Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

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Jinwook Back [a], Wonchoel Lee [a] & Rony Huys [b]

[a] Department of Life Science, College of Natural Sciences, Hanyang University, Seoul, 133-791, Korea

[b] Department of Zoology, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

Version of record first published: 03 Nov 2011.

To cite this article: Jinwook Back , Wonchoel Lee & Rony Huys (2011): A new species of Remanea Klie, 1929 (Copepoda: Harpacticoida: Paramesochridae) with a redescription of the type species, Journal of Natural History, 45:47-48, 2939-2964

To link to this article: http://dx.doi.org/10.1080/00222933.2011.622057

Journal of Natural History
Vol. 45, Nos. 47–48, December 2011, 2939–2964

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A new species of *Remanea* Klie, 1929 (Copepoda: Harpacticoida: Paramesochridae) with a redescription of the type species

Jinwook Back[a], Wonchoel Lee[a]* and Rony Huys[b]

[a]*Department of Life Science, College of Natural Sciences, Hanyang University, Seoul 133-791, Korea;* [b]*Department of Zoology, Natural History Museum, Cromwell Road, London SW7 5BD, UK*

(*Received 25 March 2011; final version received 6 September 2011; printed 27 October 2011*)

A new species of *Remanea* Klie, 1929 (Copepoda: Harpacticoida: Paramesochridae) is described from a brackish water habitat near Naksan beach on the east coast of Korea, representing the third species of the genus. The new species was assigned to the genus *Remanea* on the basis of the well-developed rostrum, the eight-segmented female antennule, the two-segmented antennary exopod and the three-segmented P1 exopod. *Remanea naksanensis* sp. nov. is most closely related to the type species, *Remanea arenicola* Klie, 1929, sharing the same armature formula of the swimming legs and the previously overlooked sexual dimorphism on the distal endopodal segment of P3. The new species can be distinguished from its congeners primarily by the morphology of the P5 in both sexes, and setal length differences in the P1 endopod and caudal rami. A brief redescription of *R. arenicola* is provided based on Klie's original type slide material. The distribution records of all three species are summarized and an updated identification key to species is presented. Partial sequences of the mitochondrial gene COI (cytochrome *c* oxidase subunit I) of *R. naksanensis* were obtained and submitted to GenBank.

Keywords: *Remanea arenicola*; *Remanea naksanensis*; Harpacticoida; Paramesochridae; barcode; Korea

Introduction

Although the family Paramesochridae (Copepoda: Harpacticoida) is known to have successfully entered the deep sea (Becker 1979; Veit-Köhler 2004, 2005; Gheerardyn and Veit-Köhler 2009; Plum and George 2009; Vasconcelos et al. 2009; Veit-Köhler and Drewes 2009), the great majority of this group typically inhabits the mesopsammic environment of subtidal and intertidal sandy substrates (Boxshall and Halsey 2004), which they colonized either by miniaturization (e.g. *Paramesochra* T. Scott, 1892; *Emertonia* Wilson, 1932; *Kunzia* Wells, 1967) or by adopting a vermiform body shape (e.g. *Biuncus* Huys, 1996; *Apodopsyllus* Huys, 2009). Several ecological studies have demonstrated that paramesochrids are frequently the dominant harpacticoids in sandy sediments (Coull and Dudley 1985; Bodin and Jackson 1989; George and Schminke 2002). Nicholls (1945) proposed the family Remaneidae for the genera *Remanea* Klie, 1929, *Leptopsyllus* T. Scott, 1894, *Paramesochra* and *Emertonia*, which

*Corresponding author. Email: wlee@hanyang.ac.kr

ISSN 0022-2933 print/ISSN 1464-5262 online

http://dx.doi.org/10.1080/00222933.2011.622057
http://www.tandfonline.com

he distinguished on the basis of general body shape, segmentation of the P1 exopod, and morphology of the mandibular palp. Nicholls' (1945) family-group name is, however, a junior synonym of Lang's (1944) Paramesochridae, which was proposed for the genera *Paramesochra*, *Leptopsyllus*, *Remanea* and *Paraleptopsyllus* Lang, 1944 [see postscript in Lang (1948: 1621)]. Lang (1948) primarily used swimming leg segmentation characters to differentiate these genera, considered *Emertonia* as a *genus incertae sedis* in the family, and divided the type genus *Paramesochra* into three species groups (*dubia*-, *robertsoni*- and *intermedia*-groups) based on the armature and segmentation of P2–P4. Kunz's revision of the family (Kunz 1962) resulted in the removal of several species from the genera *Leptopsyllus* and *Paramesochra* to four newly established genera: *Apodopsyllus* Kunz, 1962; *Intermedopsyllus* Kunz, 1962; *Kliopsyllus* Kunz, 1962; and *Scottopsyllus* Kunz, 1962. Huys (2009) pointed out that none of these generic names was available from Kunz (1962) because they failed to meet the provisions of ICZN Art. 13.3 (mandatory type fixation for names proposed after 1930). According to Huys (2009), the correct name, authorship and dates for the four genus-group names listed above are *Apodopsyllus* Huys, 2009; *Intermediopsyllus* Huys, 2009 (corrected spelling); *Emertonia* Wilson, 1932 (senior subjective synonym); and *Scottopsyllus* Apostolov and Marinov, 1988, respectively. Based on the Principle of Priority (ICZN Art. 23.3.5) both *Intermediopsyllus* and *Scottopsyllus* are now considered subgenera in the genus *Wellsopsyllus* Kunz, 1981. The morphology-based phylogenetic scheme proposed by Kunz (1981) recognized three lineages within the family (*Diarthrodella*-, *Paramesochra*- and *Scottopsyllus*-groups). It was subsequently revised by Huys (1987), who proposed two subfamilies, Paramesochrinae and Diarthrodellinae, and identified four species-groups within the type genus *Paramesochra*. The family currently comprises 13 valid genera (Wells 2007).

At present, the genus *Remanea* accommodates two valid species, *Remanea arenicola* Klie, 1929 (type species by monotypy) and *Remanea plumosa* Pennak, 1942 (known from the female only). During a study of the harpacticoid copepod fauna along the east coast of Korea, a new species of the genus *Remanea* was discovered. Here we provide an illustrated description of both sexes and the partial sequence of the mitochondrial gene COI (cytochrome *c* oxidase subunit I) as a DNA barcode of the new species and discuss its relationships to the other two congeners. To confirm its differences with the new species, we also present a partial redescription of the type species, *R. arenicola*, based on its type slide material.

Materials and methods

Specimens and scanning electron microscopy

Samples were collected from a brackish water system near Naksan beach on the east coast of South Korea. Sediment samples were fixed in 5% neutralized formalin. Specimens were dissected with the aid of an Olympus SZX12 stereomicroscope, and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with transparent nail varnish. All drawings were prepared with the aid of a drawing tube mounted on an Olympus BX51 microscope equipped with differential interference contrast optics.

For scanning electron microscopy, specimens were transferred to 70% ethanol, dehydrated through a graded ethanol series for observation in a Hitachi S-2380N

scanning electron microscope (in Hanyang University) or through an acetone series for a Philips XL-30 (in the Natural History Museum, London), critical-point dried, mounted on stubs using double-sided tape, coated with gold, and then photographed.

The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text, figures and Table 1 are: *ae*, aesthetasc; *exp*, exopod; *enp*, endopod; *P1–P6*, first to sixth thoracopods; *exp(enp)-1(2, 3)* to denote the proximal (middle, distal) segment of a three-segmented ramus. Specimens were deposited in the National Institute of Biological Resources (NIBR), Korea. Scale bars in figures are indicated in μm.

DNA sequencing

Harpacticoid samples were collected with a hand net (mesh size 63 μm) and subsequently rinsed with seawater on a 63-μm mesh size sieve and fixed in absolute ethanol. Mitochondrial cytochrome oxidase *c* subunit I (mtCOI) was amplified by polymerase chain reaction (PCR) using PCR premix (BiONEER Co., Korea). The amplification primers used were LCO-1490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′) and HCO-2198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′) (Folmer et al. 1994). The thermocycling profile was 94°C (1 min), 46°C (2 min), 72°C (3 min) and was carried out for 40 cycles. PCR products were purified with a LAboPass PCR purification Kit (COSMO Co. Ltd, Korea) and sequenced in both directions using an Applied Biosystems 3730xl DNA Analyzer (COSMO Co. Ltd).

Systematics

Family **PARAMESOCHRIDAE** Lang, 1944
Genus ***Remanea*** Klie, 1929
Remanea naksanensis sp. nov.
(Figures 1–7)

Type locality

Naksan sandy beach, east coast of South Korea (38°06′20″ N, 128°38′46″ E); washings of sandy sediments from a brackish water system (salinity 4–7 psu) near a small unnamed stream.

Material examined

Holotype female (NIBRV0000238524) dissected on six slides, and paratype male (NIBRV0000238525) dissected on four slides. Additional paratypes represented by 14 females (NIBRV0000238526) and three males (NIBRV0000238527) in ethanol. All specimens were deposited in the NIBR, Korea; seven females and four males were used

for scanning electron microscopy while 12 females were used for DNA extraction. All specimens were collected from the type locality by J. Back on 23 April 2010.

DNA-barcode (mtCOI) sequences and traces were submitted to GenBank.

Description of female

Body fusiform, slightly depressed dorsoventrally (Figure 1A, B), with sensilla as illustrated. Total body length, 553 μm ($n = 15$, mean = 541 μm); largest width (153 μm) measured at posterior margin of cephalic shield. Body somites with well-developed arthrodial membranes.

Cephalothorax and somites bearing P2–P4 with crenulate posterior hyaline frill. Cephalothorax bell-shaped, with several sensilla; pleural areas weakly developed, posterolateral angles rounded.

Urosomites (Figure 1A–C), except for anal somite, with striations on hyaline frills dorsally and laterally. Fifth urosomite and anal somite without sensilla; the latter small, without anal operculum, but with well-developed flimsy serrate pseudoperculum arising from penultimate somite. Genital somite (second urosomite) and third urosomite completely fused forming genital double-somite; genital field located in posterior half of second urosomite (proximal half of genital double-somite), with copulatory pore positioned medially, and two small pores located on either side of copulatory pore.

Caudal rami (Figures 1C, 2C, 7H) rectangular, about 1.6 times as long as wide; with three transverse spinular rows dorsally; with spinules at bases of setae III (ventrally) and VII (dorsally), and around distal margin of rami (ventrally); secretory pores located dorsally near base of seta III and ventrally near base of seta IV; with seven setae, setae I–II located halfway down the outer margin; setae III–VII located in distal third of ramus; seta II short and pinnate; seta I bare; seta III plumose; seta IV well developed and plumose, seta V longest and pinnate in distal half; seta VI pinnate; dorsal seta VII bi-articulate at base, naked.

Rostrum (Figure 1A) well developed, with rounded tip, defined at base; with two small lateral sensilla.

Antennule (Figure 2A) slender, eight-segmented; segment 1 with short row of long spinules along anterior margin and one pinnate seta; segments 1 and 2 similar in length; segment 4 with sub-cylindrical process bearing one bare seta fused basally to aesthetasc; armature formula: 1-[1 pinnate], 2-[7 pinnate + 1 spinulose + 3 bare], 3-[5 pinnate + 3 bare], 4-[3 pinnate + (1 + ae)], 5-[1 pinnate + 1 bare], 6-[3 pinnate + 1 spinulose + 1 bare], 7-[1 pinnate + 1 spinulose seta + bare], 8-[5 bare + (2 + ae)]. Acrothek consisting of apical aesthetasc and two basally fused bare setae.

Antenna (Figures 2B, 7A): coxa and basis without surface ornamentation. Exopod two-segmented; exp-1 shorter than exp-2, the former with one pinnate seta distally; exp-2 with row of strong spinules apically and with four setae; armature formula: 1-[1 pinnate], 2-[3 pinnate + 1 bare]. Endopod two-segmented; enp-1 with lateral seta, without surface ornamentation; lateral armature of enp-2 consisting of two bare setae, one small spinulose element, and one pinnate seta; distal armature of enp-2 consisting of four geniculate and two bare setae (one small bare seta laterally and one long bare seta fused at base to largest geniculate seta).

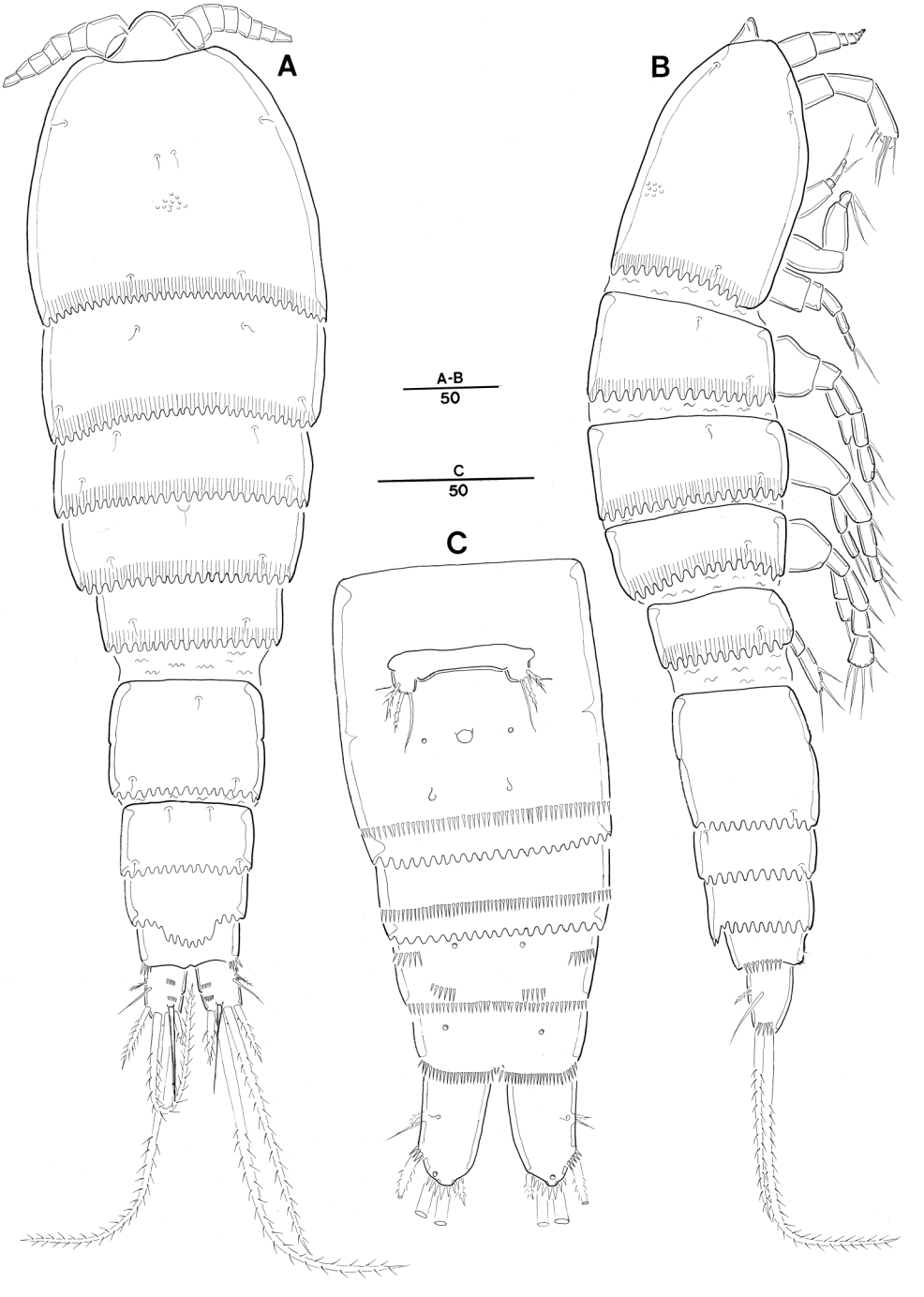

Figure 1. *Remanea naksanensis* sp. nov. Female: (A) Habitus, dorsal; (B) habitus, lateral; (C) urosome (excluding P5-bearing somite), ventral. Scale bars in μm.

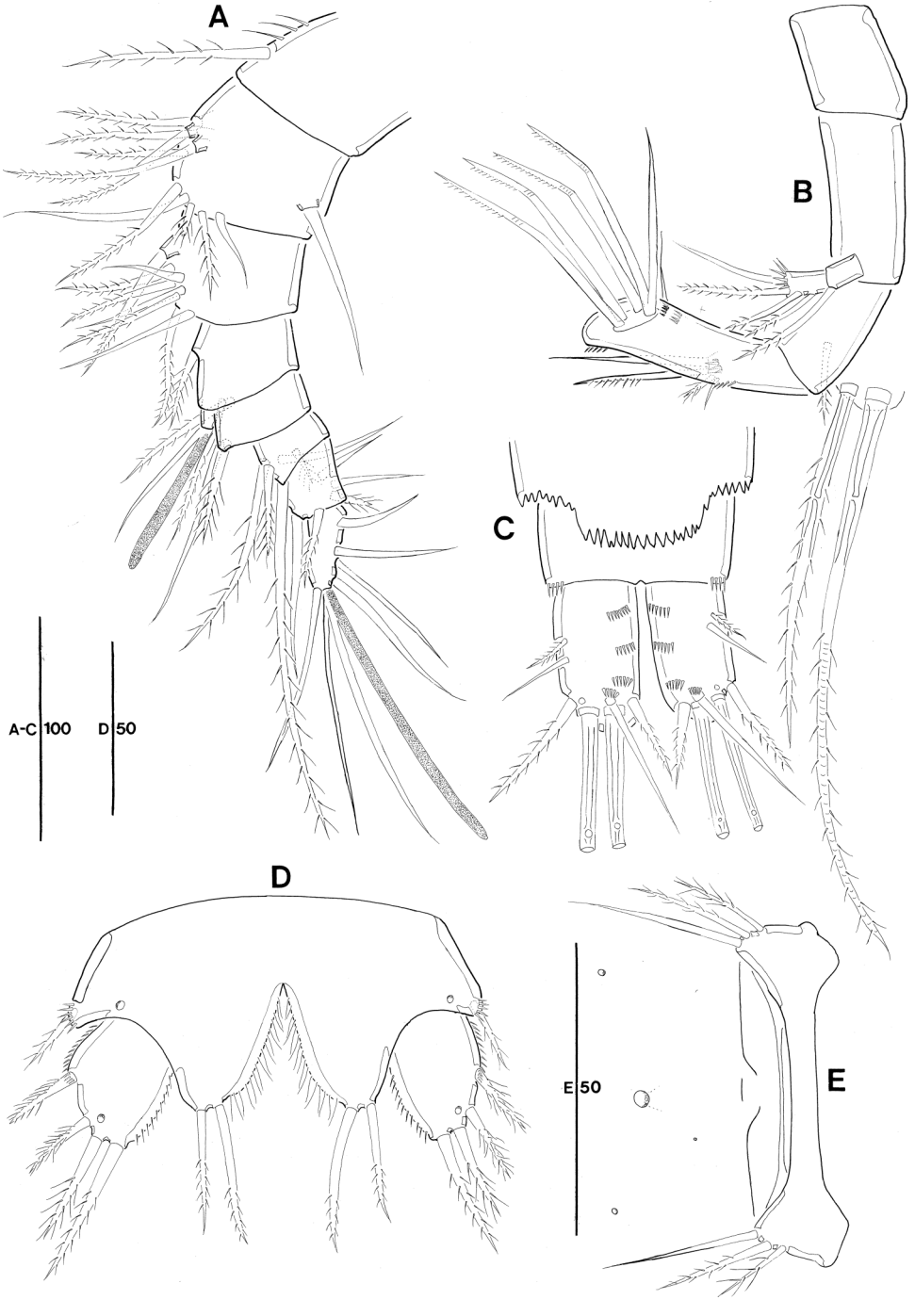

Figure 2. *Remanea naksanensis* sp. nov. Female: (A) Antennule, ventral; (B) antenna; (C) pseudoperculum, anal somite and caudal rami, dorsal (inset showing full length of setae IV–V); (D) fifth pair of legs (P5); (E) P6 and genital field. Scale bars in μm.

Mandible (Figures 3A, 7B): coxa well developed, with process; gnathobase with six small blunt teeth and one pinnate seta at dorsal corner. Palp biramous; basis elongate, with four pinnate setae; exopod one-segmented, with three inner and two distal pinnate setae, and ornamented as figured; endopod two-segmented; enp-1 as long as enp-2, with two bare distal setae; enp-2 with seven setae (two bare setae, three distal setae fused at base, and one apical long seta and one slender bare seta confluent at base).

Maxillule (Figure 3B): praecoxa subquadrate, without ornamentation, arthrite well developed, with five strong spines and one seta apically, three bare lateral elements, and two surface setae. Coxa with five pinnate setae. Basis with five setae. Exopod one-segmented, with four slender bare setae of different lengths and with lateral row of spinules. Endopod one-segmented, longer than exopod, with three apical, and two bare lateral setae.

Maxilla (Figure 3C): syncoxa with four endites. First endite small, with one pinnate and one bipinnate setae; second endite with two pinnate setae; third endite with two pinnate and one bare setae; distal endite close to third endite, with one pinnate lateral seta, two pinnate distal elements, and with one small process proximally (arrowed in Figure 3C – inset 4). Allobasis with one bare seta, one stout claw-like element, and one bare accompanying seta. Endopod two-segmented; enp-1 rectangular, with five slender setae; enp-2 with one pinnate claw, two apical, and one naked lateral setae.

Maxilliped (Figures 3D, 7C) three-segmented. Syncoxa with two rows of spinules. Basis elongate, with rows of spinules halfway down inner and outer margin. Endopod indistinctly segmented, with one bare seta proximally, one stout claw medially, two stout claw-like bi-articulate setae, and one small seta distally.

P1 (Figure 4A): coxa and basis with spinules as figured; the latter with one outer bare and one inner pinnate seta. Exopod three-segmented, shorter than endopod; exp-1 longest, with some spinules along outer margin and one pinnate outer spine; exp-2 somewhat swollen distally, with one pinnate outer spine and one spinulose inner seta; exp-3 with six spines/setae. Endopod prehensile; enp-1 elongate and approximately as long as exopod, with row of spinules along outer margin and one long plumose inner seta; enp-2 small, slightly longer than wide, apically with two strong claw-like setae and one small pinnate element.

P2–P4 (Figure 4B–D): coxae with row of long (P2) or slender (P3–P4) spinules on outer distal corner. Basis with long inner spinules and with rows of spinules on anterior surface. Exopod three-segmented; exp-1 with one strong pinnate outer spine; exp-2 shortest, with one strong pinnate outer spine and one bare inner seta; exp-3 with two pinnate outer spines, two plumose apical setae, and one bare (P2–P3) or plumose (P4) inner seta. Endopod two-segmented; enp-1 with one plumose inner seta; enp-2 as long as enp-1 (P2) or about 1.6 times as long as enp-1 (P3–P4), with one bare (P2) or pinnate (P3–P4) outer spine and two pinnate apical setae; with one pore close to inner distal corner, except for P4.

Armature formula as follows: exopod: P2, 0.1.122; P3, 0.1.122; P4, 0.1.122; endopod: P2, 1.021; P3, 1.021 (1.020 in male); P4, 1.021.

P5 (Figures 2D, 7E) with medially fused baseoendopods and discrete exopods. Baseoendopod with short pinnate outer basal seta; endopodal lobes shorter than exopods, each lobe with two apical pinnate setae of almost equal length, with long spinules along inner margin. Exopod well developed, with rows of spinules along inner and outer margins, with two pinnate apical setae and two spinulose short outer elements.

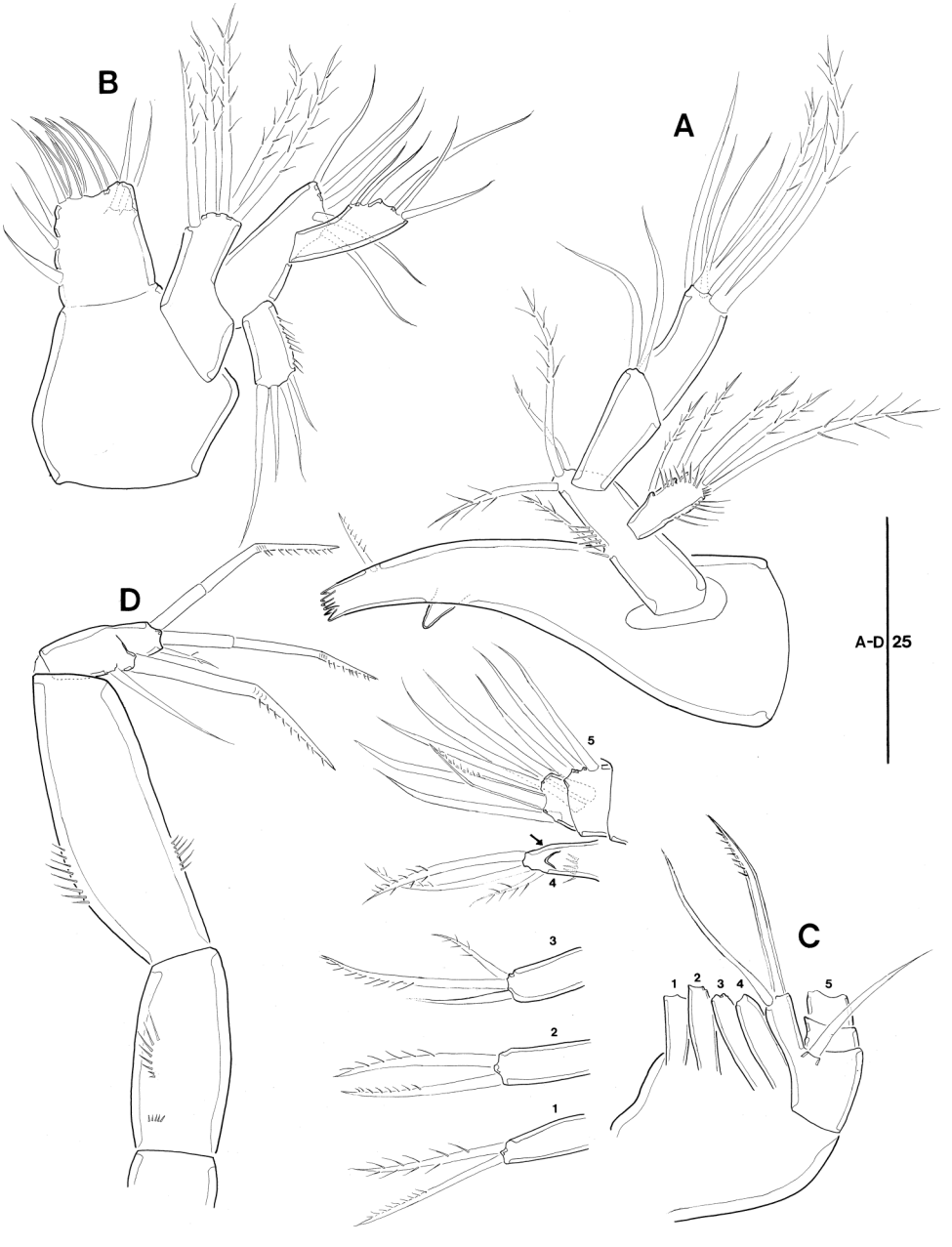

Figure 3. *Remanea naksanensis* sp. nov. Female: (A) Mandible; (B) maxillule; (C) maxilla [syncoxal endites (1–4) and endopod (5) shown in separate insets; arrow indicates minute process on distal coxal endite]; (D) maxilliped. Scale bars in μm.

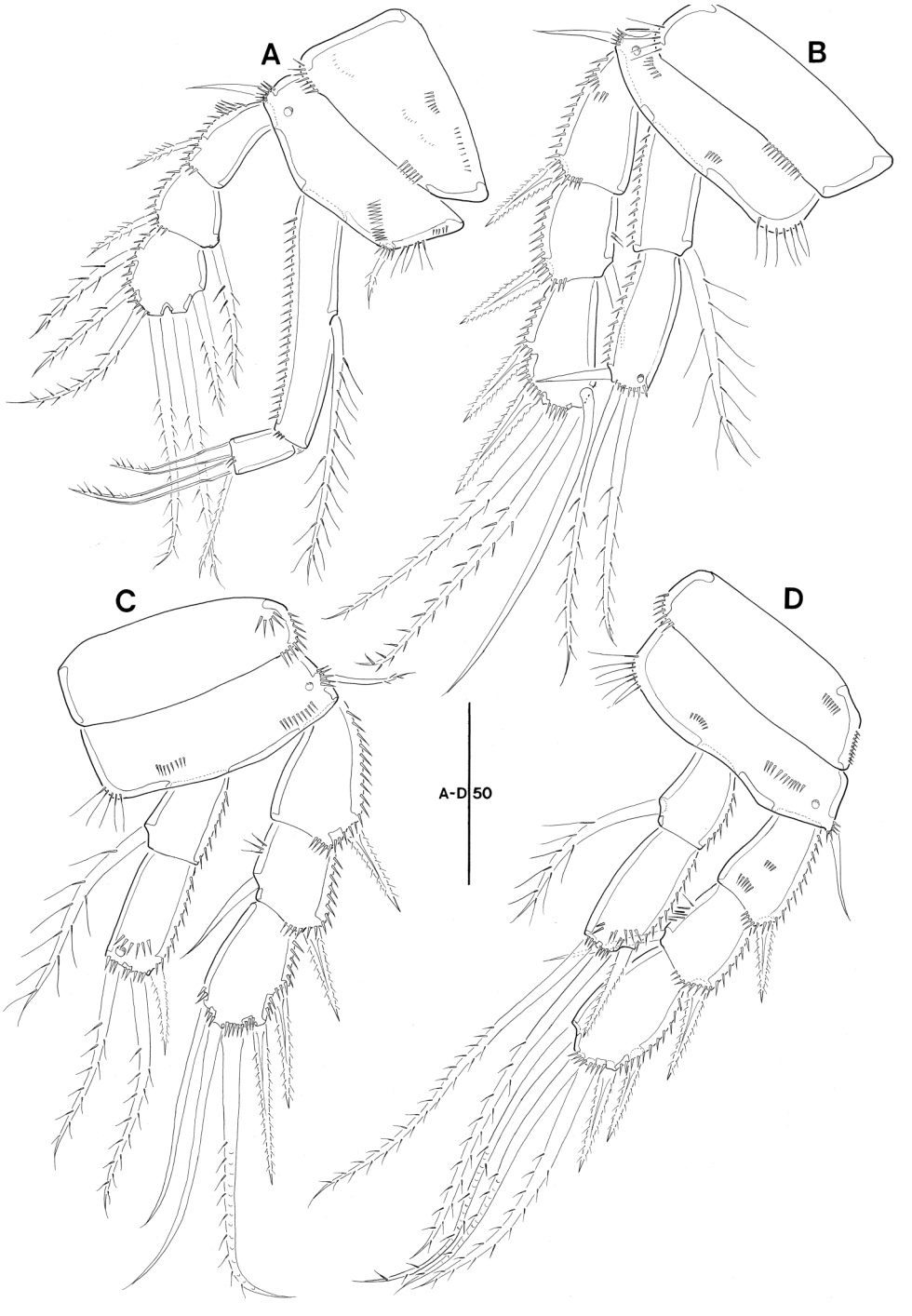

Figure 4. *Remanea naksanensis* sp. nov. Female: (A) P1, anterior; (B) P2, anterior; (C) P3, anterior; (D) P4, anterior. Scale bars in μm.

P6 (Figures 2E, 7D) represented by narrow transverse plate, armed with one bare inner seta and two pinnate outer elements of different lengths, the former longest.

Description of male

Slightly smaller and more slender than female, body length 498 μm ($n = 4$, mean = 488 μm) (Figure 5A). Largest width (92 μm) measured at posterior margin of cephalic shield. Cephalothorax (Figure 5A) slightly more angular and with more sensilla than in female. General body shape and ornamentation as in female except for separation of genital somite; additional sexual dimorphism in antennule, P2, P3, P5 and P6.

Antennule (Figures 5B, 7F): eight-segmented, subchirocer; segment 6 swollen, largest. Aesthetascs on sixth and eighth segments. Sixth segment with surface suture dorsoanteriorly (arrowed in Figure 7F). Armature formula: 1-[1 pinnate], 2-[4 bare + 1 pinnate], 3-[5 bare + 3 pinnate], 4-[3 bare + 3 pinnate], 5-[2 bare + 1 pinnate], 6-[5 bare + 6 pinnate + (1 + ae)], 7-[4 bare], 8-[7 bare + (2 + ae)].

P2 (Figure 6A) Basis with surface spinules and small outer seta. Exopod as in female. Enp-1 as in female; enp-2 armed with two long and one small bare setae apically, the latter smaller than homologous element in female. General shape, segmentation, and armature formula as in female.

P3 (Figure 6B). Coxa, basis, and exopod as in female. Endopod two-segmented; enp-1 with rows of long spinules along outer margin and with one inner plumose seta. Enp-2 twice as long as enp-1, with two apical setae and well developed outer apophysis.

P5 (Figure 6C): baseoendopods confluent, forming large transverse plate; unarmed except for outer slender bare seta on either side. Exopod ovate, with row of spinules along inner margin; with two outer spinulose setae, one long apical bare seta and one small naked inner seta.

P6 (Figure 6D): pair of P6 symmetrical, fused medially. Each P6 with one outer naked lateral seta proximally and one pinnate seta close to distal outer corner.

Etymology

The specific name refers to the type locality, the Naksan sandy beach area on the east coast of Korea.

Remanea arenicola Klie, 1929
(Figures 8, 9)

Original description. Klie (1929): 364–367; figs 44–56.

Type locality. Germany, Kiel Bay, off Bülk lighthouse (vicinity of "Nebenfahrwassertonne A"); clean coarse sand, 10 m depth.

Material examined

Zoologisches Museum der Universität Kiel. Walter Klie collection. Two females (Cop 586, 589) and two males (Cop 584, 588) dissected on individual slides.

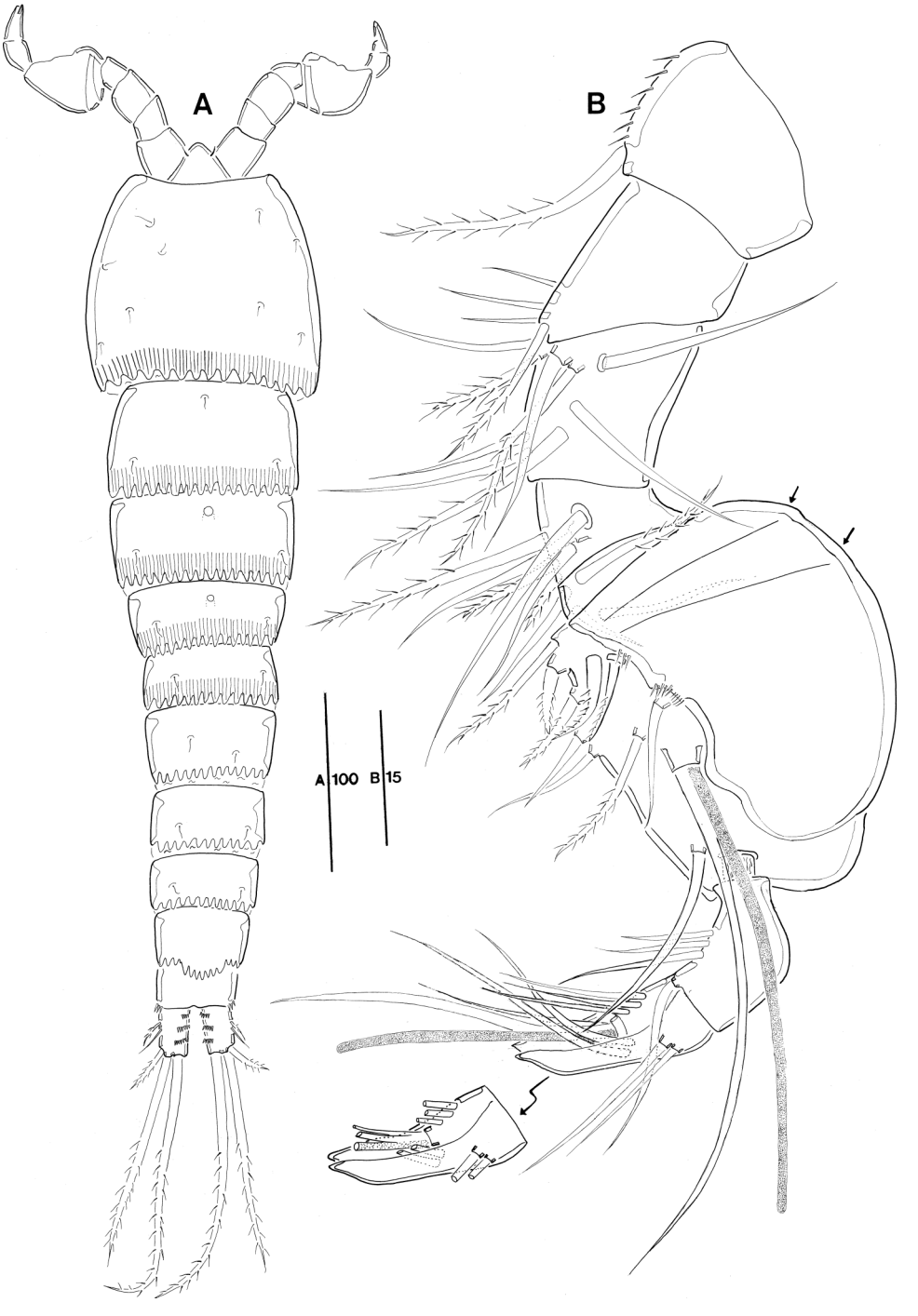

Figure 5. *Remanea naksanensis* sp. nov. Male: (A) Habitus, dorsal; (B) antennule, ventral (arrows indicate position of partial surface sutures on swollen segment 5). Scale bars in μm.

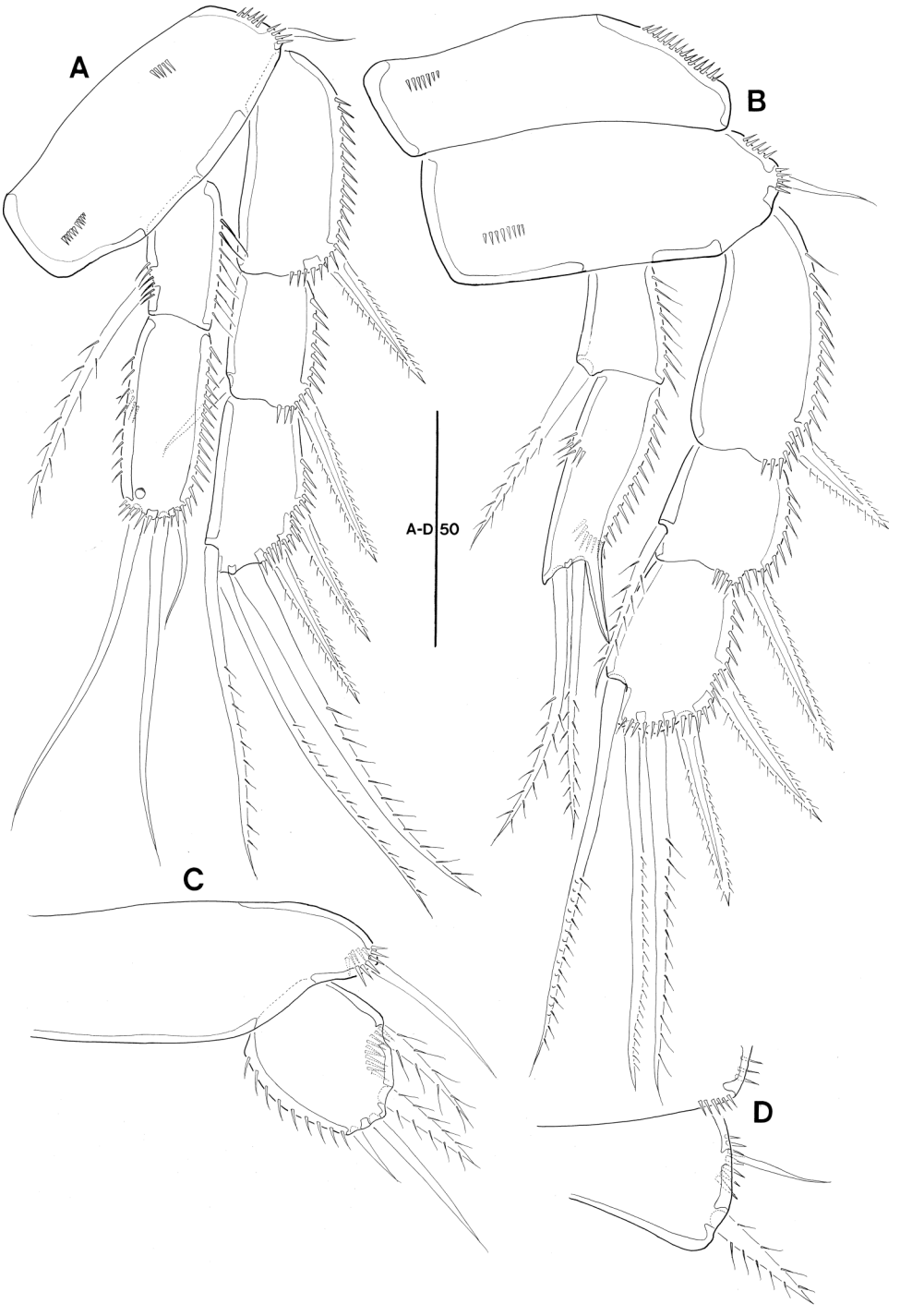

Figure 6. *Remanea naksanensis* sp. nov. Male: (A) P2, anterior; (B) P3, anterior; (C) left P5, anterior; (D) armature of left P6. Scale bars in μm.

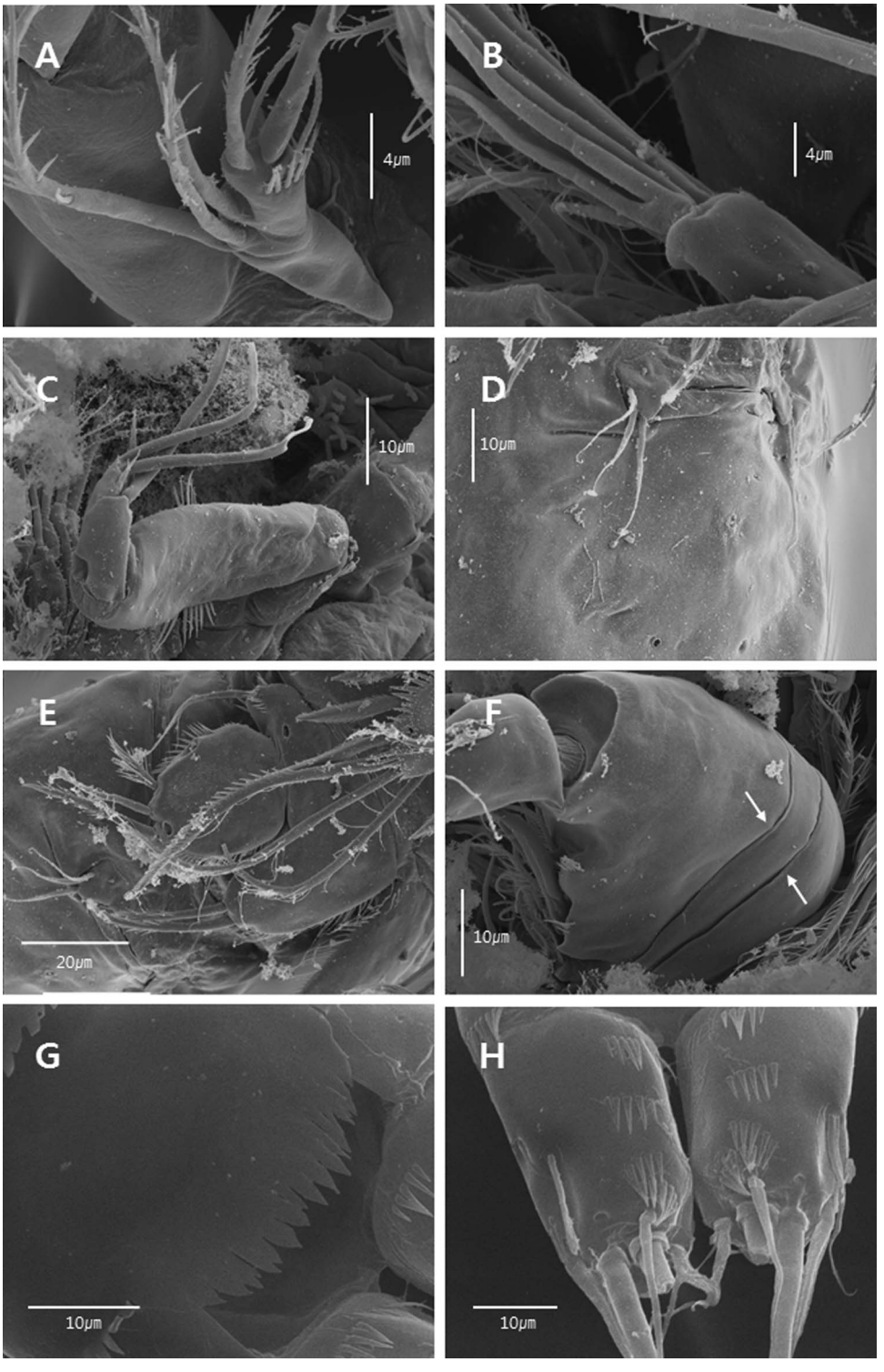

Figure 7. *Remanea naksanensis* sp. nov., scanning electron micrographs. Female: (A) Antennary exopod; (B) distal segment of mandibular palp; (C) maxilliped; (D) genital field and P6; (E) P5; (G) pseudoperculum; (H) caudal rami, dorsal. Male: (F) fifth antennulary segment with surface sutures arrowed. Scale bars in μm.

Unfortunately the slides were partly dried out and not in a sufficiently good condition to make a complete detailed redescription.

Description of female

General shape of appendages similar to those given in Klie's original description (Klie 1929).

Caudal ramus (Figure 8C) rectangular, about 1.5 times as long as wide; with three inner rows of spinules dorsally; with seven setae; setae I–II arising from anterior outer margin, setae III–VI around posterior margin, and seta VII in distal third of ramus; seta I short and bipinnate; seta II spinulose in distal half; seta III plumose; seta IV well developed and plumose, seta V longest and pinnate in distal half; seta VI spinulose; seta VII bi-articulate at base and naked. Ventral spinules present along posterior margin and at base of seta III.

Antenna (Figure 8A): basis with row of spinules distally. Exopod arising from distal margin of basis, two-segmented; exp-1 as long as exp-2; exp-1 with one long pinnate seta; exp-2 with two lateral and two pinnate apical setae. Enp-1 with pinnate seta, without surface ornamentation; enp-2 with two bare setae of different lengths and one spinulose seta laterally, with five geniculate setae and one bare seta fused with largest geniculate seta at base.

P1 (Figure 8D): coxa well developed, with rows of spinules as figured. Basis with one inner and one outer pinnate seta. Exopod much shorter than endopod; exp-1 longest, with outer spinules and one pinnate outer spine; exp-2 somewhat swollen distally, with one pinnate outer spine and one long spinulose inner seta; exp-3 with six spines/setae. Endopod prehensile; enp-1 elongate, longer than exopod, with outer row of spinules, with one long plumose inner seta in proximal third; enp-2 small, quadrangular, with two strong setae and one small pinnate apical element.

P5 (Figure 9C) with medially fused baseoendopods and discrete exopods. Baseoendopod with pinnate outer basal seta; endopodal lobes narrow, shorter than exopod, each with one short outer seta and one long slender plumose inner seta, with row of spinules along inner margin. Exopod well developed, with inner and outer rows of spinules; with two short spinulose outer setae and two plumose apical elements (subequal in length).

P6 (Figure 8B) forming small narrow transverse plate with one long outer and two bare inner setae; middle seta shortest.

Description of male

Sexual dimorphism expressed in antennule, P3 endopod, P5, P6 and urosomal segmentation.

P3 (Figure 9A). Coxa, basis, and exopod virtually similar to those of female (see Klie 1929). Endopod two-segmented; enp-1 with outer rows of spinules and one inner plumose seta; enp-2 longer than enp-1, with two apical pinnate setae and with well developed outer apophysis (see inset in Figure 9A).

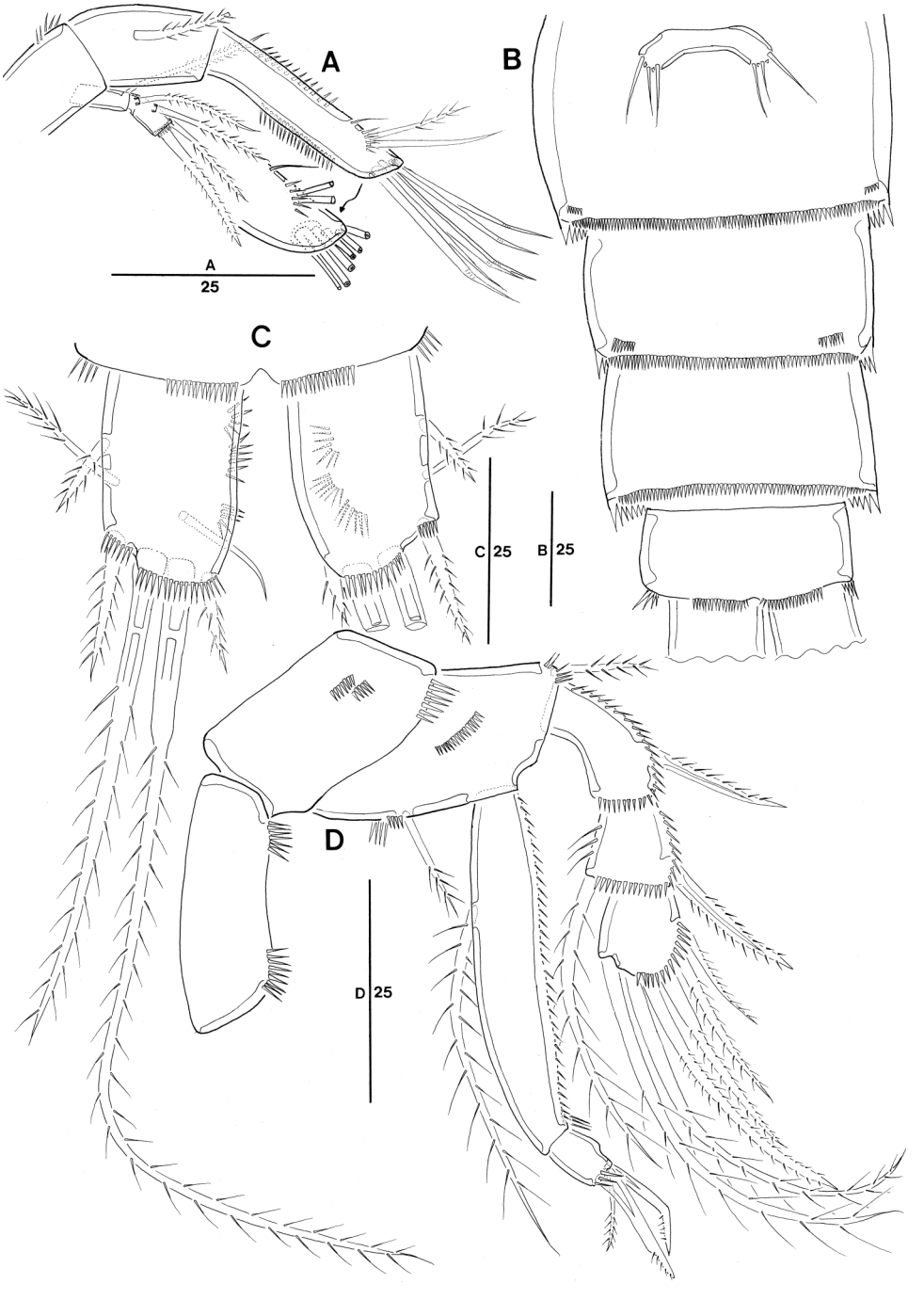

Figure 8. *Remanea arenicola* Klie, 1929. Female: (A) Antenna; (B) urosome (excluding P5-bearing somite and caudal rami), ventral; (C) caudal rami, ventral; (D) P1 and intercoxal sclerite, anterior. Scale bars in μm.

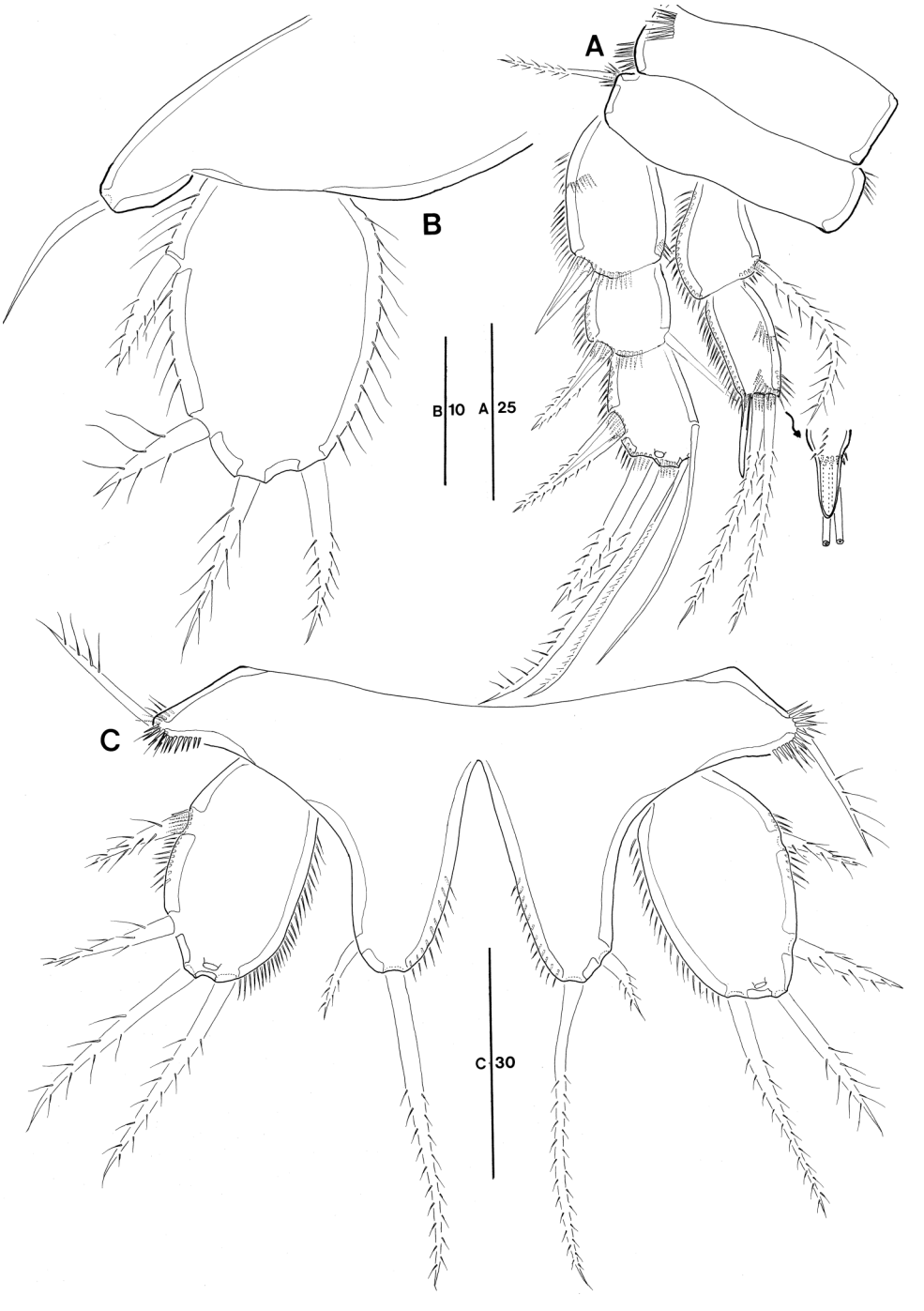

Figure 9. *Remanea arenicola* Klie, 1929. Male: (A) P3, posterior (inset showing apophysis on enp-2, outer lateral); (B) right P5, anterior. Female: (C) fifth pair of legs, anterior. Scale bars in μm.

P5 (Figure 9B). Baseoendopods confluent, each with one outer bare basal seta. Exopod ovate, discrete, with inner row of spinules, and with two spinulose outer setae, one pinnate apical element, and one pinnate inner seta.

Discussion

Review of previous descriptions and updated generic diagnosis of Remanea *Klie, 1929*

Since its original description by Klie (1929) *R. arenicola* has been the subject of a number of redescriptions (Nicholls 1945; Božić 1955; Mielke 1975; Arlt 1983) based on material from the west coast of Scotland, Brittany, the Isle of Sylt and the Baltic. Comparison reveals a great deal of alleged variation in some characters and what appear to be erroneous observations in others, hampering reliable species discrimination in the genus. These characters are reviewed below.

Ornamentation of antennulary setae

Pennak (1942a) noted that most setae in *R. plumosa* were plumose (hence the specific epithet) whereas in Klie's (1929) description of *R. arenicola* they were clearly illustrated as naked. Nicholls (1945) showed pinnate setae on segments 1 and 2, however our re-examination has confirmed that – as in *R. naksanensis* – one or more pinnate/plumose setae are present on all segments except for the apical one.

Armature of antennary exopod

Pennak (1942a) stated that the distal segment of the antennary exopod has six setae but only figured five. The outermost apical element shown in his Plate I (fig. 21) is very small and it is therefore highly conceivable that Pennak has misinterpreted one of the spinules typically found in that position (Figure 2B) as an additional armature element. Arlt (1983) claimed that his specimens from the Baltic had only three setae but his illustration suggests that he has overlooked one of the lateral elements. Our observations confirmed that the antennary exopod in both *R. arenicola* and *R. naksanensis* has a [1, 4] setal formula which is here considered as the basic pattern for the genus.

P1 enp-1 armature

One of the major morphological differences between *R. plumosa* and its congeners is the absence of the long inner seta on enp-1. Within Paramesochridae the armature pattern of P1 is typically conservative at generic level and it is therefore likely that Pennak (1942a) overlooked the inner seta, either because it was dislodged or concealed behind the long proximal endopod segment. Similar observational errors were made in his description of *Psammoleptastacus arenaridus* Pennak, 1942 (cf. Sak et al. 2008).

P1 enp-2 armature

In both the original description of *R. plumosa* and all previous descriptions (Klie 1929; Nicholls 1945; Arlt 1983 – note that the latter author mislabelled the P1 male

as P5 female and vice versa) of *R. arenicola* the distal segment of the P1 endopod has consistently been illustrated with two apical elements. Mielke (1975) listed the setal formulae for the swimming legs but did not include the P1. In both *R. arenicola* (Figure 4A) and *R. naksanensis* sp. nov., we observed an additional bipinnate seta arising from the inner distal corner. This seta is often concealed by the inner apical geniculate seta, raising the suspicion that it was overlooked in earlier descriptions. We speculate that it is probably the homologue of the minute element found at the inner distal corner of enp-2 in some *Rossopsyllus* species (Mielke 1985; Cottarelli and Baldari 1987) or of the well developed seta originating from the inner margin of enp-2 in *Tisbisoma spinisetum* Božić, 1964 (Božić 1964).

Sexual dimorphism P3 endopod

The sexual dimorphism on the P3 endopod has as yet been unnoticed. Both *R. arenicola* and *R. naksanensis* have a spiniform outer apophysis on the distal endopod segment of P3. Although this condition has yet to be confirmed in *R. plumosa* (male unknown) it is likely to be a diagnostic character for the genus. The male apophysis is the positional homologue of the outer distal seta expressed in the female. Only the primitive genera *Rossopsyllus* Soyer, 1975, *Tisbisoma* Božić, 1964 and some representatives of *Diarthrodella* Klie, 1949 possess an outer seta/spine on P3 enp-2 but none of these taxa displays sexual dimorphism on this ramus. We therefore hypothesize that the presence of an apophysis on the male P3 endopod is an autapomorphy of *Remanea* rather than the ancestral condition of the family. Sexual dimorphism in the Paramesochridae (except for the conventional modifications in the antennule, P5, P6 and urosomal segmentation) is rare. Veit-Köhler (2000) reported on the sexual dimorphism in the shape and length of caudal ramus setae in representatives of the subgenus *Wellsopsyllus* (*Scottopsyllus*) while Mielke (1984, 1985) documented modifications in the male antennary exopod of *Rossopsyllus* and some species of *Diarthrodella*. Swimming leg sexual dimorphism has only been reported for *Diarthrodella galapagoensis* Mielke, 1985 (P4 exp-3 without inner seta in the male), *Kliopsyllus regulexstans* Mielke, 1984 (inner distal corner of P2–P3 exp-3 forming small spiniform projection) and *Rossopsyllus kerguelenensis quellonensis* Mielke, 1985 (inner seta of P3–P4 enp-1 with different ornamentation).

Female sixth legs

Neither Klie (1929) nor Pennak (1942a) figured or commented on the female genital field. The first author to refer to it was Nicholls (1945) who illustrated the P6 with two naked setae. Božić (1955) remarked that his specimens from the Roscoff area had three naked setae, which was confirmed by our re-examination of the type material (Figures 1C, 2E) except that the middle and outer ones are pinnate rather than unornamented.

Pseudoperculum

The presence of a pseudoperculum covering the anal opening is a family diagnostic for the Paramesochridae. It consists of a posterior hyaline extension originating from the

penultimate somite. Early workers have often overlooked such transparent structures and none of Klie (1929), Pennak (1942a) or Nicholls (1945) made reference to it. Božić (1955) illustrated it as a deeply incised frill in *R. arenicola*, which was confirmed in our material of the type species and *R. naksanensis*.

Caudal ramus ornamentation

Kunz (1962) used the number of elements on P2–P3 exp-3 and the spinular ornamentation on the caudal ramus to differentiate *R. arenicola* and *R. plumosa*. Pennak's (1942a) description of *R. plumosa* showed multiple transverse spinule rows on the median half of the caudal ramus while Klie (1929) illustrated the caudal ramus of *R. arenicola* with only one dorsal spinule row (" . . . auf der dorsalen Fläche, gleichlaufend mit dem Innenrande, eine Leiste aus feinen Haaren"). The redescription by Nicholls (1945) adds further confusion because it does not show any ornamentation on the caudal ramus. Although his illustration of the urosome appears to suggest that it was drawn in dorsal aspect because of the presence of a "dorsal" seta on the caudal rami, the spinule rows around the posterior margin of the anal somite indicate that it is a ventral view, in which case it would explain the absence of the spinules in the median half of the caudal ramus [see Figure 8C and Mielke (1975: Abb. 50B)]. The "dorsal" seta of Nicholls (1945) is located far proximally near the rear margin of the anal somite and hence cannot possibly be the real seta VII, which typically arises from near the posterior margin of the caudal ramus in each of the three congeners. Božić's (1955) partial redescription and our observations (Figure 8C) confirmed that the spinular ornamentation on the dorsal surface of the caudal ramus is essentially identical in *R. arenicola* and *R. plumosa* and can no longer be used as a species discriminant.

Updated generic diagnosis of* Remanea *Klie, 1929

Paramesochridae

Body broad anteriorly, rather flattened; with distinct separation between prosome and urosome; dorsal and lateral hyaline frills of cephalothorax and body somites well developed, crenulate. Rostrum defined at base. Pseudoperculum well developed, incised. Caudal rami with seven setae, seta I well developed, seta VII positioned near posterior margin of ramus. Antennule eight-segmented in both sexes, subchirocer in male; with pinnate setae on segments 1–7 in female and segments 1–5 in male. Antennary exopod two-segmented with one seta on exp-1 and four setae on exp-2. Mandible with four setae on basis; two-segmented endopod and one-segmented exopod. Maxilla with four endites on syncoxa; endopod one- or two-segmented. Maxilliped with elongate basis; endopod one-segmented with three or four setae and claws. P1–P4 biramous, with three-segmented exopods and two-segmented endopods; P2 endopod with weak sexual dimorphism (*R. naksanensis*); P3 endopod with outer apical spinous apophysis on enp-2 (unconfirmed in *R. plumosa*). P1–P4 armature formulae: exopods: P1, 0.1.222; P2, 0.1.[0–1]22; P3, 0.1.[0–1]22; P4, 0.1.122; endopods: P1, 1.030; P2, 1.02[0–1]; P3, 1.021 (1.020 in male); P4, 1.021.

P5 with medially fused baseoendopods in both sexes. Endopodal lobe well developed in female, with two apical setae; not developed in male, unarmed. Exopod

discrete in both sexes; with five elements in female and four in male. P6 with three setae in female and two in male.

Type species: *Remanea arenicola* Klie, 1929.

Additional species: *R. plumosa* Pennak, 1942a, *R. naksanensis* sp. nov.

Species discrimination

Remanea naksanensis is placed in the genus *Remanea* on account of the three-segmented P1 exopod, the eight-segmented female antennule, the armature formulae of the swimming legs, and the shape of the caudal rami. The new species resembles *R. arenicola* in most characters except for the morphology of the P5 in both sexes: (a) the general shape of the endopodal lobe in the female (more robust and distinctly shorter in *R. naksanensis* sp. nov.; compare Figures 2D and 9C), (b) the relative length of the endopodal setae in the female (inner seta slightly longer than exopod and outer seta in *R. naksanensis* sp. nov., but inner seta clearly longer than exopod and outer seta very small in *R. arenicola*), and (c) in *R. naksanensis* the exopod in the male is armed with one small naked inner seta, one bare terminal seta, and two pinnate outer setae, while in *R. arenicola* it is armed with two pinnate outer setae, and one terminal and one inner well-developed pinnate seta (compare Figures 6C and 9B). The new species has the distal segment of P1 endopod armed with three setae; however, *R. arenicola* also has the same number of setae (see Figure 8D). Additional morphometric differences separating both species are summarized in Table 1.

Key to species of **Remanea** *Klie, 1929*

1. P2–P3 exp-3 with four setae/spines; enp-2 with two elements . . . . . *R. plumosa*
   P2–P3 exp-3 with five setae/spines; enp-2 with three elements 2
2. P5 of female endopodal inner seta 0.25 the length of outer seta; P5 of male inner exopodal seta bipinnate . . . . . *R. arenicola*
   P5 of female endopodal inner seta 0.85 the length of outer seta; P5 of male inner exopodal seta naked . . . . . *R. naksanensis* sp. nov.

Distribution

From a biogeographical point of view, it would appear that *R. arenicola* is confined to western Europe, assuming a distribution along the Atlantic seaboard from Sweden to Portugal. It is widely distributed in the Baltic but absent from the Mediterranean basin. Plum and George (2009) listed *R. arenicola* as a "cosmopolitan" species and cite Australia as one of the records. This is a mistake based on an erroneous interpretation of Nicholls (1945), which dealt with a new species of *Paramesochra* from Australia and included a redescription of *R. arenicola*; however, the author stated explicitly (p. 94) that the latter was based on material collected from the Firth of Clyde in Scotland. Unlike its congeners, *R. arenicola* is found in sandy substrata in

Table 1. Morphological comparison of the species of *Remanea* Klie, 1929.

Character	*R. arenicola*	*R. plumosa*	*R. naksanensis* sp. nov.
Antennary exopod	exp-1>exp-2	exp-1<exp-2	exp-1<exp-2
P1			
exp-3 inner seta/inner distal seta	equally long	equally long	less than half the length
exp-3 inner seta	naked	naked	bipinnate
length longest apical seta enp-2/enp-1	0.35	0.95	0.55
P2–P3			
armature exp-3	122	122	022
armature enp-2	021	020	021
P5 ♀			
exopod L /W	1.5	1.4	1.2
endopodal outer seta/inner seta	0.25	0.50	0.85
inner margin endopodal lobe	pinnate in distal half	pinnate in distal third	setulose along entire margin
P5 ♂			
exopod L/W	1.4	?	1.1
inner exopodal seta	bipinnate	?	naked
inner lateral/inner apical exopodal seta	0.9	?	0.17
Caudal ramus seta V/seta IV	1.85	2.1	1.6
Body size (μm)			
♀	350 (Klie 1929)	330–420 (Pennak 1942a)	541 (this study)
	380 (Nicholls 1939) ± 500 (Božić 1955)		
	330–360 (Mielke 1975)		
♂	350 (Klie 1929)	unknown	488 (this study)
	320–350 (Mielke 1975)		
no sex specified	290–360 (Arlt 1983)		

both intertidal beaches (e.g. Nicholls 1939; Noodt 1952; Harris 1972a, b) and subtidal localities (e.g. Klie 1929; Drzycimski 1974; Arlt 1983; Willems et al. 2009). Its distribution records are summarized below.

Sweden: Skåne County, Simrishamn (Noodt 1955a; Brinck et al. 1956); Västra Götaland County, Koster-area (Willems et al. 2009).
Denmark: southwest of the isle of Bornholm in the Baltic (Arlt 1983).
Germany: Isle of Sylt (Noodt 1952, 1956, 1957; Mielke 1975) and Jade Bay (Rose and Seifried 2006) along the North Sea coast; off Bülk lighthouse (Klie 1929), Weißenhaus and Bottsand (Noodt 1956, 1957), and Schilksee (Kunz 1935, 1937) in the Kiel Bay (Kieler Bucht).
Poland: Puck Bay (Demel 1936; Drzycimski 1967), Southern Baltic (Drzycimski 1974, 1975, 1986; Sywula 1982).

Russia: Kaliningrad oblast, Curonian Spit (Kurishe Nehrung) (Kunz 1939).
Scotland: Isle of Cumbrae in the Firth of Clyde (Nicholls 1939, 1945).
Wales: Traeth Bychan, Anglesey (Geddes 1972).
England: Isles of Scilly (Wells 1961, 1970; R. Huys unpublished data); Cornwall, Whitsand Bay (Harris 1972a, b).
Belgium: coastal area (Vandepitte et al 2010).
France: Brittany, Kernic (Božić 1955). Noodt (1955b, c) recorded a single juvenile from Contis-Plage (Landes) (as *Remanea* spec.) and remarked that it most likely belonged to *R. arenicola*.
Portugal: Porto District, Francelos and Cabedelo (Galhano 1970).

The only confirmed records of *R. plumosa* are those by Pennak (1942a, b) who found numerous specimens just above the low tide mark at North Cape Cod beach and Falmouth beach near Woods Hole, Massachusetts. The record by Collette (1983) of *R. arenicola* from Canoe beach in Nahant, Massachusetts, almost certainly refers to *R. plumosa*.

Baguley (2004) listed "*Remanea texana*" in a checklist of harpacticoid copepods from the deep sea in the northern Gulf of Mexico but since no description has been published so far this name is to be regarded a *nomen nudum*.

Barcoding

So far, the taxonomy of harpacticoid copepods has been based on morphological characters. For the identification of species, morphological data are of primary importance; however, molecular sequence data are often required to confirm differences among species that closely resemble each other (e.g. Castro-Longoria et al. 2003), or to study phylogenetic relationships. Molecular methods can be a useful tool for the rapid identification of species. Recent studies have demonstrated that a fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene can be used as a DNA barcode for species-level resolution among crustacean lineages (Hebert et al. 2003; Costa et al. 2007; Bradford et al. 2010). Moreover, some researchers have already begun adopting a DNA-based phylogenetic approach to study copepods, especially lineages where morphological characters have not yielded resolution (e.g. Caudill and Bucklin 2004; Eyun et al. 2007). Recently, Handschumacher et al. (2010) elucidated the genetic relationships of *Tigriopus brevicornis* (Müller, 1776), a harpacticoid with a worldwide distribution, using mitochondrial DNA sequencing. To date, partial or complete mtCOI sequences have been submitted to GenBank of only 11 harpacticoid species, representing six families: *Tigriopus brevicornis*, *Tigriopus fulvus* (Fischer, 1860), *Tigriopus californicus* (Baker, 1912), *Tigriopus japonicus* Mori, 1938, *Tigriopus* sp., *Macrosetella gracilis* (Dana, 1847), *Miracia efferata* Dana, 1849, *Cletocamptus deitersi* (Richard, 1897), *Cletocamptus helobius* Fleeger, 1980, *Coullana* sp., Cletopsyllidae sp. and Clytemnestridae sp. Ideally, morphological descriptions of new species should be accompanied by the submission of a barcode sequence to GenBank/EMBL and the deposition in an appropriate institution (ICZN Recommendations 16C and 72F) of voucher specimens preserved in an adequate storage reagent (e.g. RNA*later*®) for future molecular studies. The sequences of mtCOI of *R. naksanensis* was submitted to GenBank under accession numbers JN222346–JN222357.

Acknowledgements

This research was supported by the Basic Science Research Programme of the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology (2009-0075502), and by the Discovery of Korean Indigenous Species Project, NIBR (National Institute of Biological Resources).

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