



A REAPPRAISAL OF THE GENERA *NANNOPUS* BRADY, 1880  
AND *ILYOPHILUS* LILLJEBORG, 1902 (COPEPODA, HARPACTICOIDA,  
NANNOPODIDAE) WITH A DESCRIPTION OF *N. PARVIPILIS* SP. NOV.  
FROM SOUTH KOREA

BY

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ABSTRACT

The genera *Nannopus* Brady, 1880 and *Ilyophilus* Lilljeborg, 1902 are reappraised based on the characteristic features of a new species, *Nannopus parvipilis* sp. nov., collected from the brackish mud flat on Jindo Island, South Korea. *Nannopus* species have long been known as having a two-segmented P3 endopod. However, we discovered *N. parvipilis* sp. nov. having a one-segmented P3 endopod in accordance with the description of the genus by Brady. It implies that Brady's generic diagnosis was appropriate and tentatively correct, and such species having a two-segmented P3 endopod but still being placed in *Nannopus* should be excluded from the genus. The genus *Ilyophilus* Lilljeborg, 1902, which has been regarded as a junior synonym of *Nannopus*, is revived to accommodate these *Nannopus* species. Thus, *Nannopus* is now composed of only two species, *N. palustris* and *N. parvipilis* sp. nov. and *Ilyophilus* comprises eight species: *I. flexibilis* Lilljeborg, 1902, *I. perplexus* Sars, 1909b comb. nov., *I. unisegmentatus* (Shen & Tai, 1964) comb. nov., *I. didelphis* (Fiers & Kotwicki, 2013) comb. nov., *I. hirsutus* (Fiers & Kotwicki, 2013) comb. nov., *I. procerus* (Fiers & Kotwicki, 2013) comb. nov., *I. scaldicola* (Fiers & Kotwicki, 2013) comb. nov., and *I. ganghwaensis* (Vakita, Kihara & Lee, 2016). In addition, *N. palustris* sensu Canu, 1892, which was commonly considered as representing the criterion of *N. palustris*, is established as a new species, *I. canui* sp. nov., based on the characteristic feature of the P3. A detailed description and illustrations of *N. parvipilis* sp. nov. are provided.

Key words. — Harpacticoids, *Ilyophilus*, morphology, *Nannopus*, new species, taxonomy

RÉSUMÉ

Les genres *Nannopus* Brady, 1880 et *Ilyophilus* Lilljeborg, 1902 sont réévalués à partir des traits caractéristiques d'une nouvelle espèce, *Nannopus parvipilis* sp. nov., collectée dans une vase

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saumâtre sur l'île de Jindo, Corée du Sud. Les espèces de *Nannopus* sont connues depuis longtemps comme ayant un endopodite de P3 bi-segmenté. Cependant, nous avons découvert *N. parvipilis* sp. nov. qui possède un endopodite de P3 uni-segmenté en accord avec la description du genre par Brady. Cela implique que cette diagnose du genre par Brady était appropriée et provisoirement correcte, et les espèces avec un endopodite de P3 bi-segmenté et encore placées dans le *Nannopus* devraient être exclues de ce genre. Le genre *Ilyophilus* Lilljeborg, 1902, qui a été considéré comme synonyme junior de *Nannopus*, est rétabli pour traiter ces espèces de *Nannopus*. Ainsi, *Nannopus* est maintenant composé de seulement deux espèces, *N. palustris* et *N. parvipilis* sp. nov. et *Ilyophilus* comprend huit espèces: *I. flexibilis* Lilljeborg, 1902, *I. perplexus* Sars, 1909b comb. nov., *I. unisegmentatus* (Shen & Tai, 1964) comb. nov., *I. didelphis* (Fiers & Kotwicki, 2013) comb. nov., *I. hirsutus* (Fiers & Kotwicki, 2013) comb. nov., *I. procerus* (Fiers & Kotwicki, 2013) comb. nov., *I. scaldicola* (Fiers & Kotwicki, 2013) comb. nov., et *I. ganghwaensis* (Vakita, Kihara & Lee, 2016). De plus, *N. palustris* sensu Canu, 1892, qui était couramment considéré comme représentant le critère de *N. palustris*, est établi comme une nouvelle espèce, *I. canui* sp. nov., sur la base du trait caractéristique de P3. Une description détaillée et des illustrations de *N. parvipilis* sp. nov. sont fournies.

Mots clés. — Harpacticoïdes, *Ilyophilus*, morphologie, *Nannopus*, nouvelle espèce, taxonomie

## INTRODUCTION

Brady (1880) erected the genus *Nannopus* Brady, 1880 for *N. palustris* Brady, 1880 based on a single specimen with insufficient description and illustrations. The outright vagueness of description for the type species gave rise to taxonomic confusion on the reinterpretation of the boundaries of *N. palustris* for subsequent authors (Canu, 1892; Scott, 1902; Sars, 1909a; etc.). To date, the specimens of Canu (1892) and Scott (1902) have been accepted as suitable standards for *N. palustris*, although they differ from the generic definition of Brady (1880) (Wells, 1971; Fiers & Kotwicki, 2013). Thereafter, many descriptions of specimens identified as *N. palustris* have been provided worldwide. However, recent studies based on morphological and molecular characterization have revealed that most previous reports of *N. palustris* are composed of several pseudo-sibling species (Staton et al., 2005; Garlitska et al., 2012; Fiers & Kotwicki, 2013). These species called *N. palustris* have to be re-examined in the viewpoint of modern taxonomy (Fiers & Kotwicki, 2013).

Lilljeborg (1902) introduced the genus *Ilyophilus* Lilljeborg, 1902. This genus, with type species *I. flexibilis* Lilljeborg, 1902, was subsequently synonymized into the genus *Nannopus* with *N. palustris* by Sars (1909a). However, Fiers & Kotwicki (2013) have recently reported that there are several noticeable differences between the two species, i.e., *N. palustris* Brady, 1880 and *N. palustris* sensu Lilljeborg, 1902 (= *I. flexibilis* Lilljeborg, 1902). They have re-instated the former as a separate species, i.e., *N. flexibilis* (Lilljeborg, 1902). *Nannopus* is currently composed of the following nine valid species: *N. palustris* Brady, 1880, *N. flexibilis* (Lilljeborg, 1902), *N. perplexus* (Sars, 1909b), *N. unisegmentatus* Shen & Tai,

1964, *N. didelphis* Fiers & Kotwicki, 2013, *N. scaldicola* Fiers & Kotwicki, 2013, *N. procerus* Fiers & Kotwicki, 2013, *N. hirsutus* Fiers & Kotwicki, 2013, and *N. ganghwaensis* Vakati, Kihara & Lee, 2016 (Brady, 1880; Lilljeborg, 1902; Sars, 1909b; Shen & Tai, 1964; Fiers & Kotwicki, 2013; Vakati et al., 2016).

During our study of harpacticoid copepods from Korean waters, a new *Nannopus* species was collected. Here we describe this new species, *Nannopus parvipilis* sp. nov., collected from the intertidal flat on Jindo Island in South Korea. Its relationships with other members of the genus are discussed here.

#### MATERIAL AND METHODS

Materials were obtained from brackish mud flat using a 212- $\mu$ m-mesh sieve. Sorted copepods were preserved in 99% ethanol solution. Before dissection, line drawings of habitus were prepared from whole specimens mounted temporarily in lactophenol. Specimens were dissected and mounted in lactophenol on a slide under a stereo microscope (Discovery V8; Zeiss, Göttingen, Germany). All line drawings of habitus and appendages were made using a light microscope (Eclipse 80i; Nikon, Tokyo, Japan) equipped with a drawing tube. Materials examined in this study were deposited at the National Institute of Biological Resources (NIBR, Incheon and the National Marine Biodiversity Institute of Korea (MABIK, Seocheon) in South Korea). Scale bars in figures are given in  $\mu$ m.

Descriptive terminology follows that of Huys & Boxshall (1991). Abbreviations used in text and figures are as follows: P1-P6, first to sixth thoracic legs; exp, exopod; enp, endopod; exp(enp)-1(-2,-3), the proximal (middle, distal) segment of a ramus.

#### SYSTEMATIC PART

Order HARPACTICOIDA Sars, 1903

Family NANNOPODIDAE Brady, 1880

Genus *Nannopus* Brady, 1880

Amended diagnosis.— Nannopodidae. Body fusiform, slightly depressed dorsoventrally; posterior margins of somites dentate except for anal somite. Rostrum bell-shaped, fused to cephalothorax basally, with 1 pair of sensilla subdistally. Caudal rami with 7 setae; seta IV small, seta V well-developed. Antennule 5-segmented, short in female. Antenna with 2 abexopodal setae on allobasis; exopod with 4 setae. Mandibular palp 1-segmented, broad, with 5 setae. P1-P4 exopods 3-segmented; P1-P2 endopods 1- or 2-segmented; P3-P4 endopods 1-segmented, with 1 apical seta. P5 endopodal lobe not developed. P6 represented by 1 seta.

Male with sexual dimorphism on antennule, P5, and P6. Antennule 5-segmented, chirocer. P5 exopod 1-segmented, fused to baseoendopod basally. P6 represented by 2 setae.

Type species.— *Nannopus palustris* Brady, 1880.

Other species.— *Nannopus parvipilis* sp. nov.

### ***Nannopus parvipilis* sp. nov. (figs. 1-4)**

(Korean name: Jjal-beun-tyeol-kko-ma-bal-jang-su-no-beol-re, new)

Material examined.— Holotype female (NIBRIV0000470371) dissected on seven slides. Allotype adult male (NIBRIV0000470372) dissected on 12 slides. Paratypes: one female (NIBRIV0000470373) dissected on four slides; one female (NIBRIV0000470374) dissected on two slides; one male (NIBRIV0000470375), dissected on two slides; two females (MABIKCR00240716, MABIKCR00240717) preserved in each vial with 80% ethanol. All this material was collected from the type locality on 9 April 2013.

Type locality.— Brackish mud flat of Jindo Island (34°21'49.48''N 126°9'43.68''E); Namdong-ri, Imhoe-myeon, Jindo-gun, Jeollanam-do, Korea.

Etymology.— The composite epithet of the specific name, *parvipilis*, is a combination of Latin *parvus* and *pilus*. This name means 'small seta' referring to the shape of the setae placed on endopods of P3-P4.

Description.— Female. Habitus (fig. 1A) semi-cylindrical, depressed, tapering posteriorly, usually rolling up when preserved in alcohol; total body length 662  $\mu\text{m}$ , measured from tip of rostrum to end of caudal rami, long; prosome 1.8 times as long as urosome. Surface covered with dispersedly small cuticular ridges except for anal somite; ridges (fig. 1D) composed of cuticular ellipsoid. Posterior margin of each somite dentate, except for anal somite. Rostrum (fig. 2A) triangular, fused to cephalothorax, reaching mid-length of second segment of antennule; apex bluntly rounded, furnished with setules posteriorly; lateral margin with 1 sensillum at one third anteriorly. Cephalothorax tapering anteriorly, as long as three succeeding somites combined, about 224  $\mu\text{m}$  in length; surface and posterior margin ornamented with paired sensilla; surface with 2 ridges; P1-bearing somite partially exposed in lateral view. P2- to P5-bearing somites with 8, 6, 8 and 6 ridges on dorsal surfaces, respectively. Urosome (fig. 1B, C) tapering posteriorly. Genital double-somite (composed of genital somite and urosomite 3) slightly shorter than 2 succeeding somites combined; partially fused ventrally, but divided dorsally and laterally by transverse chitinous stripe; posterior margin of urosomite 3 ventrally dentate, with 4 sensilla; dorsal surfaces of genital somite and urosomite 3 with 4 and 6 ridges, respectively; genital field (fig. 1F) with separate genital organs on each side, each with 1 plumose seta representing P6. Urosomite 4 with 6 ridges on dorsal surface, 2 pairs of sensilla on ventral surface; posterior margin dentate. Urosomite 5 without sensillum on posterior margin. Anal somite about 2 times as

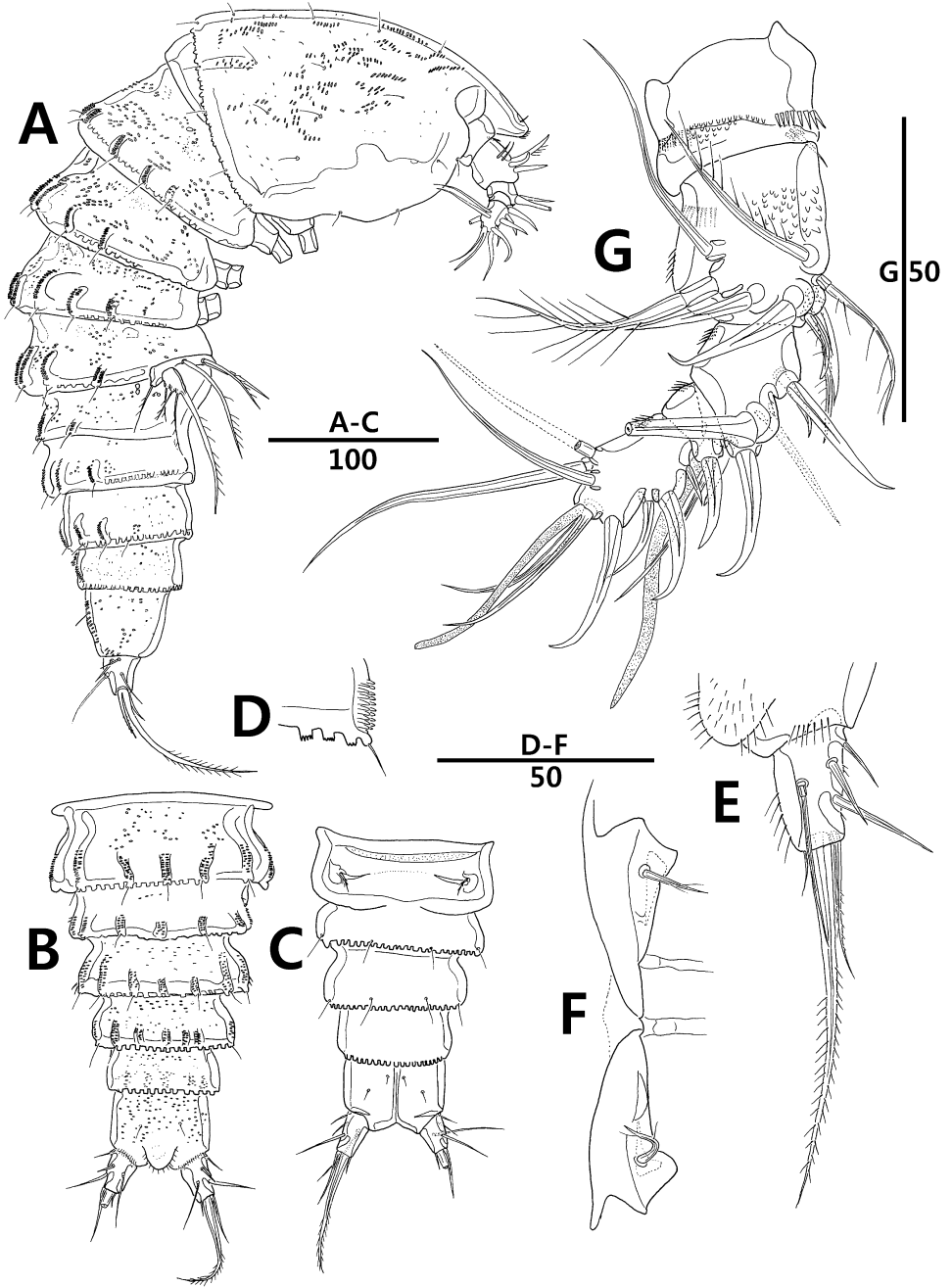


Fig. 1. *Nannopus parvipilis* sp. nov., female. A, habitus, lateral; B, urosome, dorsal; C, urosome, ventral; D, ridge on body surface; E, caudal ramus, dorsal; F, genital field; G, antennule.

long as preceding one, with 1 pair of sensilla on dorsal surface, 2 pairs of sensilla on ventral surface; operculum well-developed, covered with minute setules; dorsal posterior margin with 1 row of setules.

Caudal rami (fig. 1E) cylindrical, tapering posteriorly, about 1.5 times as long as wide, with 1 row of setules on inner margin, 7 accessory setae; setae I and II bare, small; seta III bare slightly longer than ramus in length; seta IV pinnate, as long as seta III; seta V well-developed, pinnate, about 3 times as long as caudal ramus; seta VI minute, naked; dorsal seta VII articulated at base, slightly longer than seta IV in length.

Antennule (fig. 1G) short, robust, 5-segmented. First segment short, robust, covered with papilla, with 1 row of setules, 1 row of spinules, and 1 small seta. Second segment longest, with 2 rows of setules and 9 setae; surface covered with papilla. Third segment with 1 group of setules, 7 setae and 1 aesthetasc. Fourth segment smallest, with 1 group of setules and 1 seta. Fifth segment about 3 times as long as preceding one, with 1 group of setules, 9 setae, and 1 aesthetasc. Each aesthetasc on both segments 3 and 5 fused basally to slender seta.

Antenna (fig. 2B). Coxa small, with 1 patch of papillae and 1 row of setules. Allobasis with 2 plumose setae on abexopodal margin; surface covered with minute spinules. Exopod 1-segmented, short, with 4 bare setae. Endopod shorter and narrower than allobasis; abexopodal margin with 1 row of long spinules, 1 group of stout spinules, and 2 stout spine-like elements; inner margin with 1 hyaline frill subdistally; distal margin with 1 hyaline frill and 4 spine-like elements.

Mandible (fig. 2C). Gnathobase well-developed, with 2 rows of setules; cutting edge armed with 1 main bicuspid, 3 bicuspid and 1 recurved teeth; inner distal corner with 2 pinnate setae fused basally, inner one armed with 2 pointed process. Palp 1-segmented, broad; surface covered with 2 rows of long spinules; basal endite with 2 long plumose setae; exopod small, fused to basis, with 1 apical seta; endopod incorporated into basis, represented by 2 small setae.

Maxillule (fig. 2D). Praecoxa with 1 row of spinules on surface and 1 row of setules on outer margin; arthrite well-developed, armed with 6 stout spines, 1 pinnate spine, and 1 naked spine on distal margin, with 1 long recurved and 1 slender pinnate setae along medial margin; surface with 2 parallel setae anteriorly and 1 tube pore posteriorly. Coxa with 1 group of spinules anteriorly; endite small, armed with 2 rows of spinules, with 2 apical elements. Basal endite elongate; surface armed with 1 row of spinules anteriorly, with 2 uniplumose setae; distal margin 1 stout unipinnate seta and 2 naked setae. Exopod 1-segmented, fused to basis, with 2 apical setae. Endopod incorporated into basis, represented by seta.

Maxilla (fig. 2E). Syncoxa with 3 groups of spinules along outer margin and 2 endites; proximal endite with 3 spinulose setae, two of which fused to endite; distal

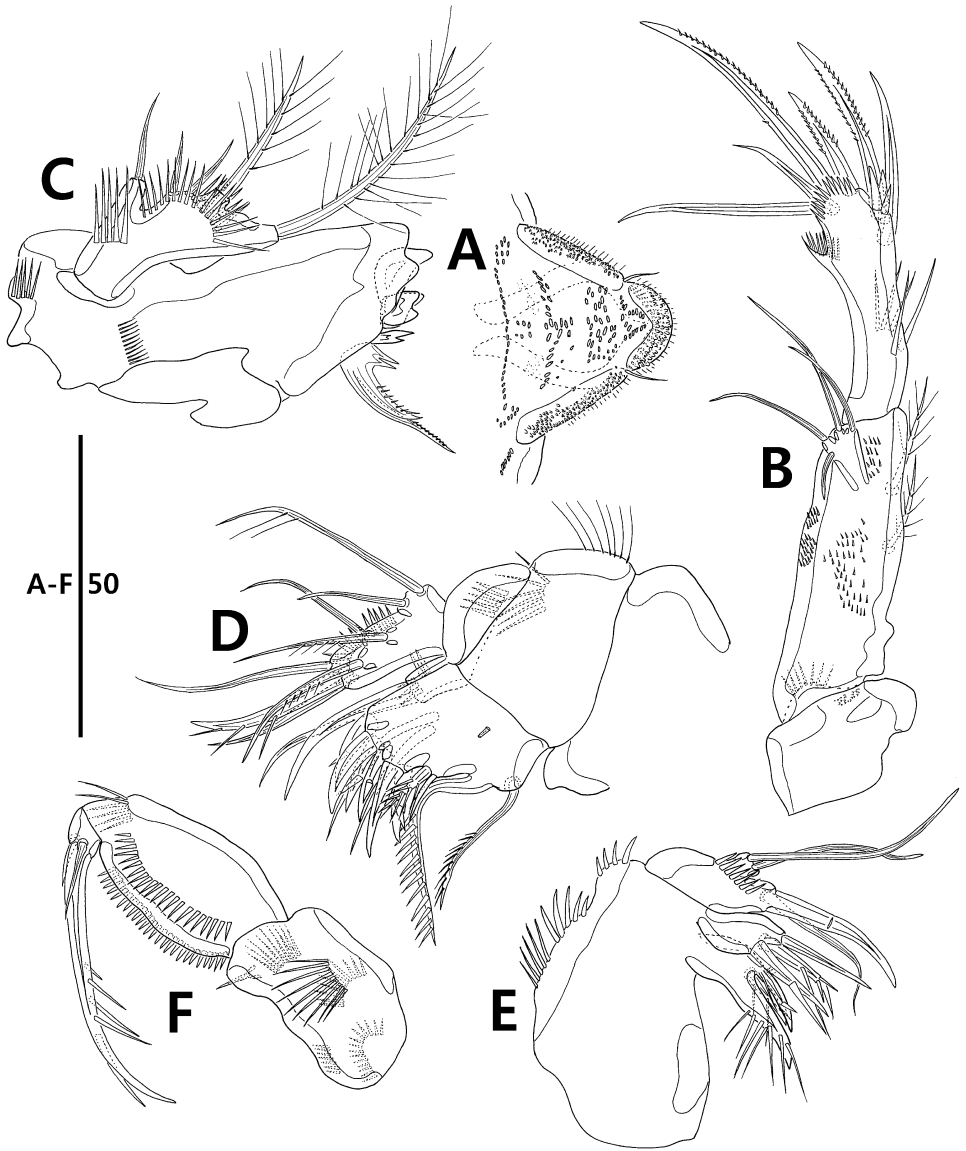


Fig. 2. *Nannopus parvipilis* sp. nov., female. A, rostrum; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped.

endite with 1 naked seta and 2 spinulose setae. Basal endite drawn out into claw, with 1 long seta; surface with 1 row of spinules. Endopod 1-segmented, confluent with basis, with 2 long apical setae.

Maxilliped (fig. 2F) 3-segmented, subchelate. Syncoxa elongate, with 1 small seta on inner distal corner and 5 rows of spinules on surface. Basis elongate, ovate, longer than preceding one, with 1 row of setules on outer margin distally and 2

rows of spinules along palmer margin. Endopod 1-segmented, small, with 1 claw bearing 1 row of spinules and 2 accessory setae.

P1 (fig. 3A). Intercoxal sclerite wide; proximal margin convex midway. Prae-coxa large, triangular, with 1 row of setules on distal margin. Coxa wide, with 2 rows of spinules on distal margin. Basis with 3 rows of spinules on anterior surface; distal margin convex; inner spine pinnate distally, with 1 small setule; outer peduncle with 1 naked seta. Exopod 3-segmented; each segment armed with outer spinules and inner setules; exp-1 and exp-2 with pinnate outer spine; exp-3 with 2 outer spines and 2 apical setae. Endopod 1-segmented; anterior surface fused, but posterior one with chitinous suture vestigially; outer margin with 1 group of spinules; distal margin with 1 group of stout spinules and 1 serrate spines; inner margin with 1 inner seta posteriorly.

P2 (fig. 3B). Intercoxal sclerite wide; proximal margin slightly convex midway. Coxa wide, with 2 rows of spinules. Basis longer and narrower than coxa, with 1 outer seta and 2 rows of spinules. Exopod 3-segmented; each segment armed with outer spinules and inner setules; exp-1 with 1 long pinnate seta on outer margin; exp-2 with 1 plumose inner seta and 1 pinnate outer spine; exp-3 with 2 outer spines, 2 apical setae, and 1 inner seta. Endopod 2-segmented; enp-1 with 1 row of spinules on outer margin; enp-2 with 1 row of spinules along distal margin, 1 pinnate apical spine, and 1 delicate spine on posterior surface.

P3 (fig. 3C). Intercoxal sclerite wide and slightly convex. Coxa smaller than that of P2, with 2 rows of spinules on anterior surface. Basis with 2 rows of spinules on anterior surface and 1 long plumose seta on outer margin. Exopod 3-segmented; each segment armed with outer spinules and inner setules; exp-1 and exp-2 similar to those of P2; exp-3 with 2 outer spines, 2 apical setae, and 2 inner setae. Endopod 1-segmented, very small, with 1 small apical seta.

P4 (fig. 3D). Intercoxal sclerite similar to that of P3. Coxa with 1 row of spinules on anterior surface. Basis with 2 rows of stout spinules and 1 row of minute spinules on anterior surface, 1 long plumose seta on outer margin. Exopod similar to that of P3 except for exp-3; exp-3 with 2 outer spines, 2 apical setae, and 1 inner seta; inner seta on exp-3 stout and pinnate distally. Endopod smaller than that of P3, with 1 delicate apical seta.

P5 (fig. 3E). Baseoendopod wide, plate-like, with 1 row of setules on posterior surface and 3 plumose setae on distal margin; innermost seta on distal margin pinnate distally; endopodal lobe not extended; outer peduncle with 1 row of setules and 1 long plumose seta. Exopod 1-segmented, rectangular, with 4 setae; innermost seta well-developed, fused to exopod basally; posterior surface with 2 rows of setules.

Male. Habitus (fig. 4A) similar to that of female, but smaller than female; total length 500  $\mu\text{m}$  long in lateral view; genital somite and urosomite 3 separate.



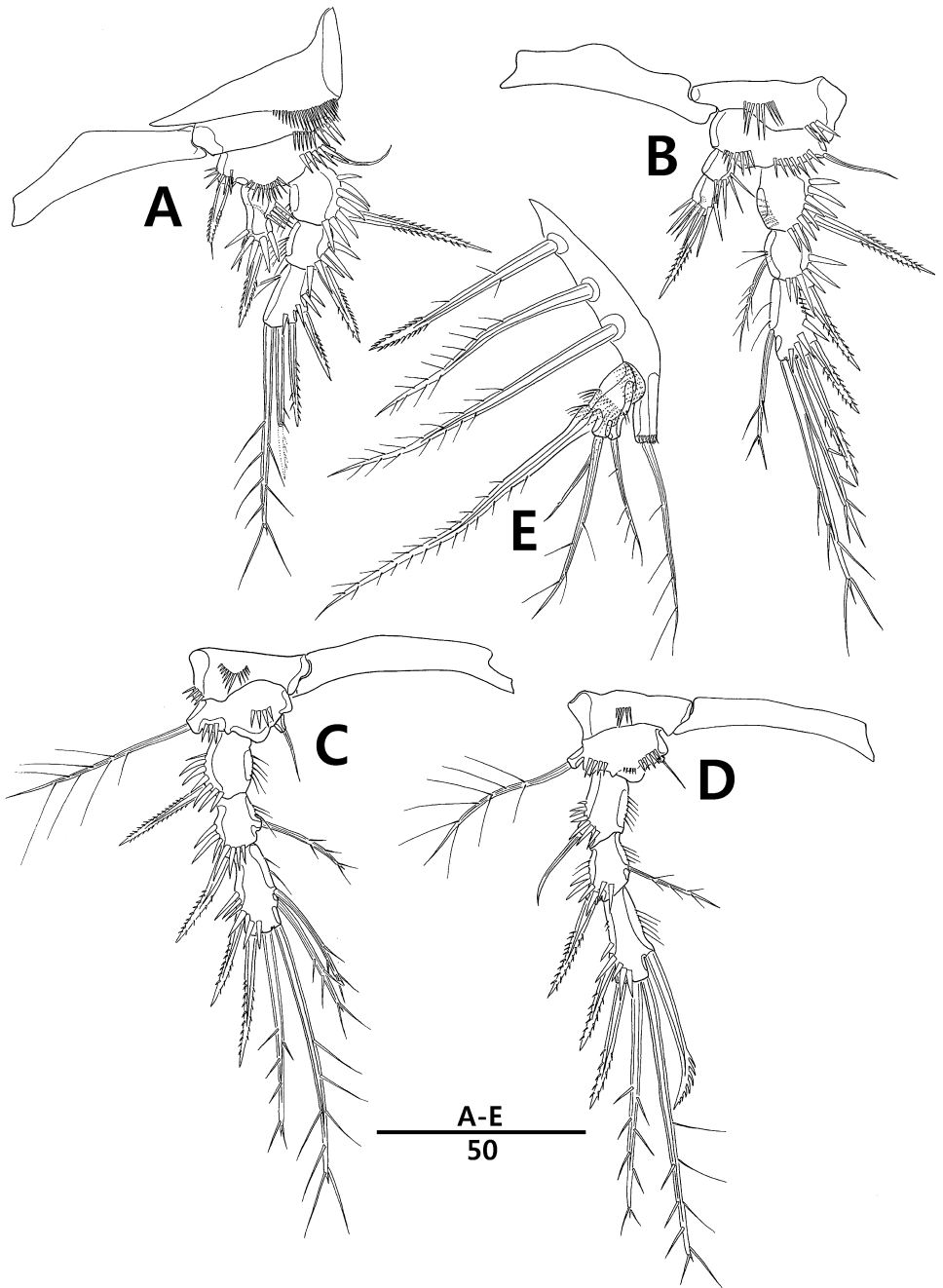


Fig. 3. *Nannopus parvipilis* sp. nov., female. A-E, P1-P5.

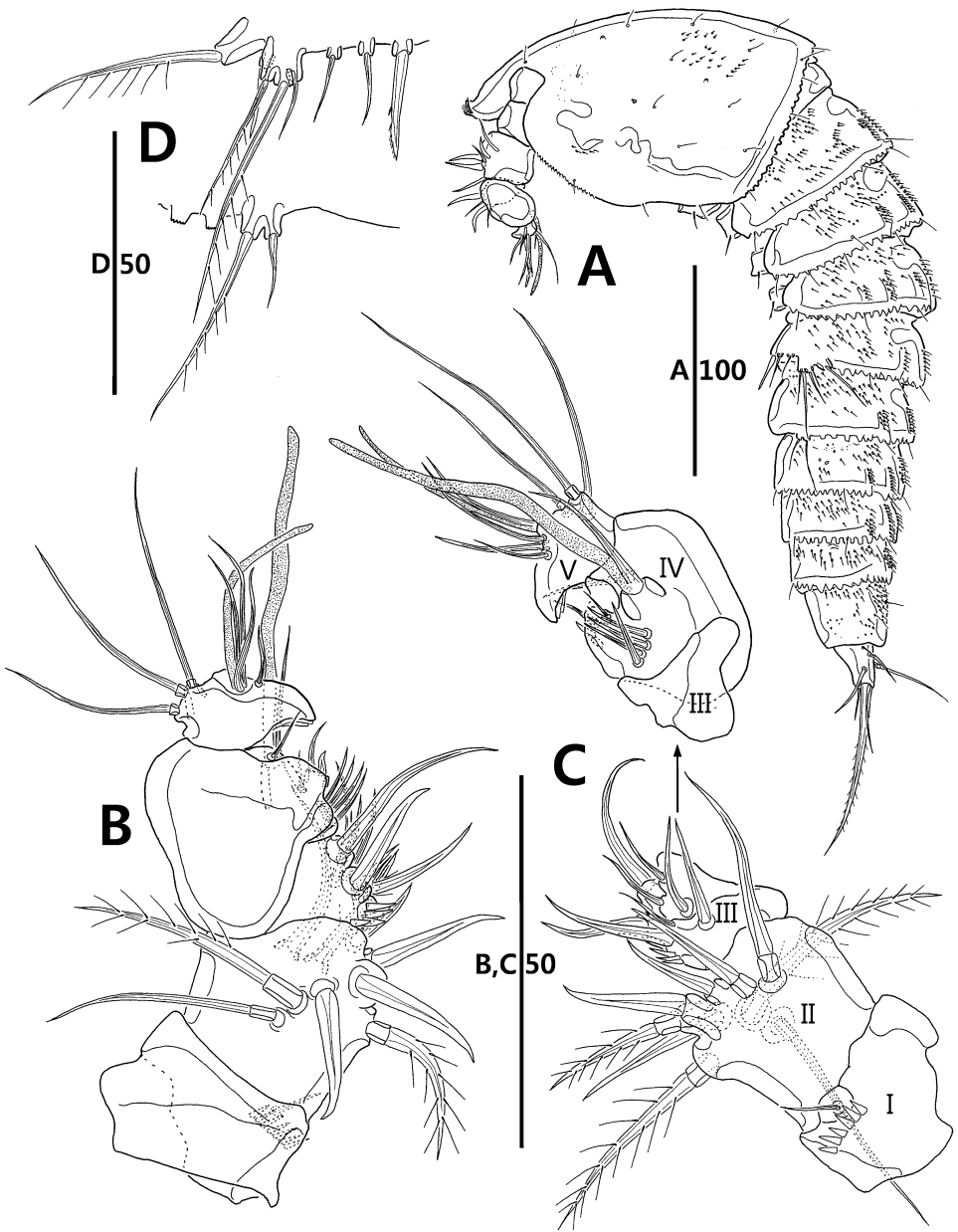


Fig. 4. *Nannopus parvipilis* sp. nov., male. A, habitus, lateral; B, antennule, anterior; C, antennule, posterior; D, P5 and P6.

Antennule (fig. 4B, C) 5-segmented, chirocer. First segment small with 1 row of spinules and 1 minute seta. Second segment with 9 setae. Third segment triangular in shape, with 1 row of spinules proximally and 8 setae. Fourth segment stout,

semi-ovate, with 6 setae, 1 large peduncle bearing 1 seta and 1 aesthetasc, 1 small peduncle bearing 1 small seta and 1 spine-like element. Fifth segment smallest, tapering distally, with 7 setae and 1 aesthetasc. Each aesthetasc on fourth and fifth segments fused to seta basally.

P5 (fig. 4D). Baseoendopod small, with 3 peduncles each with 1 apical seta; innermost seta on baseoendopod stout; outer peduncle with 1 long plumose seta. Exopod fused to baseoendopod, with 2 plumose and 2 naked setae.

P6 (fig. 4D) symmetrical, small, with 1 plumose and 1 bare setae on apical margin.

Remarks.— To date, there are several obvious discrepancies between the definition of the genus *Nannopus* by Brady (1880) and the concept of the genus accepted at present (Canu, 1892; Scott, 1902; Sars, 1909a; Gurney, 1932; Shen & Tai, 1964; Wells, 1971; Kikuchi & Yokota, 1984; Yoo & Lee, 1995; Kornev & Chertoprud, 2008; Fiers & Kotwicki, 2013; Vakati et al., 2016; etc.). Brady (1880) described that “inner branches of the third and fourth pairs rudimentary, and consisting only of a few setae” in the definition of the genus *Nannopus* and “In place of the inner branch of the third and fourth pairs is a small tubercle, which gives attachment to a long plumose seta and two or three very small cilia” in the description of *N. palustris* Brady, 1880. While the present concept of *Nannopus* considers that P3 and P4 are two- and one-segmented, respectively. Such discrepancies were originated from Canu’s (1892) reinterpretation of Brady’s thoracic legs. Canu (1892) first found out that the illustration of P1 expresses the absence of the median spine on the basis, which is essential in harpacticoid copepods. Canu (1892) has suggested that this figure represents P2 or P3. He also believed that Brady’s figure 20 captioned as P3 actually expressed the P4 of *N. palustris* without providing reasons (Canu, 1892). This reinterpretation has been accepted by subsequent authors when reporting *Nannopus* species (Scott, 1902; Sars, 1909a; Gurney, 1932; Shen & Tai, 1964; Wells, 1971; Kikuchi & Yokota, 1984; Kornev & Chertoprud, 2008; Fiers & Kotwicki, 2013; Vakati et al., 2016).

However, this currently accepted concept of *Nannopus* might be incorrect by the discovery of *N. parvipilis* sp. nov. collected from Korea. The new species shows a one-segmented P3 endopod in accordance with the definition of the genus described by Brady (1880). Considering the segmentation of thoracic legs present in *N. parvipilis* sp. nov., we suggest that Brady did not make a mistake in the illustration of P3 at least and Canu’s (1892) assumption for P3 was incorrect. We also think that the segmentation of P3 endopod is sufficient to be a generic characteristic to differentiate *Nannopus* species from others and such species having a two-segmented P3 endopod but still being placed in *Nannopus* should be excluded from the genus. By the way, the known diagnosis of the genus *Ilyophilus*

Lilljeborg, 1902, which has long been regarded as a junior synonym of *Nannopus* after Sars (1909a), is well accorded with the characteristic features appeared in P3 and P4 of these *Nannopus* species. Therefore, we revive the genus *Ilyophilus* to accommodate these eight species: *I. flexibilis* Lilljeborg, 1902, *I. perplexus* Sars, 1909b comb. nov., *I. unisegmentatus* (Shen & Tai, 1964) comb. nov., *I. didelphis* (Fiers & Kotwicki, 2013) comb. nov., *I. hirsutus* (Fiers & Kotwicki, 2013) comb. nov., *I. procerus* (Fiers & Kotwicki, 2013) comb. nov., *I. scaldicola* (Fiers & Kotwicki, 2013) comb. nov., and *I. ganghwaensis* (Vakati, Kihara & Lee, 2016) comb. nov. Although the knowledge of *N. palustris* is poor because of insufficient description and illustrations in the original description (Brady, 1880), the revival of *Ilyophilus* can be supported by the differences between *N. parvipilis* sp. nov. and above eight *Ilyophilus* species in the following characteristics: the rostrum in *N. parvipilis* sp. nov. is furnished with ventral setules vs. dorsal setules in *Ilyophilus* species; the mandibular palp in *N. parvipilis* sp. nov. has five setae vs. four setae in *Ilyophilus* species, except for *I. unisegmentatus* having five setae; the sexual dimorphism on P3 endopod in *N. parvipilis* sp. nov. is absent vs. present in *Ilyophilus* species; the male P6 in *N. parvipilis* sp. nov. is represented by two setae vs. three setae in *Ilyophilus* species.

*Nannopus parvipilis* sp. nov. is very close to the original description of *N. palustris* by Brady (1880) in sharing a one-segmented endopod on P3-P4. However, it differs from the latter in the following features: all P1-P4 exp-3 have two outer spines, whereas *N. palustris* has three spines at P1 exp-3 (currently considered as P2); both P3-P4 endopods have a very small seta, whereas P3 (currently considered as P4) of *N. palustris* has a long plumose seta exceeding the end of the exopod; and its body surface is ornamented with ridges, while the body surface of *N. palustris* is even without ridges.

#### Genus *Ilyophilus* Lilljeborg, 1902

Amended diagnosis.— Nannopodidae. Body fusiform, slightly depressed dorso-ventrally; posterior margins of somites serrate usually, but smooth in *I. perplexus*. Rostrum bell-shaped, fused to cephalothorax basally; anterior margin furnished with setules. Caudal rami about 2 times as long as wide; seta I inserted close to proximal margin; seta III inserted ventrally at midlength of outer margin; seta V well-developed. Antennule 5-segmented in female; both segments 3 and 5 with 1 aesthetasc. Antennal allobasis with 2 abexopodal setae usually, but 1 seta in *I. perplexus*; exopod 1-segmented, with 4 setae usually, but 3 setae in *I. perplexus*; endopod with 6 spines, but 7 spines in *I. perplexus*. Mandibular palp 1-segmented, broad, with 3 or 4 setae usually, but 5 setae in *I. unisegmentatus*. Maxillule with 2 pinnate setae on praecoxal arthrite; exopod represented by 2

setae; endopod represented by 1 seta. Maxilla with 2 endites on syncoxa; each endite with 3 elements; endopod small, represented by 2 setae. Maxilliped 1 small seta on syncoxa; endopod small, with 1 claw, 2 accessory setae. P1 exopod 3-segmented; exp-2 with inner setae; exp-3 with 2 outer, 2 apical setae; endopod 1- or 2-segmented, not prehensile. P2-P4 exopods 3-segmented. P2-P3 endopods 2-segmented. P4 endopod 1-segmented, very small, with 1 long plumose and 1 small bare setae usually, but small seta absent in *I. perplexus*. Female P5 baseoendopod plate-like, with 3 or 4 setae; exopod separate usually, but fused basally in *I. perplexus*, with 4 or 5 setae.

Male with sexual dimorphism in antennule, P3, P5 and P6. Antennule 5- or 6-segmented, chirocer. P3, outer element on distal margin of enp-2 confluent with segment. P5, exopod 1-segmented, fused to baseoendopod basally. P6 represented by 3 setae.

Type species.— *Ilyophilus flexibilis* Lilljeborg, 1902.

Other species.— *Ilyophilus perplexus* Sars, 1909b comb. nov., *I. unisegmentatus* (Shen & Tai, 1964) comb. nov., *I. didelphis* (Fiers & Kotwicki, 2013) comb. nov., *I. hirsutus* (Fiers & Kotwicki, 2013) comb. nov., *I. procerus* (Fiers & Kotwicki, 2013) comb. nov., *I. scaldicola* (Fiers & Kotwicki, 2013) comb. nov., *I. ganghwaensis* (Vakati, Kihara & Lee, 2016) comb. nov., and *I. canui* sp. nov.

Remarks.— Lilljeborg (1902) erected the genus *Ilyophilus* Lilljeborg, 1902 for *I. flexibilis* Lilljeborg, 1902 having a two-segmented P3 endopod and a one-segmented P4 endopod. However, this genus was synonymized into *Nannopus* Brady, 1880 by Sars (1909a) who synonymized *I. flexibilis* with *N. palustris* Brady, 1880. The genus *Ilyophilus* is revived by the present study based on the discovery of *N. parvipilis* sp. nov. that is well in accordance with Brady's (1880) generic description of *Nannopus*.

Canu (1892) first reinterpreted the characteristics in P3 endopod of *N. palustris* sensu Brady, 1880 based on those of *N. palustris* sensu Canu, 1892 having a two-segmented P3 endopod. Since then, Canu's specimen had long been considered as the criterion of *N. palustris* before Fiers & Kotwicki's (2013) who doubted the taxonomic status of so-called *N. palustris* in their revision on *Nannopus*. *Nannopus palustris* sensu Canu, 1892 should now be placed in *Ilyophilus* because of the characteristic feature of two-segmented P3 and the reinstatement of *Ilyophilus*. We here name this species *I. canui* sp. nov. in honour of Dr. E. Canu who was the original author of this species.

Fiers & Kotwicki (2013) identified divergent character states in *Nannopus* species, which are now placed into *Ilyophilus* in the present study, and assumed that there are two groups characterized by conditions of the inner subdistal element on P4 exp-3 and the male genital apparatus. However, it was not supported

by *I. ganghwaensis* in discordance with their assumption (Vakati et al., 2016). Among nine *Ilyophilus* species, on the other hand, two species show discrepancy with remaining their congeners, respectively. *Ilyophilus perplexus* differs from its congeners by the following characteristic features: the posterior border of somites is smooth, while it is serrate in congeners; antennary exopod has three setae, while it has four setae in congeners; antennary allobasis has one abexopodal setae, while it has two setae in congeners; antennary endopod with seven spines, while it has six spines in congeners; P4 endopod has only one long plumose setae, while it has one long plumose and one small setae in congeners; the female P5 exopod is fused to baseoendopod, while it is separated in congeners. *Ilyophilus unisegmentatus* is also discriminated from its congeners by the number of setae on the mandibular palp (5 setae in *I. unisegmentatus* vs. 3 or 4 setae in its congeners) and the segmentation of P1 endopod (1-segmented in *I. unisegmentatus* vs. 2-segmented in its congeners). Considering diverse conditions of the character states within *Ilyophilus* species as mentioned above, this genus seems to be a polyphyletic group and could be subdivided into several groups by further studies.

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