsally recurved in lateral view, apical portion between sensilla convex, pore absent on ventral surface.

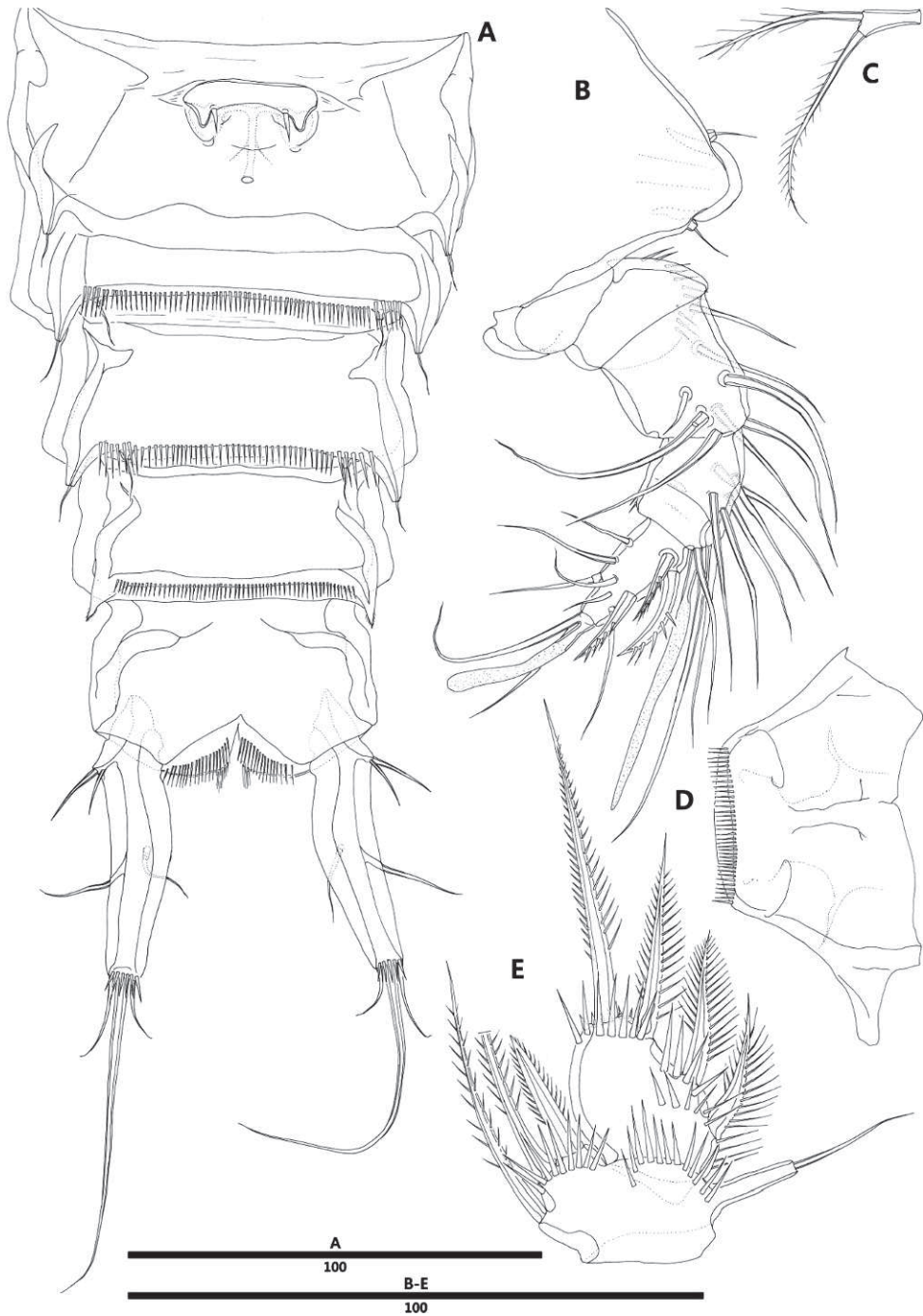


Fig. 13. *Geehydrosoma intermedia* (Chislenko, 1978) Holotype (♀) from Russia. A, urosome, ventral; B, rostrum and antennule, dorsal; C, antennary exopod; D, labrum; E, P5, anterior.

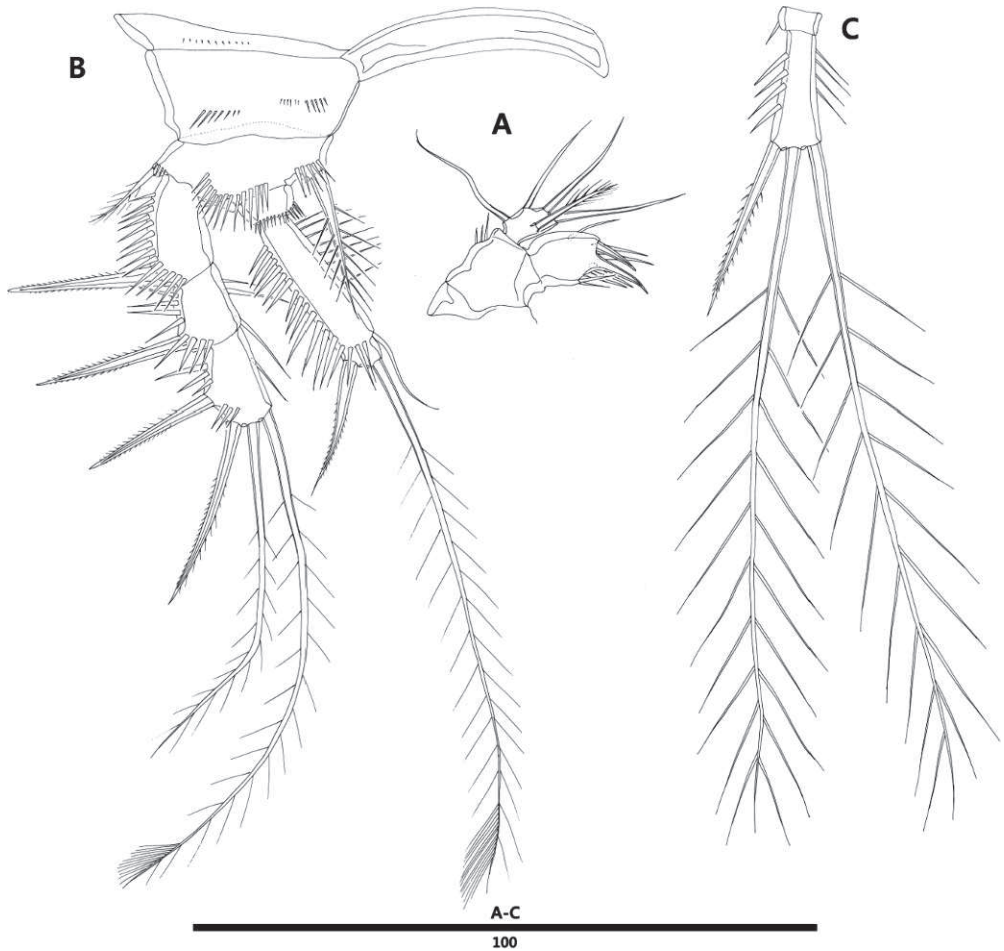


Fig. 14. *Geehydrosoma intermedia* (Chislenko, 1978) Holotype (♀) from Russia. A, maxillule; B, P1, anterior; C, endopod of P4, anterior.

Prosoma (Figs. 9A, B, 10A, B, 11A, B, D) four-segmented, including cephalothorax and three free pedigerous somites. Cephalothorax with longitudinally ridged dorsal surface and posterior margin ornamented with minute spinules. Free pedigerous somites with short spinules and pairs of papillary socles (each bearing one sensillum apically) on posterior margin; pair of small ridges on dorsal surface of each segment.

Urosome (Figs. 9A, 10A, 11A, 13A) five-segmented, including P5-bearing somite, genital double-somite, and three free abdominal somites. Dorsal surface of all urosomites, except anal somite, with spi-

nules and pairs of papillary socles on posterior margin. Additional socles on ventroposterior margin of urosomites 3–4.

Genital double-somite (Figs. 11A, 13A, 18A) with dorsal subcuticular ridge indicating line of fusion, but fused midventrally. Genital apertures forming common transverse genital slit; covered by vestigial P6, represented by one naked seta and small triangular lobe on each side; midventral copulatory pore moderately small and located at midlength of somite.

Anal somite (Figs. 9E, 10E, 11E, 13A) partially cleft medially; anal operculum dentate, semicircular.

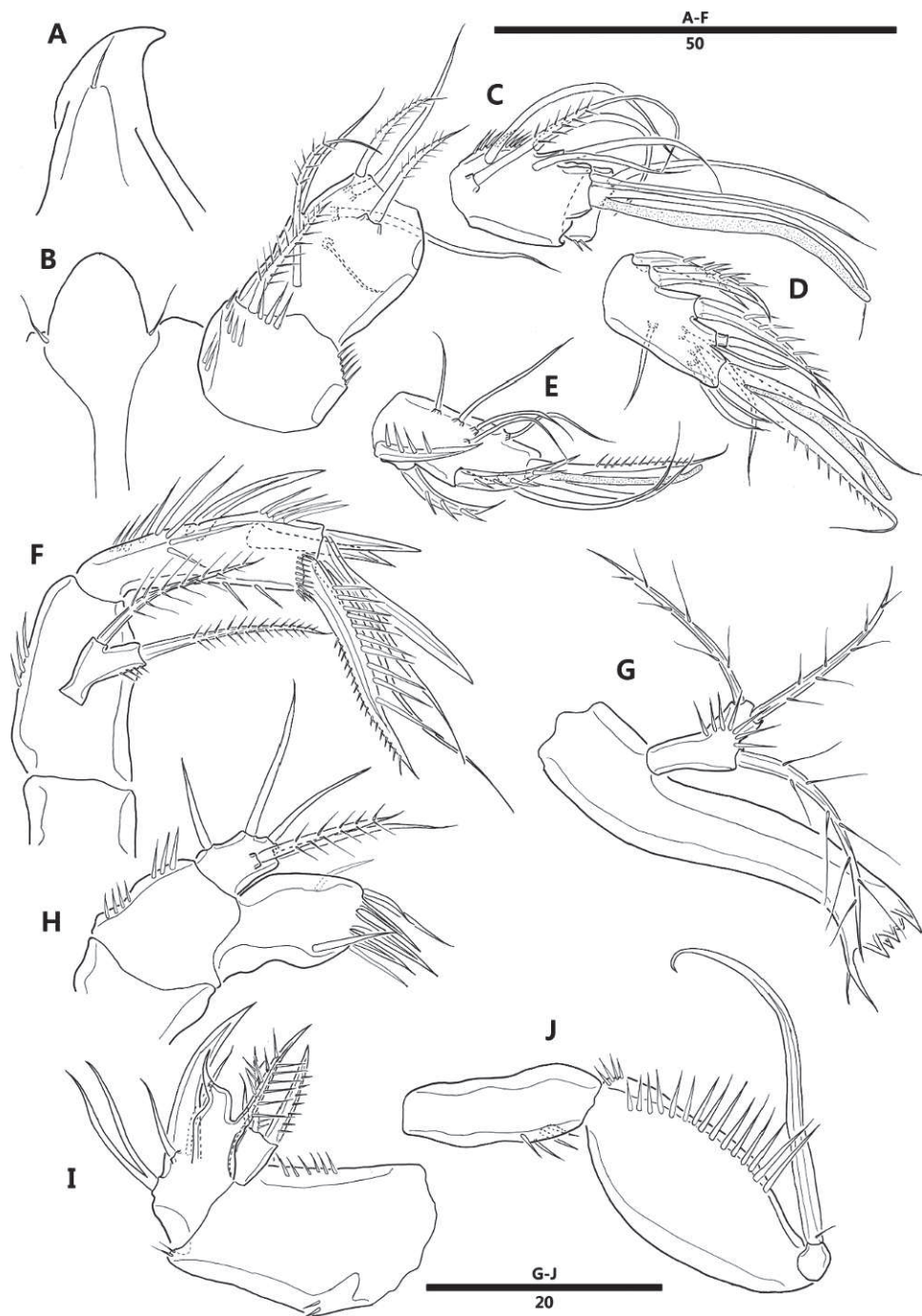


Fig. 15. *Geehydrosoma intermedia* (Chislenko, 1978) (♀) from Korea. A, rostrum, lateral; B, rostrum and segments 1 and 2 of antennule, ventral; C, segments 3 and 4 of antennule, ventral; D, segment 5 of antennule, ventral; E, segment 5 of antennule, dorsal; F, antenna; G, mandible; H, maxillule; I, maxilla; J, maxilliped.

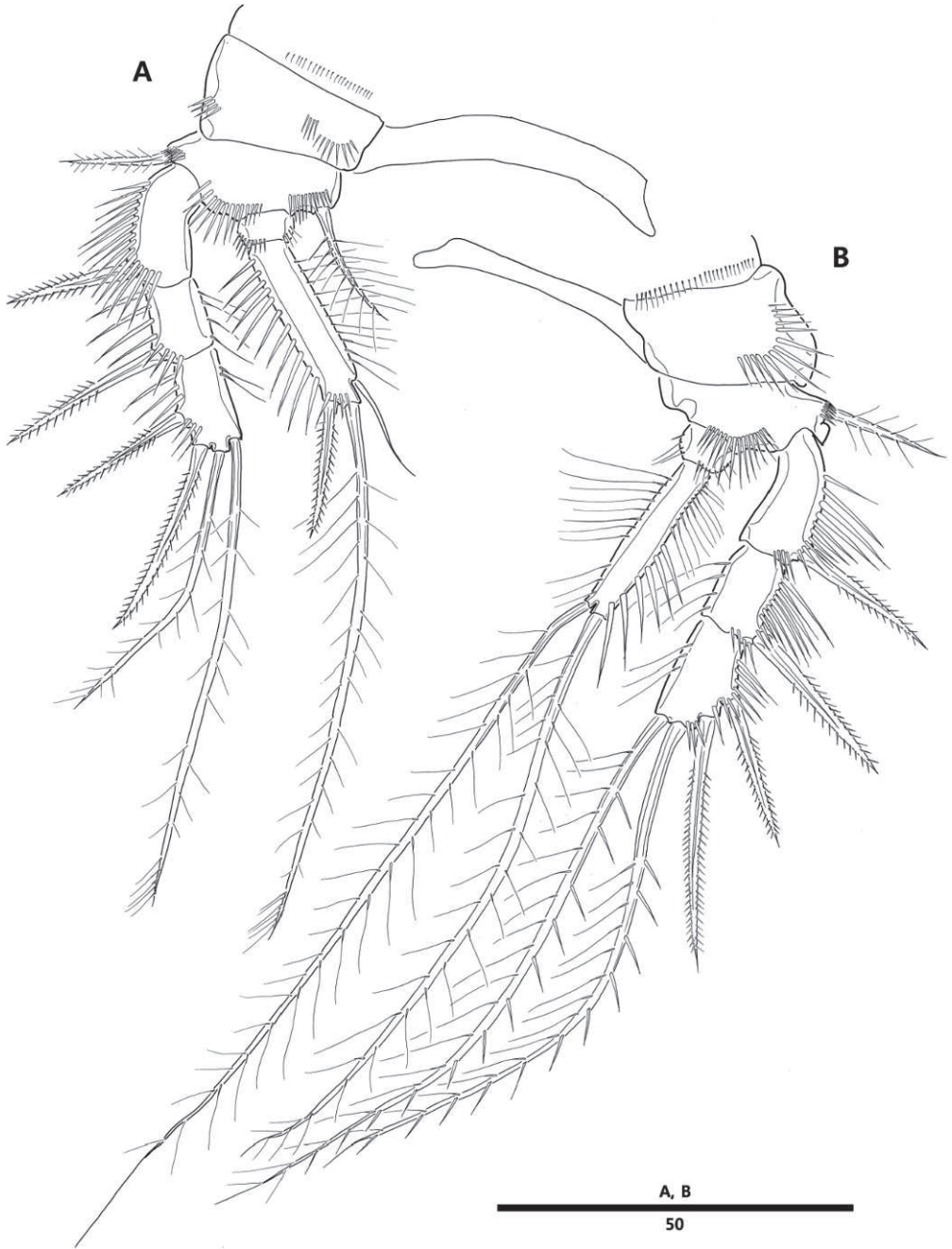


Fig. 16. *Geehydrosoma intermedia* (Chislenko, 1978) (♀) from Korea. A, P1, anterior; B, P2, anterior.

Caudal rami (Figs. 9E, 10E, 11E, 13A, 18E) divergent, cylindrical, from 3.5 to 4.1 times as long as wide (posterior part more elongated in Korean specimens), more or

less densely covered with hair-like spinules, broad at base and tapering posteriorly, sparsely covered by small setules, one Y-shaped tube pore near base of seta III,

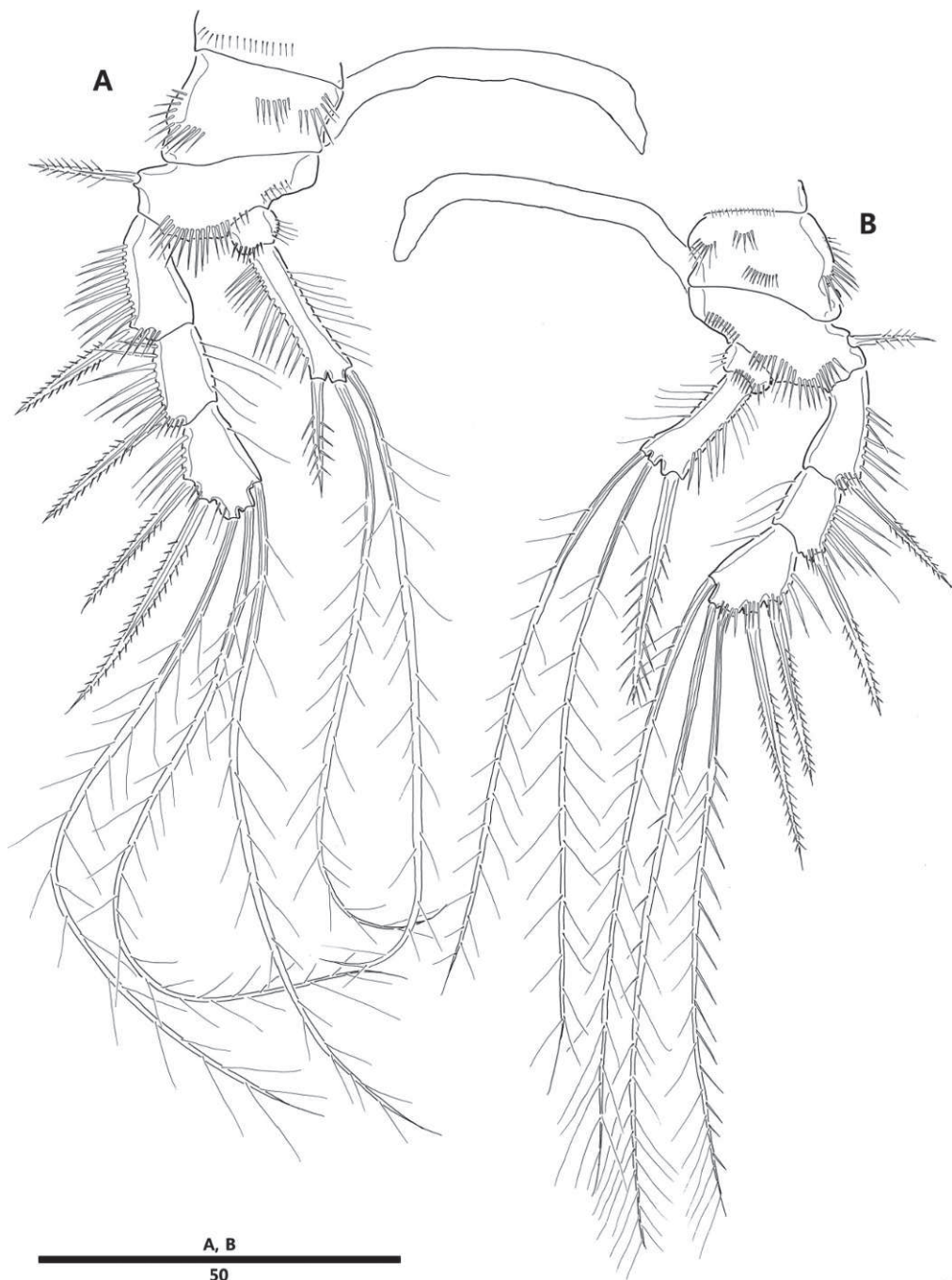


Fig. 17. *Geehydrosoma intermedia* (Chislenko, 1978) (♀) from Korea. A, P3, anterior; B, P4, anterior.

distal margin serrate, 5.5 times longer than wide. All caudal setae bare; setae I and II located proximally on outer margin and naked, seta II two times longer than seta I;

seta III located at middle of outer margin and three times longer than seta I; setae IV and V fused at bases, seta IV similar in length to seta III; seta V longest, as long as

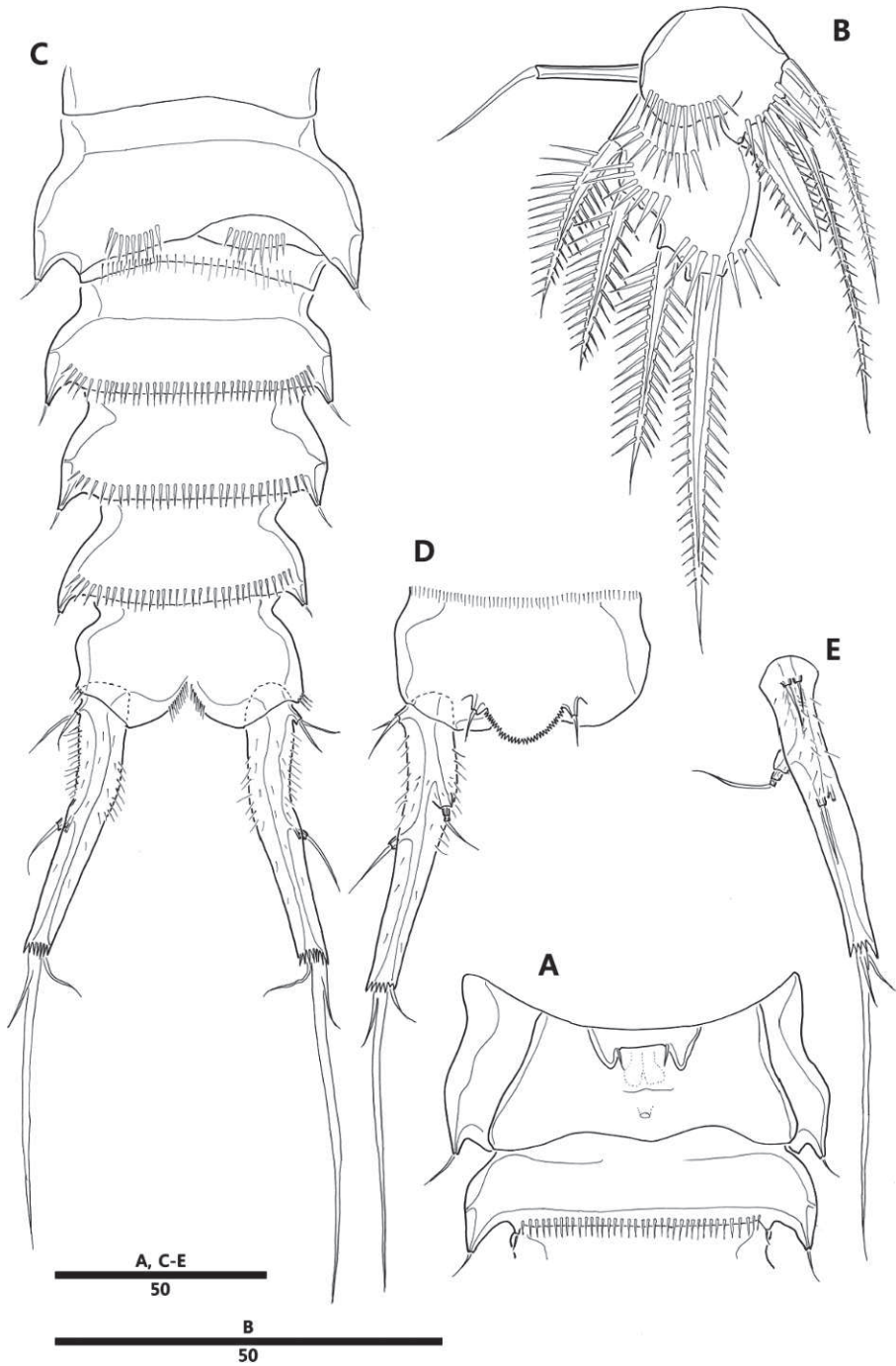


Fig. 18. *Geehydrosoma intermedia* (Chislenko, 1978) (δ) from Korea. A, P6 and genital field, ventral (♀); B, P5, anterior (♀); C, urosome, ventral (δ); D, caudal ramus and anal somite, dorsal (♀); E, caudal ramus, lateral (♀).

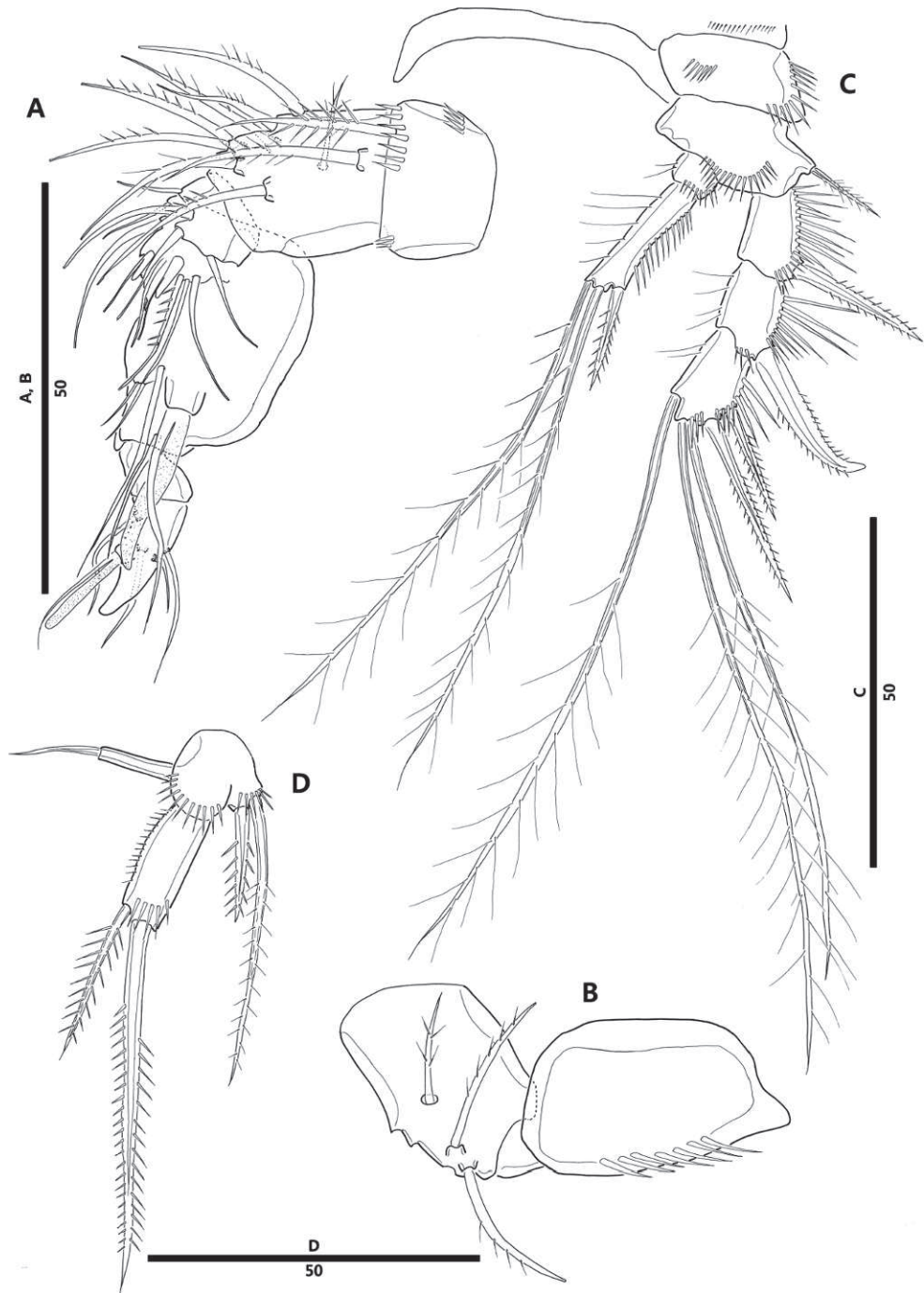


Fig. 19. *Geehydrosoma intermedia* (Chislenko, 1978) (δ) from Korea. A, antennule, ventral; B, segments 2-4 of antennule, dorsal; C, P3, anterior; D, P5, anterior.

caudal ramus; seta VI slightly shorter than seta IV; seta VII as long as seta II, arising from rounded protrusion located on inner proximal portion of dorsal surface.

Antennule (Figs. 11F, 13B, 15A–E) short, stout, five-segmented. First segment with spinular rows; second segment with small plumose seta implanted in circular depression on dorsal surface (Fig. 11F); third segment with aesthetasc fused basally to seta; fourth segment smallest; last segment with apical acrothek consisting of two setae and aesthetasc. Armature formula: 1-[1 pinnate], 2-[4 + 3 pinnate], 3-[5 + 1 pinnate + (1 + ae)], 4-[1], 5-[6 + 3 pinnate + acrothek].

Antenna (Figs. 13C, 15F). Coxa well developed. Basis and first endopodal segment completely fused, forming allobasis; abexopodal margin with spinular row and without seta. Exopod one-segmented with two bipinnate setae and row of spinules near distal seta. Free endopodal segment with spinular rows as illustrated; two stout naked spines located on posterior surface and five elements distally (one stout bipinnate spine, two long naked setae, one stout naked spine and one short naked spine).

Labrum (Fig. 13D). Trapezoidal; short setules set densely along posterior margin.

Mandible (Fig. 15G). Syncoxa slender, recurved. Gnathobase with several teeth along distal margin and naked seta at dorsal corner. Palp one-segmented with three bipinnate setae and ornamented with row of spinules.

Maxillule (Figs. 14A, 15H). Praecoxal ornamented with rows of spinules, arthrite with one surface seta and eight distal elements (two of them possibly spinules). Coxa and basis fused; bearing one bipinnate surface seta (originating from coxa), three naked distal setae (originating from basis), and one lateral naked seta (representing endopod).

Maxilla (Fig. 15I). Syncoxa with two spinular rows and single endite. Syncoxal endite (proximal one) with one stout

unipinnate spine, one slender bipinnate seta, and one short naked seta. Distal endite armed with two elements (one bipinnate seta and one strong modified spine, fused to endite at their base). Basal endite with smooth spine fused at base, naked seta on each surface. Endopod represented by two setae fused at their bases.

Maxilliped (Fig. 15J). Syncoxa with spinular row on outer margin, and without seta at inner distal corner. Basis with spinular rows on inner margin. Endopod with curved slender claw, distinct from endopodal segment, and short naked accessory seta.

P1 (Figs. 14B, 16A) with thin and wide intercoxal sclerite. Praecoxa well developed, with spinular row. Coxa broad, with three spinular rows as illustrated. Basis with bipinnate outer seta, pectinate inner spine, and three spinular rows. Exopod three-segmented, each segment longer than wide; exp-1 with outer bipinnate spine and spinular row along outer margin, inner margin smooth; exp-2 with outer bipinnate spine, spinular row along outer margin, and setular row on inner margin; exp-3 bearing two outer bipinnate spines and two distal setae with penicillate tips, ornamented with spinular row along outer margin and setular row along inner margin. Endopod two-segmented; enp-1 wider than long, ornamented with row of slender setules on inner margin and row of spinules along outer margin; enp-2 four times longer than wide, long setules along inner margin and row of spinules along outer and distal margins, bearing one inner naked seta, one distal bipinnate seta, and one outer bipinnate spine at outer distal corner.

P2 (Fig. 16B) with thin and wide intercoxal sclerite. Praecoxa with spinular row. Coxa with long spinular row on anterior surface as illustrated. Basis with two spinular rows and bearing outer plumose seta. Exopod three-segmented, each segment longer than wide; exp-1

ornamented with spinular row along outer margin, inner margin smooth, bearing one bipinnate spine at outer distal corner; exp-2 ornamented with spinular row along outer margin and long setules along inner margin, bearing one bipinnate spine at outer distal corner; exp-3 with spinular rows on outer margin and setules on inner margin, bearing two bipinnate outer spines and two plumose distal setae. Endopod two-segmented, each segment ornamented with setules and spinules; enp-1 wider than long; enp-2 4.5 times longer than wide, bearing two plumose setae distally.

P3 (Fig. 17A) with thin and wide intercoxal sclerite. Praecoxa with short spinular row. Coxa ornamented with three spinular rows on anterior surface. Basis with two spinular rows and bearing outer bipinnate seta. Exopod three-segmented, each segment longer than broad, all segments ornamented with spinules along outer margin; exp-1 and exp-2 with bipinnate spine at outer distal corner; exp-3 with two outer spines, two distal setae, and one inner seta, all elements bipinnate. Endopod two-segmented, each segment ornamented with setules on inner margin and spinules on outer margin; enp-1 wider than long; enp-2 four times longer than wide, bearing two distal setae and one outer spine at distal corner.

P4 (Figs. 14C, 17B) with thin and wide intercoxal sclerite. Praecoxa with short spinular row distally. Coxa with four spinular rows. Basis ornamented with two rows of spinules and bearing outer bipinnate seta. Exopod three-segmented, each segment longer than wide, all segments ornamented with spinules along outer margin; exp-1 and exp-2 with bipinnate spine at outer distal corner; exp-3 with two outer spines, two distal setae, and one inner seta, all elements bipinnate. Endopod two-segmented, each segment ornamented with setules on inner margin and spinules along outer margin; enp-1 wider than length; enp-2 2.5 times longer than wide, bearing two distal bipinnate

setae and one long outer spine at distal corner.

Armature of P1–P4 as follows:

| | Exopod | Endopod |
|----|---------|---------|
| P1 | 0.0.022 | 0.111 |
| P2 | 0.0.022 | 0.020 |
| P3 | 0.0.122 | 0.021 |
| P4 | 0.0.122 | 0.021 |

P5 (Figs. 9F, 10F, 13E, 18B) biramous, comprising triangular exopod and short baseoendopod. Exopod ornamented with three rows of spinules on anterior surface and bearing four bipinnate spines along distal slope. Baseoendopod with long cylindrical setopore bearing basal seta on outer margin; ornamented with two spinular rows; bearing two long bipinnate setae and one stout bipinnate spine on inner margin.

First description of male.—As in female, except in urosome, genital area, antennule, P3, and P5. Body (Fig. 12A) slightly more slender and shorter than female, length 400–463 μm (measured from anterior margin of cephalic shield to posterior margin of caudal rami, mean = 435 μm , $n = 5$). Urosomites-2 and -3 not fused. Caudal rami (Figs. 12B, 18C, D) slightly more elongated. Mouth appendages (Fig. 12D) and P1 (Fig. 12E) armature and ornamentation as in female.

Antennule (Figs. 12C, 19A, B) six-segmented, short, subchirocer. First segment with rows of spinules and bearing one pinnate seta; second segment bearing short plumose seta implanted in circular depression on dorsal surface as in female; third segment short; fourth segment swollen, with spinules on anterior surface and bearing two modified elements; fifth segment bare; apex of seventh segment recurved. Armature formula: 1-[1 pinnate], 2-[9 pinnate], 3-[4], 4-[8 + 1 pinnate + 2 modified elements + (1 + ae)], 5-[0], 6-[4 + acrothek].

P3 (Fig. 19C). Protopod and endopod as in female. Endopod two-segmented, enp-2 without apophysis. Exopod three-segment-

Table 2.—Average pairwise maximum likelihood distances (TN model) among mtCOI sequences from nine specimens of Cletodidae from Korea and Russia (for details on specimens studied see Table 1), and *Coullana* sp. (family Canuellidae), its sequences available from GenBank prior to this study [AF315015].

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|--------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1 KC39 <i>Enhydrosoma intermedia</i> | | | | | | | | | |
| 2 KC35 <i>E. intermedia</i> | 0.004 | | | | | | | | |
| 3 KC36 <i>E. intermedia</i> | 0.004 | 0.000 | | | | | | | |
| 4 KC37 <i>E. intermedia</i> | 0.004 | 0.000 | 0.000 | | | | | | |
| 5 KC16 <i>E. coreana</i> | 0.287 | 0.286 | 0.286 | 0.286 | | | | | |
| 6 KC17 <i>E. coreana</i> | 0.284 | 0.282 | 0.282 | 0.282 | 0.018 | | | | |
| 7 KC18 <i>E. coreana</i> | 0.282 | 0.280 | 0.280 | 0.280 | 0.016 | 0.002 | | | |
| 8 KC40 <i>Stylicletodes</i> sp. | 0.300 | 0.296 | 0.296 | 0.296 | 0.273 | 0.275 | 0.273 | | |
| 9 KC41 <i>Stylicletodes</i> sp. | 0.300 | 0.296 | 0.296 | 0.296 | 0.273 | 0.275 | 0.273 | 0.000 | |
| 10 AF315015 <i>Coullana</i> sp. | 0.287 | 0.286 | 0.286 | 0.286 | 0.263 | 0.270 | 0.268 | 0.296 | 0.296 |

ed. Exp-2 bearing enlarged outer spine at outer distal corner.

P5 (Figs. 12F, 19D). Fifth pair of legs not fused medially. Baseoendopod with elongated setophore bearing outer basal seta; endopodal lobe shorter than exopod, bearing bipinnate spine and seta on inner margin, ornamented with rows of spinules on anterior surface. Exopod cylindrical, about 2.5 times longer than wide; ornamented with rows of spinules and bearing two bipinnate apical setae.

P6 (Fig. 18A, C). Asymmetrical; each side represented by small plates with rows of spinules, left plate fused to urosomite and right plate functional, covering gonopore.

Molecular Results

DNA was extracted and the mtCOI fragment successfully PCR-amplified from nine cletodid copepod specimens (Table 1), belonging to three different morpho-species. Fragments ranged in length from 567 to 679 base pairs. All sequences were translated into protein, using MEGA, and showed 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 (AF315015) from the species *Coullana* sp. (family Canuellidae) was included in our phylogenetic analyses for rooting the trees.

Average pairwise distances between morpho-species were very high (Table 2), all in excess of 26%, suggesting only a remote relationship between the taxa studied. The divergence between the two cletodid congeners studied morphologically in this paper (*E. intermedia* and *E. coreana*; 28.3%) is even higher than that between *E. coreana* and the remotely related cletodid species from the genus *Stylicletodes* (27.4%) or between *E. coreana* and a completely unrelated species from a different harpacticoid family (*Coullana* sp.; 26.7%). The highest average pairwise distance (29.7%) was observed between *Stylicletodes* sp. and *E. coreana*. These high divergence values are certainly indicative of distinct species by comparison with other crustaceans (Lefébure et al. 2006) and are comparable to those among some well-accepted harpacticoid genera from the families Canthocamptidae, Parastenocarididae, and Miraciidae (Karanovic & Cooper 2011a, 2011b, 2012; Karanovic & Kim 2014).

The highest divergences within morpho-taxa were those among three specimens of *E. coreana* (1.2 %), which all came from the same sampling location in Korea (St. 10; Table 1) and were collected on the

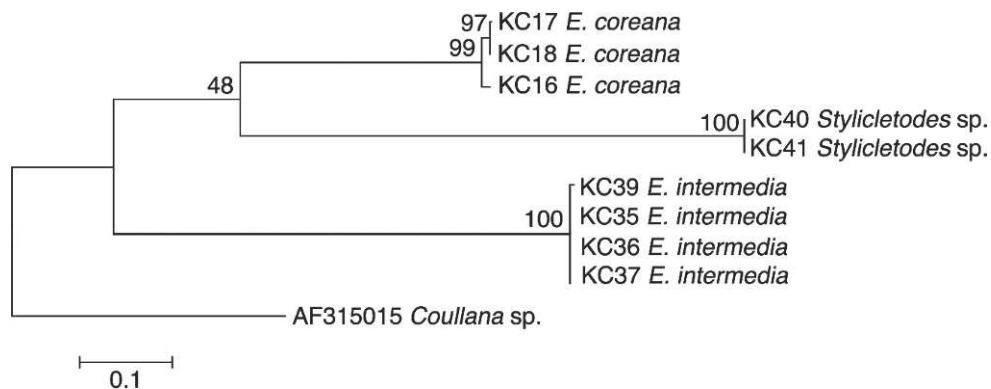


Fig. 20. Maximum likelihood (ML) tree based on mtCOI sequence data of nine Cletodidae specimens from Gwangyang Bay (Korea) and Posyet Bay (Russia), constructed using MEGA v. 5.2.2 and an HKY+G model of evolution, with numbers on branches representing bootstrap values from 500 pseudoreplicates. Cladogram is drawn to scale and specimen codes correspond to those in Table 1. Tree is rooted with *Coullana* sp. (family Canuellidae), whose sequences were available from GenBank prior to this study [AF315015].

same date. Divergences among three specimens of *E. intermedia* from Korea were zero, while those between the Russian specimen of this species and Korean specimens were only 0.4% (i.e., two nucleotides). These are all indicative of intra-specific variability (Lefébure et al. 2006). Sequences of the only other species of which we had more than one specimen (two Korean specimens of *Stylicletodes* sp.) showed zero divergence.

All analyses (Fig. 20) supported the presence of at least four highly divergent lineages, and all three of the multisample lineages were supported with high bootstrap values (>99% for ML). The tree topology in our NJ analysis was the same as in the ML analysis (Fig. 20), except the support for the clade formed by *E. coreana* and *Stylicletodes* was slightly higher (50% for NJ vs. 48% for ML). This low support for the basal nodes could be explained by the low phylogenetic resolution of the mtCOI, possibly due to saturation at third-codon positions (Karanovic & Cooper 2012), and only future analysis of some more slowly evolving genes may shed more light on this problem. However, none of our analyses suggested a sister relationship between *E. intermedia* and *E. coreana*, which we interpret as strong support for

their different generic placement (see above).

Discussion

Enhydrosoma coreana shares a number of rare morphological features with the type species, *E. curticauda* Boeck, 1872 (see Gee 1994), such as a strongly bifid rostrum with centrally inserted sensilla, endopodal lobe of the P5 with a peduncle, and a characteristic shape of the female genital field. This type of rostrum is unique in the family, except perhaps in several species of *Kollerua* Gee, 1994 (see Borutzky 1928, Ranga Reddy 1979, Kikuchi et al. 1993). The P5 with a peduncle is found elsewhere only in three species of the genus *Kollerua*, but this genus differs from *Enhydrosoma* by a number of morphological characters, most importantly by a one-segmented endopod of the P4. However, it is possible that the one-segmented condition of the P4 endopod may have arisen several times independently in cletodids, which would lend support for the suggestion that the genus *Kollerua* is polyphyletic. Further support for this may be found in the very variable nature of the P5 in this genus, but this is outside of the scope of our study

and would require molecular data and redescription of several species to be tested properly. *Enhydrosoma coreana* differs from *E. curticauda* in the armature formula of the mandible (three vs. four setae on the palp), P1 endopod (the minute seta absent), and P5 exopod (three vs. four setae), size of the P5 peduncle (reaching beyond the distal margin of the exopod), and minor details in the ornamentation of several somites. Although the new species slightly bridges the gap between the type species and other congeners, the two still have a very isolated position within *Enhydrosoma*. Most of the morphological differences are in fact synapomorphies of these two species, which would make it easy to separate them, but because one of them is the type species of *Enhydrosoma* it would mean that all other members would have to be transferred into a newly erected genus. This would only perpetuate the problem of supporting extremely heterogeneous groups (see above), and we feel reluctant to attempt any such revision without the use of molecular data and redescription of species that are presently inadequately described.

Our re-examination of the holotype (which is partly damaged due to desiccation) and newly collected material from and near the type locality of *G. intermedia* showed that several features described and illustrated by Chislenko (1978) were not correct. For example, this species does not have a seta on the maxillipedal syncoxa (see Figs. 12D, 15J) and has only three setae on the P1 endopod (Figs. 12E, 14B, 16A). In both cases Chislenko (1978) probably mistook a strong spinule or some external contamination for an armature element, because his other drawings are of a relatively high standard. These inaccuracies and the lack of known males probably prevented Gómez (2004) from noticing a very close relationship between this Russian Far Eastern species and his new species from the Pacific coast of Mexico (*G. brevipedum*). Our first description of

the male of *G. intermedia* reveals that both species share the same type of sexual dimorphism (more precisely the lack of it) in the swimming legs, and also that their morphological similarities extend to minute details of ornamentation of the somites and caudal rami. Needless to say, they share the same armature formula of all appendages. The major difference between these two sister species is in the length of their caudal rami, which are about four times as long as wide in the Russian/Korean species and more than eight times as long as wide in the Mexican species. We transfer them into a newly erected genus *Geehydrosoma*, its major autapomorphy in the family being a very short female P5 exopod armed with four elements. It is very unlikely that this structure has arisen independently in these two species, because they share a large number of other morphological features. Furthermore, the shortened female P5 exopod is not merely a simple reduction in size, because the segment is still robust and armed with four strong setae (more than in most species of *Enhydrosoma*), and the homologous structure in males is still elongated (i.e., retaining its plesiomorphic condition). The occurrence of this new genus in the North Pacific is congruent with likely dispersal routes of the presumed immediate ancestor of these two congeners.

The morphological proximity of *E. coreana* to the type species of *Enhydrosoma*, and the very high average pairwise distances in the mtCOI gene between *E. coreana* and *G. intermedia* (more than 28%, see above) are interpreted here as further support for separating *G. intermedia* from the genus *Enhydrosoma*. We base this interpretation on some recent molecular work, which showed comparable divergences in the same gene between some well-established genera in three different harpacticoid families. Karanovic & Cooper (2011b) showed divergences among three genera of the family Parastenocar-

ididae Chappuis, 1940 (*Dussartstenocaris* Karanovic & Cooper, 2011; *Kinnecaris* Jakobi, 1972; and *Parastenocaris* Kessler, 1913) to be in excess of 22%. Karanovic & Cooper (2012) similarly showed divergences among three genera of the family Canthocamptidae Brady, 1880 (*Australocamptus* Karanovic, 2004; *Cletocamptus* Schmankevitch, 1875; and *Elaphoidella* Chappuis, 1928) to be in excess of 27%. Finally, Karanovic & Kim (2014) showed divergences among four stenheliine genera and one diosaccine genus of the family Miraciidae Dana, 1846 to be between 17 and 38%.

A very small divergence value between the Russian and Korean specimens of *G. intermedia* (0.4 %) is in stark contrast to those observed between two sister-species pairs of stenheliine harpacticoids (10.1% and 7.1%) collected from the same localities (Karanovic & Kim 2014), which suggests that different groups of harpacticoids have different dispersal potentials despite their apparently similar lifestyles. In fact, the divergence values are greater between three specimens of *E. coreana* that all come from the same Korean sampling site (1.2%), than those between two disjunct populations of *G. intermedia* that span more than 1200 km of coastline. We believe these disjunct populations to be a consequence of a natural long-distance dispersal and not anthropogenic translocation (see Karanovic & Krajicek 2012a), as the Korean population is homogenous and differs from the Russian population in two nucleotides.

By separating a new genus from *Enhydrosoma* without conducting a proper phylogenetic analysis that would include all its members, we risk making *Enhydrosoma* paraphyletic, especially because many species are known from a very limited set of morphological characters. However, we see this as a minor problem in comparison with its probable polyphyletic nature, already hypothesized by several researchers (Mielke 1990, Gee 1994,

2001; Gee & Huys 1996). Lumping them together, despite the overwhelming morphological and molecular evidence that shows only a remote relationship, would certainly be a greater mistake. At this stage, we can only speculate on where the bulk of *Enhydrosoma* species would nest between the *E. curticauda*/*E. coreana* and *Geehydrosoma* clades of the family.

Absence of sexual dimorphism in the male P3 endopod has been recorded in at least ten other species of *Enhydrosoma* (see Gómez 2004) and several other genera of cletodids; a recurved and enlarged outer spine on the male P3 second exopodal segment has been reported for three species (*E. gariene* Gurney, 1930; *E. latipes* [A. Scott, 1909]; and *E. pericoense* Mielke, 1990); the maxilliped without a seta on the syncoxa has been observed in more than ten species (Gee 1994); and a one-segmented maxillular palp that bears only five setae has been reported in at least ten species (Lang 1948, Raibaut 1965, Wells 1967, Bell & Kern 1983, Mielke 1990, Gee 1994, Gómez 2003). While some of these characters of *Geehydrosoma* (and many others not mentioned here) may have originated convergently (especially those involving reduced armature), it is possible that at least some of them have a broader phylogenetic value and should be used in future phylogenetic studies.

Acknowledgments

This research was financially supported by grants from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment of the Republic of Korea (NIBR No. 2013-02-001), as well as a grant from the Basic Science Research Programme of the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology of the Republic of Korea (2012R1A1A2005312). Loan of the holotype of *E. intermedia* from St. Petersburg, Russia, was made possible

through efforts of Dr. Elena Chertoprud (Moscow State University).

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