Journal of Species Research 6(Special Edition):185-214, 2017

Two new *Phyllopodopsyllus* (Copepoda, Harpacticoida) from Korean marine interstitial

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The genus *Phyllopodopsyllus* T. Scott, 1906 is nearly cosmopolitan and contains around 60 valid species, but has not been previously recorded in Korea. One of the reasons is probably the paucity of research in marginal habitats, such as marine interstitial. I describe two new species here. Numerous specimens of both sexes of *P. kitazimai* sp. nov. were collected from a beach near Yeongdeok, while only two females of *P. busanensis* sp. nov. were collected from a beach near Busan. The new species differ in numerous macro-morphological characters, such as the segmentation and armature of the antennula, armature of the mandibula, maxillula, maxilliped, and the first three swimming legs, as well as the shape of the caudal rami and the female genital field. However, they show very little difference in the number and position of cuticular organs (pores and sensilla) on all somites, which might prove these rarely used micro-characters to be useful in the reconstruction of phylogenetic relationships in this group of harpacticoids. Both species have their closest relatives in Japan. *Phyllopodopsyllus kitazimai* is morphologically most similar to *P. punctatus* Kitazima, 1981, but can be distinguished by much longer third exopodal segments of the third and fourth swimming legs. *Phyllopodopsyllus busanensis* shares the largest number of morphological similarities with *P. setouchiensis* Kitazima, 1981, but can be distinguished by shorter caudal rami. A key to species is also provided.

Keywords: Crustacea, cuticular organs, meiofauna, species key, taxonomy, Tetragonicipitidae

DOI:10.12651/JSR.2017.6(S).185

Introduction

The tetragonicipitid genus *Phyllopodopsyllus* T. Scott, 1906 is one of the most speciose marine harpacticoid genera (Walter and Boxshall, 2017), and contains the largest number of newly described species in the second half of the twentieth century (Bodin, 1997; Wells, 2007). The most important autapomorphy of this genus is its foliaceous female fifth leg that forms a completely sealed brooding chamber with urosomal somites; this character is unique among copepods and the same basic structure can be observed even in morphologically very divergent species. Lang (1944) tried to subdivide it into two genera (*Phyllopodopsyllus* and *Paraphyllopodopsyllus* Lang, 1944), based upon the shape of the second segment of the antennula and the setation of the second and third swimming legs in females (see also Lang 1948). Many authors followed this revision, and Vervoort (1964) provided a key to species of the genus *Phyllopodopsyllus*, although not of *Paraphyllopodopsyllus*. After several species were described with intermediate characteristics, Lang (1965) synonymized *Paraphyllopodopsyllus* with *Phyllopodopsyllus* and compiled a key to 21 species then recognized. He subdivided the genus into three morphological groups based on the second antennular segment. Coull (1973) presented a detailed survey of the genus *Phyllopodopsyllus*, and compiled an instructive table listing the most salient morphological characteristics. His key included 33 species and subspecies. Kunz (1984) reviewed the genus, and tabulated the setal formulae of the second, third, and fourth swimming legs in female, as well as the antennulae segmentation and shape. Based on these characters, he subdivided the genus into nine species groups. Fiers (1995) doubted the "naturalness" of these groups, but proposed nothing new, placing his new species within one of Kunz's groups. Karanovic *et al*. (2001) described a new species from Australia that did not fit into any of these nine groups, and suggested that they should be abandoned. They also provided a key to 54 species and subspecies they considered valid. Finally, Wells (2007) listed 60 species and subspecies he considered valid, although he was not able to include some in his key and some were included only provisionally; also, several species were included in more than one place, reflecting their polymorphy and potential for representing species complexes. Subsequent to this last review of the genus only two new species have been described, both from Brazil by Björnberg and Kihara (2013): *P. iuanamai* Björnberg and Kihara, 2013 and *P. pseudokunzi* Björnberg and Kihara, 2013. The genus is most specious in the tropics, where its members can be found in various marine sediments at different depths (Boxshall and Halsey, 2004). Karanovic *et al.* (2001) and Karanovic (2006) reported the occurrence of representatives in subterranean continental waters of Australia, but with increased salinity and not far from the sea.

Large harpacticoid genera frequently accumulate numerous synonyms during the course of their taxonomic history. The genus *Phyllopodopsyllus* is especially rich in synonyms, many known of long standing. In such a way *P. pirgos* Apostolov, 1969 is a synonym of *P. briani* Petkovski, 1955, which was noticed already by Coull (1973) and accepted by Apostolov and Marinov (1988), although Kunz (1984) claimed it to be a synonym of *P. thiebaudi* Petkovski, 1955. Lang (1965) suggested that *P. intermedius* (Noodt, 1955) is a synonym of *P. thiebaudi*. Two species were synonymized by their authors themselves: Kunz (1963) synonymized his *P. trichophorus* (Kunz, 1951) with *P. mossmani* T. Scott, 1912, and Apostolov (1972) synonymized his *P. ponticus* Apostolov, 1968 with *P. pauli* Crisafi, 1960. *Phyllopodopsyllus mielkei mielkei* Kunz, 1984 and *P. mielkei californicus* Kunz, 1984 are synonyms of *P. setouchiensis* Kitazima, 1981, which was first noticed by Mielke (1992); Karanovic *et al.* (2001) also considered *P. crenulatus* Wells and Rao, 1987 to be a synonym of *P. setouchiensis*. Karanovic *et al.* (2001) also considered *Phyllopodopsyllus g. gertrudi* Kunz, 1984 and *P. gertrudi costaricensis* Mielke, 1992 as synonyms of *P. aegypticus* Nicholls, 1944, mostly based on the description of *P. g. costaricensis* by Mielke (1992), who unintentionally returned the species *P. gertrudi* within the range of the species *P. aegypticus*, because the only traditionally used differentiating character (i.e. third exopodal segment of the third swimming leg with 5 or 6 elements) become invalid (see Kunz, 1984; Wells and Rao, 1987; Mielke, 1992). The same authors considered *P. yucatanensis* Piers, 1995 as an obvious synonym of *P. parafurciger* Geddes, 1968. They also drew attention to several other species pairs that could prove to be synonymous with more in-depth study, although keeping them as separate in their key: *P. curtus* Marcus, 1976 and *P. stigmosus* Wells and Rao, 1987; *P. carinatus* Mielke, 1992 and *P. paraborutzky* Kunz, 1975; *P. galapagoensis* Mielke, 1989 and *P. chavei* Coull, 1970; and *P. petkovskii* Kunz, 1984 and *P. briani* Petkovski, 1955. The latter pair they considered as subspecies, and two species they considered as incertae sedis because of the incompleteness of their descriptions: *P. minor* (T. and A. Scott, 1903) and *P. tristanensis* (Wiborg, 1964).

Here I describe two new species from marine interstitial habitats in South Korea. Some 23 higher metazoan taxa have been reported so far from this ecosystem (Vincx, 1996; Preker, 2005). However, wide areas in Africa, South America, Australia, and Asia still remain *terra incognita* (Giere, 2009). The macrofauna and the interstitial fauna of sandy beaches comprise distinct communities, with few or no trophic links (Brown and McLachlan, 1990). The interstitial system is a carbon sink that processes organic materials flushed into the sand through mineralization by a food chain consisting of heterotrophic bacteria at its base and predatory meiofauna, including copepods, at the apex. Some three-quarters of the world's ice-free coastlines consist of sandy shores (Brown and McLachlan, 1990) and Korea has 12,478 kilometers of coastline along three seas (Pruett and Cimino, 2000). Like in most other developed economies, these ecosystems are under constant anthropogenic pressure and, being a marginal habitat, are rarely included in protected natural reserves. However, marine interstitial harbours disproportionate level of biodiversity (Gray, 1997; Thrush *et al.*, 2006; Karanovic, 2008), which is yet to be fully appreciated and understood (Armonies and Reise, 2000; Gray, 2002; Zeppelli *et al.*, 2015).

South Korea has become one of the most actively researched areas for invertebrate diversity in the last decade or so, mostly thanks to the efforts of the National Institute of Biological Resources in Incheon and supporting funding from the Korean Ministry of Environment (Lee and Karanovic, 2012). According to the most current review (Cho *et al.*, 2011), the national inventory of Korea totals 36,921 species, consisting of 5,230 vascular plants and bryophytes, 4,587 algae, 4,085 fungi and lichens, 1,374 protists, 647 prokaryotes, 1,841 vertebrates, 13,384 insects, and 5,773 invertebrates other than insects. Copepods are relatively well studied here, both as free-living forms in marine (Soh, 2010; Lee *et al.*, 2012) and freshwater environments (Chang, 2009; 2010), as well as parasites of other organisms (Kim, 2008). However, surveys of marginal and previously understudied habitats (Karanovic *et al.*, 2012a; 2012b; Karanovic, 2014; Karanovic and Lee, 2016) or utilization of novel taxonomic methods, such as the study of microstructures (Karanovic and Cho, 2012; Karanovic and Lee, 2012; Karanovic *et al*., 2013a; Karanovic and Cho, 2016; 2017) and DNA (Karanovic and Kim, 2014a; 2014b; Kim *et al*., 2014; Karanovic *et al*., 2014; 2015a), have resulted in numerous recent additions to the Korean copepod fauna. While most of the recent additions are elements of neighbouring faunas that were previously unknown here (Kim *et al*., 2011; Park *et al*., 2011; 2012; Nam and Lee, 2012), some are actually endemic elements (Chang and Lee, 2012; Kim, 2014). Two harpacticoid species that I report in this paper belong to the latter group. They were both collected in the intertidal zone of sandy marine beaches, in a single location each.

Materials and Methods

All specimens of the Korean new species were collected from the intertidal zone, using the Karaman-Chappuis method. It consisted of digging a whole down to the water level and then decanting the inflowing interstitial water and filtering it through a plankton hand net (mesh size 30 μm). All samples were fixed in 99% ethanol, sorted in the laboratory also in 99% ethanol using an Olympus SZX12 dissecting microscope with PLAPO objectives and magnification of up to 200×. Locality data and number of specimens are listed for each species separately and all types are deposited in NIBR.

Some specimens were dissected and mounted on microscope slides in Faure's medium (see Stock and von Vaupel Klein, 1996), and dissected appendages were then covered by a coverslip. For the urosome or the entire animal, two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, equipped with N-PLAN (5×, 10×, 20×, 40× and 63× dry) or PL FLUOTAR (100×oil) objectives. Specimens that were not drawn were examined in glycerol and, after examination, were stored in 99.9% ethanol. Specimens for scanning electron microscopy (SEM) were transferred into pure iso-amyl-acetate, critical-point dried, mounted on stubs, coated in gold, and observed under a Hitachi S-4700 scanning microscope on the in-lens detector, with an accelerating voltage of 10 kV and working distances between 12.3 and 13.4 mm; micrographs were taken with a digital camera.

The terminology for macro-morphological characters follows Huys and Boxshall (1991), except for the numbering of setae on the caudal rami and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), as an attempt to standardise the terminology for homologous appendages in different crustacean groups. Sensilla and pores on each somite (body segment) and caudal rami were numbered consecutively from the anterior to posterior end of body and from the dorsal to ventral side; sensilla were numbered using Arabic numerals, and pores using Roman numerals. The same numbers on different somites do not necessarily indicate serially homologous structures; serial homology was hypothesised in the description of cuticular organs (see below). However, same numbers do denote homologous structures between species and between sexes. As a tentative terminology for cuticular organs in the description, I combined abbreviations for the cephalothorax (Ct), free prosomites (Fp1 to Fp3), urosomites (U1 to U6), and caudal rami (Cr) hyphenated with a given Arabic or Roman numeral (for example, sensilla pair Fp1-3; see Karanovic *et al*., 2016).

Results

***Phyllopodopsyllus kitazimai* sp. nov.**
(Figs. 1A, B and 2-10)

Type locality. Korea, East Coast, Gyeongsangbuk-do province, Yeongdeok-si city, Woncheok-ri village, beach, intertidal sand, interstitial water from a Karaman-Chappuis hole, 36°18.309′N 129°22.648′E.

Specimens examined. Holotype female (NIBR IV 0000287257) dissected on one slide; allotype male (NIBR IV 0000287258) dissected on one slide; ten paratype females (NIBR IV 0000287259-0000287268) and nine paratype males (NIBR IV 0000287269-0000287277) dissected on one slide each; five paratype females and five paratype males *in toto* on one SEM stub (NIBR IV 0000287278); 100 paratype females and 50 paratype males together in one alcohol vial (NIBR IV 0000287279); all collected from the type locality, 6 May 2016, leg. T. Karanovic.

Etymology. The species is named in honour of late Dr T. Kitazima, as a recognition of his contribution to the taxonomy of this genus. The specific name is a noun in the genitive singular.

Description. Female (based on holotype and 15 paratypes). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae and appendages) from 509 to 536 μm. Colour of preserved specimen yellowish (Fig. 1A). Nauplius eye not visible. Prosome comprising cephalothorax (Ct) with completely fused first pedigerous somite and 3 free pedigerous somites (Fp1-Fp3); urosome comprising six urosomites (U1-U6), which include fifth pedigerous somite (U1), genital double-somite (fused genital (U2) and first abdominal (U2) somites), two free abdominal somites without appendages (U4 and U5), and anal somite

Fig. 1. Light photograph of two new Korean *Phyllopodopsyllus* Scot T., 1906 species, on the same slide in glycerol: A, *P. kitazimai* sp. nov., holotype female; B, *P. kitazimai* sp. nov., allotype male; C, *P. busanensis* sp. nov., holotype female.

(U6) with caudal rami (Cr) on posterior margin. Habitus (Figs. 1A, 2A, 3A) cylindrical, slender, without distinct demarcation between prosome and urosome in dorsal view, but with sharp bend in lateral view; prosome/urosome ratio about 0.9 (in dorsal view); greatest width at posterior end of cephalothorax; cephalothorax only 1.15 times as wide as genital double-somite in dorsal view. Body length/width ratio about 5.4. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument of all somites relatively well sclerotized, generally very smooth, covered with numerous shallow cuticular pits; several irregular rows of minute spinules present on each somite except cephalothorax, but majority of surface devoid of spinules. Hyaline fringe of all somites narrow; that of cephalothorax and first free pedigerous somite smooth, those of other somites finely serrated (Figs. 2, 3). Surface of somites and caudal rami with total maximum of 185 cuticular organs (29 pairs of cuticular pores, 58 pairs of sensilla, one unpaired dorsal sensillum, and ten unpaired dorsal pores).

Rostrum (Figs. 2B, C, 3B, C) small, weakly demarcated at base from cephalothorax, linguiform, about as wide as long, its anterior tip hardly reaching beyond anterior margin of lateral wings of cephalothoracic shield, with single dorsal pair of sensilla (Ct-1) at about 2/3 of its length.

Cephalothorax (Figs. 2B, C, 3B, C) smooth, cylindrical in dorsal view, tapering towards anterior end in lateral view, about 1.7 times as long as wide in dorsal view (including rostrum); representing nearly 30 % of total body length. Hyaline fringe of cephalothoracic shield narrow and smooth. Cephalothoracic shield with nine pairs of pores (Ct-II and Ct-IV to Ct-XI), 28 pairs of sensilla (Ct-2 to Ct-13 and Ct-15 to Ct-30), one unpaired dorsal sensillum (Ct-14), and two unpaired dorsal pores (Ct-I and Ct-III); all pores of similar size, about as large as circular base of sensilla; all sensilla of similar size, long, simple, and slender; sensilla pair Ct-2 at base of rostrum; lateral marginal zone includes sensilla Ct-5, Ct-8, Ct-13, Ct-19, and Ct-28 (see Fig. 3B, C); posterior marginal zone includes only sensilla Ct-29 to Ct-30 (see Figs. 2B, 3B).

Pleuron of first free prosomite (second pedigerous somite) (Figs. 2D, 3D) mostly smooth, with several irregular dorsal rows of minute spinules in anterior half and several minute spinules in anterior lateral corner, with only five pairs of long sensilla (Fp1-1 to Fp1-5), one unpaired dorsal pores (Fp1-I), and one pair of lateral anterior pores (Fp1-II); posterior marginal zone includes sensilla Fp1-1, Fp1-2, Fp1-4, and Fp1-5, while sensilla pair Fp1-3 situated slightly more anteriorly; posterior marginal sensilla pair Fp1-1 probably serially homologous to sensilla Ct-29 on cephalothorax, while serial homology of other sensilla and pores difficult to determine; hyaline fringe narrow and smooth.

Pleuron of second free prosomite (third pedigerous somite) (Figs. 2D, 3D) very similar in shape and size to that of first free prosomite, except hyaline fringe finely serrated dorsally; also with five pairs of sensilla (Fp2-1 to Fp2-5) but with different relative position: sensilla pair Fp2-1 probably serially homologous to sensilla Sp1-2, Fp2-2 to Fp1-3, Fp2-3 to Fp1-4, and Fp2-5 to Fp1-5, while sensilla pair Fp2-4 without homologoues on first free prosomite; single unpaired dorsal pore (Fp2-I) serially homologous to that on first free prosomite (Fp1-I) and one lateral pair (Fp2-III) with serial homologoues on first free prosomite (Fp1-II), while second pair of pores (Fp2-II) without homologoues on first free prosomite.

Pleuron of third free prosomite (fourth pedigerous somite) (Figs. 2E, 3E) similar in shape to that of second free prosomite but slightly narrower and shorter, with only four pairs of sensilla (Fp3-1 to Fp3-4) and two pairs of cuticular pores (Fp3-I and Fp3-II); sensilla Fp3-1 to Fp3-3 probably serially homologous to their counterparts with same Arabic numerals on pleuron of second free prosomite, but sensilla Fp3-1 and Fp3-2 much closer to each other; sensilla pair Fp3-4 serially homologous to sensilla Fp2-5; pores Fp3-I and Fp3-II with serial homologoues on second free prosomite (Fp2-II and Fp2-III respectively); hyaline fringe finely serrated dorsally, smooth laterally.

First urosomite (fifth pedigerous somite) (Figs. 2E, 3E) slightly longer than pleuron of third free prosomite, with four pairs of sensilla (U1-1 to U1-4) and three pairs of pores (U1-I to U1-III); all sensilla probably serially homologous to their counterparts with same Arabic numerals on pleuron of third free prosomite, although sensilla U1-3 and U1-4 closer to each other; serial homology of pores not obvious, except that single unpaired dorsal pore (U1-I) serially homologous to that on first and second free prosomites (Fp1-I and Fp2-I); hyaline fringe as in third free prosomite finely serrated dorsally and smooth laterally.

Second urosomite (Figs. 2F, 3F, 6A-C) fused with third urosomite into genital double-somite, with finely serrated dorsal fringe and lateral internal ridges as only evidence of ancestral segmentation, with four pairs of posterior sensilla (U2-1 to U2-4), one unpaired dorsal pores (U2-I), and two pairs of dorso-lateral anterior pores (U2-II and U2-III); dorsal pore (U2-I) and two dorsal sensilla (U2-1 and U2-2) with serial homologoues on first urosomite with same numbers, but other cuticular organs of uncertain serial homology.

Third urosomite (Figs. 2F, 3F, 6A-C) fused with second urosomite, with wide and finely serrated hyaline fringe, but lonest combs on ventro-lateral conrers, one unpaired dorsal pores (U3-I), three pairs of anterior pores (U3-II to U3-IV), and three pairs of posterior sensilla: one dorsal (U3-1), one lateral (U3-2), and one ventral (U3-3); establishing serially homologous sensilla of third and second urosomites not easy, except for dorsal pore.

Genital double-somite about 1.2 times as long as wide (ventral view). Genital complex (Figs. 6C, 8A) with single large and round copulatory pore in distal part of third urosomite, long and narrow copulatory duct, two small and ovoid seminal receptacles in distal part of second urosomite, and central genital aperture in anterior part of second urosomite; aperture covered by reduced sixth legs.

Fourth urosomite (Figs. 2G, 3G, 6A-C) narrower and shorter than genital double-somite, with several ventral rows of long hair-like spinule in place where distal part of fifth legs rests, wide and finely serrated hyaline fringe with long combs ventrally and short dorsally, three pairs of posterior sensilla (U4-1 to U4-3), single central dorsal pore (U4-I), and two pairs of lateral pores (U4-II and U4-III); all sensilla and pores with serial homologoues with same numbers on third urosomite, but ventral pair of spinules (U4-3) closer to each other.

Fifth urosomite (preanal) (Figs. 2G, 3G, 6A-C) significantly narrower and slightly shorter than fourth urosomite, without sensilla, with single central dorsal pore (U5-I) and one pair of ventro-lateral pores (U5-II); hyaline fringe wide and finely serrated.

Sixth urosomite (anal) (Figs. 2H, 3H, 6A-C) slightly narrower and significantly longer than fifth urosomite, cleft medially in posterior part, with one pair of large dorsal sensilla (U6-1), single central dorsal pore (U6-I), two pairs of lateral pores (U6-II and U6-III), one pair of ventral pores (U6-IV), and posterior row of spinules along ventral margin of medial cleft and along dorso-lateral cuticular wing; anal operculum broad, narrow, and convex, with finely serrated posterior margin, representing about 54% of somite's width; anal sinus (Fig. 2H) widely opened, without any chitinous projections, with weakly sclerotized walls and three rows of long, hair-like spinules boarding anus.

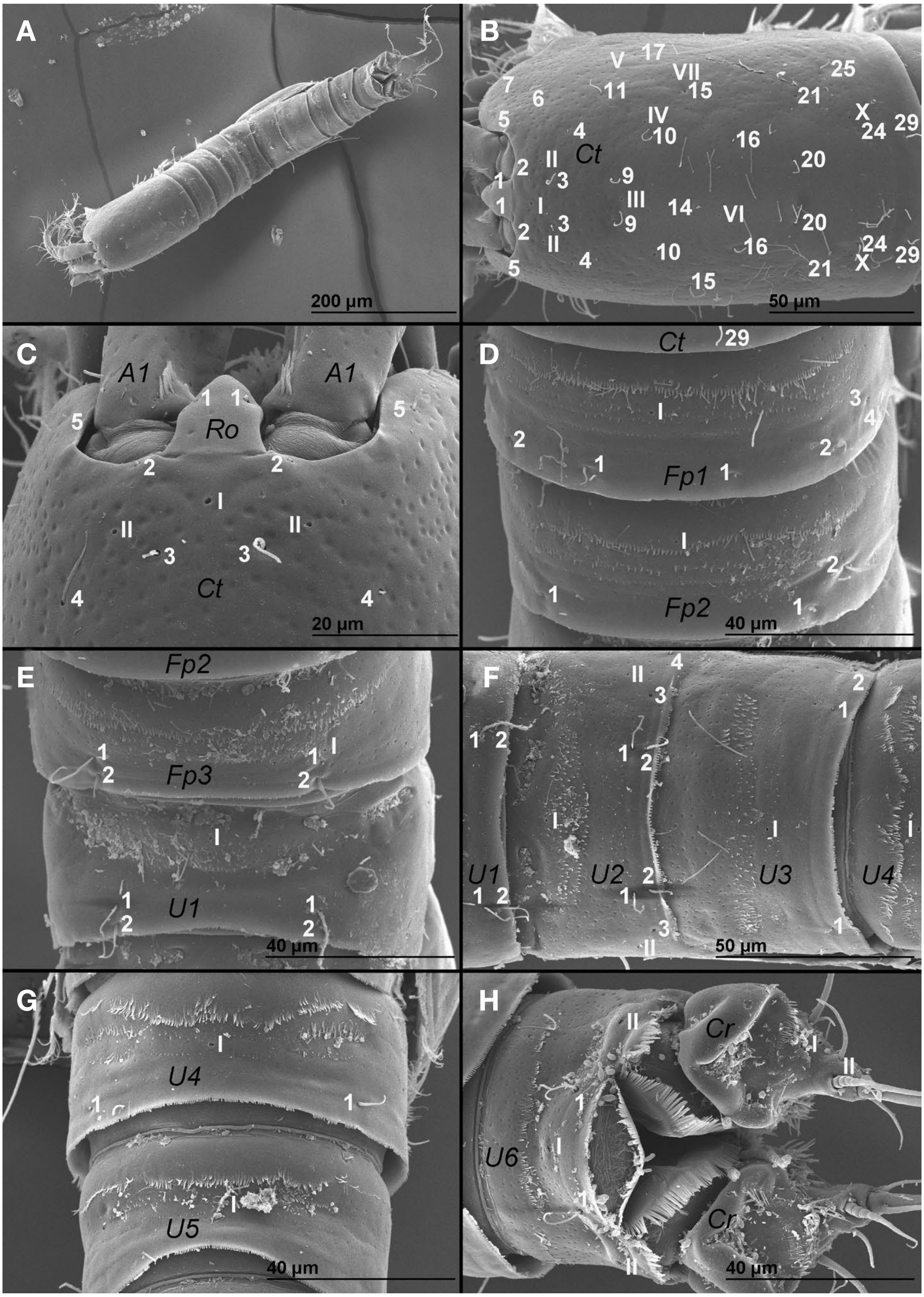

Fig. 2. *Phyllopodopsyllus kitazimai* sp. nov., paratype female 1, SEM photographs: A, habitus, dorsal; B, cephalothorax (Ct), dorsal; C, anterior part of cephalothorax (Ct) with rostrum (Ro) and first segment of antennula (A1), dorsal; D, tergites of first (Fp1) and second (Fp2) free prosomites, dorsal; E, tergites of third free prosomite (Fp3) and first urosomite (U1), dorsal; F, second (U2) and third (U3) urosomites, dorsal; G, fourth (U4) and fifth (U5) urosomites, dorsal; H, sixth urosomite (U6) and caudal rami (Cr), dorsal. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side.

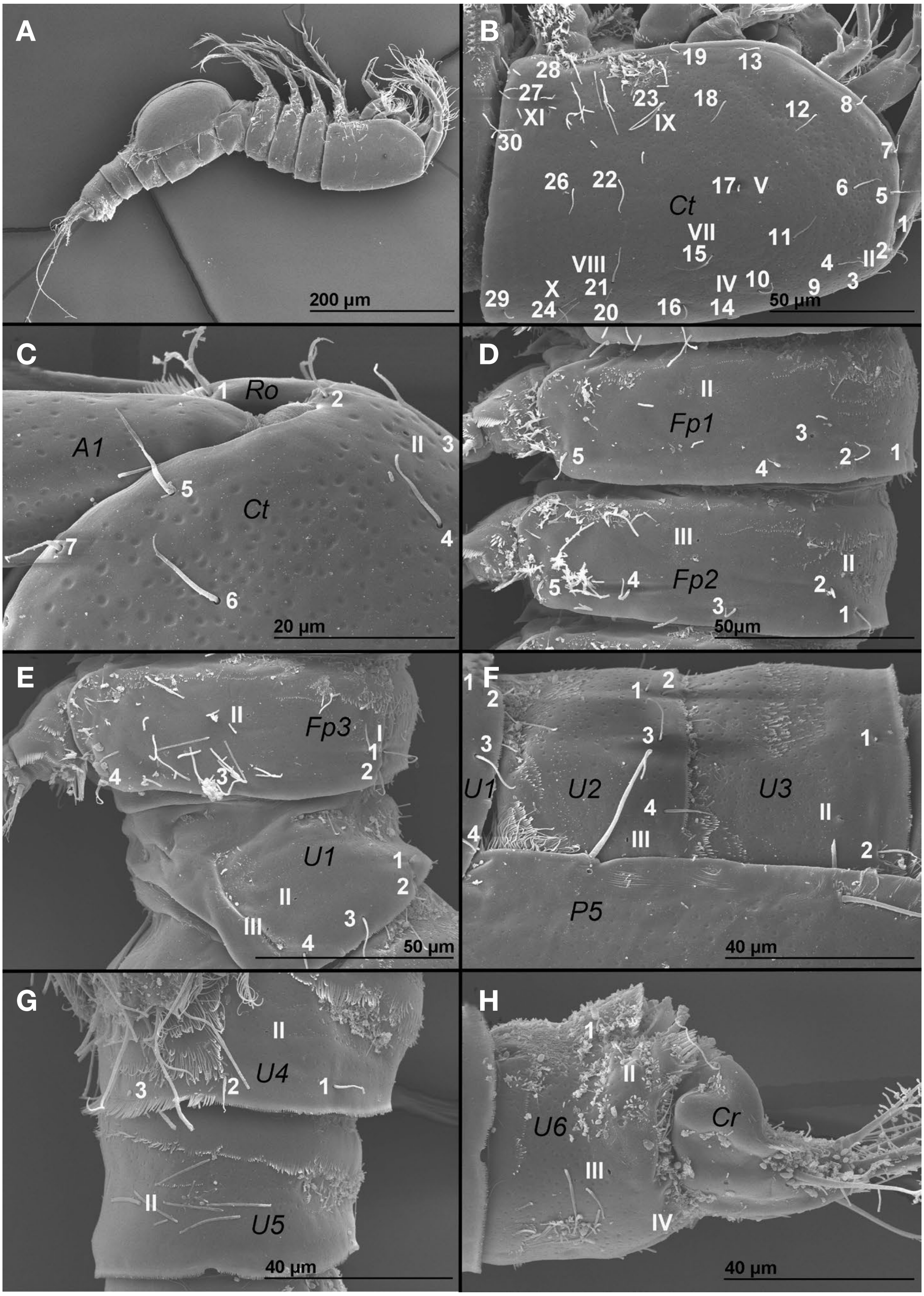

Fig. 3. *Phyllopodopsyllus kitazimai* sp. nov., paratype female 2, SEM photographs: A, habitus, lateral; B, cephalothorax (Ct), lateral; C, anterior part of cephalothorax (Ct) with rostrum (Ro) and first segment of antennula (A1), lateral; D, tergites of first (Fp1) and second (Fp2) free prosomites, lateral; E, tergites of third free prosomite (Fp3) and first urosomite (U1), lateral; F, partly fused second (U2) and third (U3) urosomites with outer part of transformed fifth leg (P5), lateral; G, fourth (U4) and fifth (U5) urosomites, lateral; H, sixth urosomite (U6) and caudal ramus (Cr), lateral. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side.

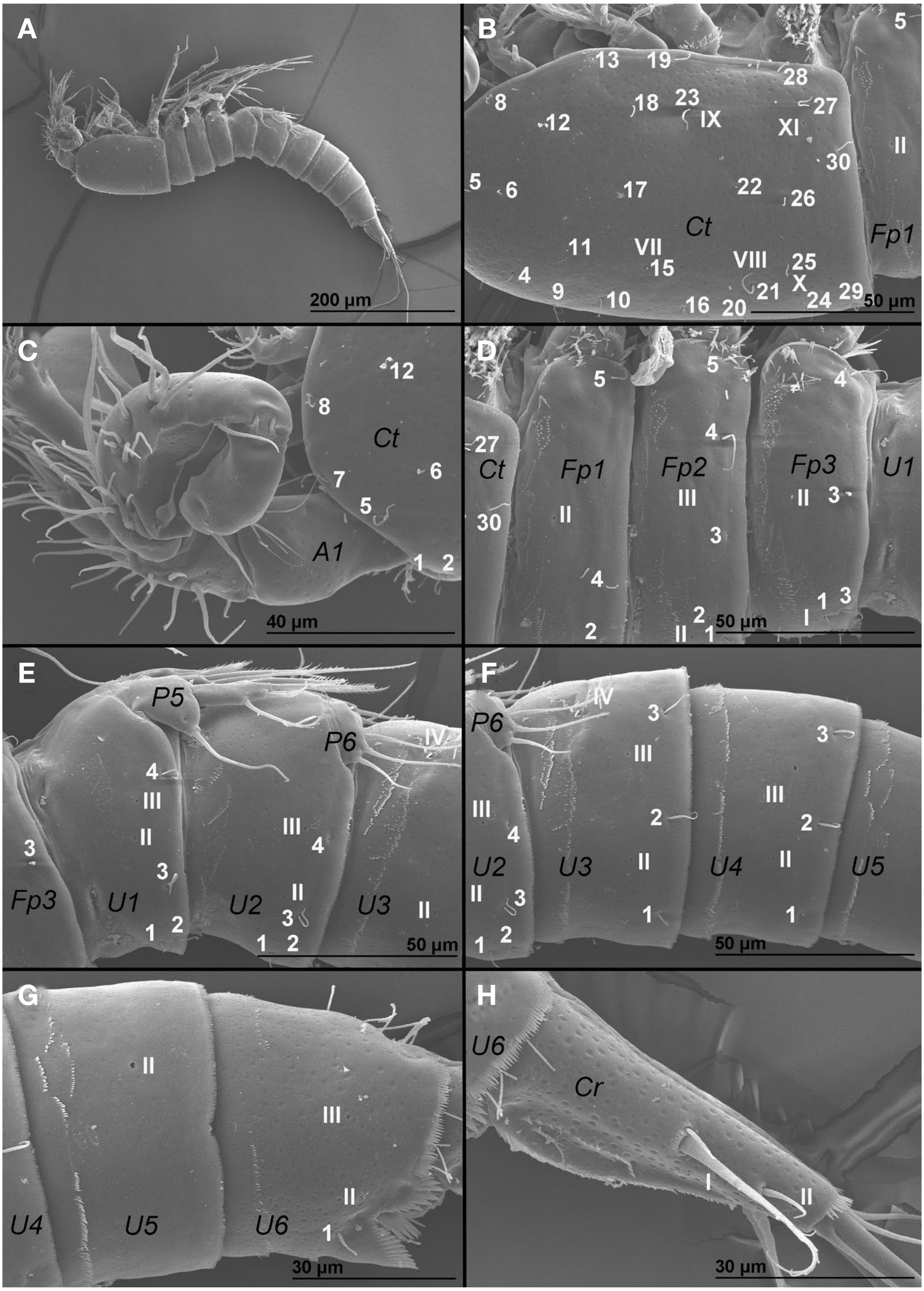

Fig. 4. *Phyllopodopsyllus kitazimai* sp. nov., paratype male 1, SEM photographs: A, habitus, lateral; B, cephalothorax (Ct), lateral; C, anterior part of cephalothorax (Ct) with antennula (A1), lateral; D, tergites of three free prosomites (Fp1-Fp3), lateral; E, first (U1) and second (U2) urosomites with fifth (P5) and sixth (P6) legs, lateral; F, third (U2) and fourth (U3) urosomites, lateral; G, fifth (U5) and sixth (U6) urosomites, lateral; H, caudal ramus (Cr), lateral. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side.

Caudal rami (Figs. 2H, 3H, 6A-C) strongly sclerotized, conical but with particularly inflated anterior dorsal region, with finely serrated ventral posterior margin, about as long as greatest width, with narrow space between them; ornamented with several short rows of large spinules along inner margin, one outer dorsal transverse row of small spinules, and two small lateral pores (Cr-I and Cr-II); armed with seven setae (three lateral, one dorsal, and three apical). Dorsal seta slender and smooth, about as long as ramus, inserted close to posterior margin, triarticulate at base (i.e., inserted on two pseudojoints). Proximal lateral setae inserted very close to each other at about midlength; ventral one minute, shorter than most sensilla; dorsal one slender and unipinnate, 1.2 times as long as ramus. Distal lateral seta also slender and smooth, inserted at 3/4 of ramus length, and about half as long as ramus. Innermost apical seta smooth, slender, and small, about half as long as ramus. Central (principal) apical seta without breaking plane, very strong, distally pinnate, about 3.5 times as long as caudal ramus, basally fused to outer principal seta. Outer apical seta also without breaking plane, much more slender than central apical seta, smooth, about 1.3 times as long as caudal ramus.

Antennula (Figs. 2C, 3C, 5A, 7A) eight-segmented, about as long as cephalothorax, with robust and long aesthetasc on fourth segment fused basally to slightly longer seta, slender and much shorter apical aesthetasc on eighth segment fused basally to two slightly longer setae, and setal formula 1.9.8.3.2.4.4.7. Two lateral setae on seventh segment and four lateral setae on sixth segment biarticulate (i.e., inserted on short pseudojoint); all setae slender and only one seta on second segment and single seta on first segment pinnate. Only ornamentation short arched row of spinules at base of first segment, on dorso-median surface. Length ratio of antennular segments, from proximal end and along caudal margin, 1 : 0.5 : 0.5 : 0.4 : 0.2 : 0.2 : 0.2: 0.4. First segment also strongest, about 2.2 times as long as wide; fourth segment slender, with prominently protruded anterior distal corner at base of large easthetasc.

Antenna (Figs. 5A, 7B) comprising coxa, allobasis (fused basis and first endopodal segment), two-segmented endopod, and much smaller one-segmented exopod. Coxa very short, 0.3 times as long as wide, unarmed, and unornamented. Allobasis cylindrical, 1.8 times as long as wide and nearly seven times as long as coxa, also unarmed, ornamented with longitudinal row of minute spinules along inner margin. First endopodal segment also cylindrical, 2.2 times as long as wide, and about 1.2 times as long as allobasis, unarmed, ornamented with longitudinal row of minute spinules along inner margin. Second endopodal segment most robust, more slender proximally but also generally cylindrical, three times as long as wide, 1.2 times as long as first endopodal segment, with two surface frills distally and row of large spinules along inner margin; lateral armature consisting of two strong, smooth spines, flanking slender and short seta; apical armature consisting of seven elements: one smooth, slender, short seta, one smooth short spine, one pinnate slender seta, and four geniculate unipinnate setae, longest fused basally to slender pinnate seta; all geniculate setae of similar length, slightly longer than second endopodal segment. Exopod slender, cylindrical but slightly curved, about four times as long as wide and half as long as allobasis; ornamented with posterior row of minute spinules; armed with one lateral and two apical unipinnate setae; outer apical seta strongest and spiniform, fused basally to exopod, about 1.2 times as long as inner apical seta, and 0.8 times as long as lateral seta.

Labrum (not illustrated) large, trapezoidal, rigidly sclerotized, with slightly convex cutting edge, ornamented with numerous slender apical and subapical spinules, those on outer distal corners strongest.

Mandibula (Figs. 5A, 7C, D) composed of large coxa and equally large palp; palp composed of basis, one-segmented endopod and one-segmented exopod; cutting edge of coxa narrow, armed with three large bi- or tricuspidate teeth, one unipinnate dorsal seta, and dorsal row of 6-7 slender spinules. Basis pentagonal, about 0.7 times as long as coxa, 2.4 times as long as wide, unornamented, armed with three apical pinnate setae of similar length and about 0.7 times as long as basis. Endopod cylindrical, 6.4 times as long as wide and 1.2 times as long as basis, unornamented, armed with two lateral and seven apical smooth and slender setae; lateral setae inserted very close to each other, about half length of endopod. Exopod conical, minute but distinct segment, twice as long as wide and only 0.13 times as long as endopod, unornamented, armed with one minute and smooth lateral seta and one pinnate apical seta.

Maxillula (Fig. 7E) composed of praecoxa, coxa, basis, one-segmented endopod, and one-segmented exopod. Praecoxa large, arthrite highly mobile, armed apically with seven strong spines (ventralmost smooth, others unipinnate) and dorsalmost unipinnate seta, with additional three smooth setae (or large spinules?) on dorsal surface, and additional two slender and smooth seta on anterior surface. Coxa small, unornamented, armed with one outer slender seta and three inner curved and strong setae, all pinnate and of similar length. Basis significantly wider and twice as long as coxa, about 2.6 times as long as wide, unornamented, armed with five unipinnate and three smooth setae along inner margin. Endopod 0.7 times as long as basis and about 2.7 times as long as wide, ornamented with hair-like spinules along outer margin, armed with one inner and three apical bipin-

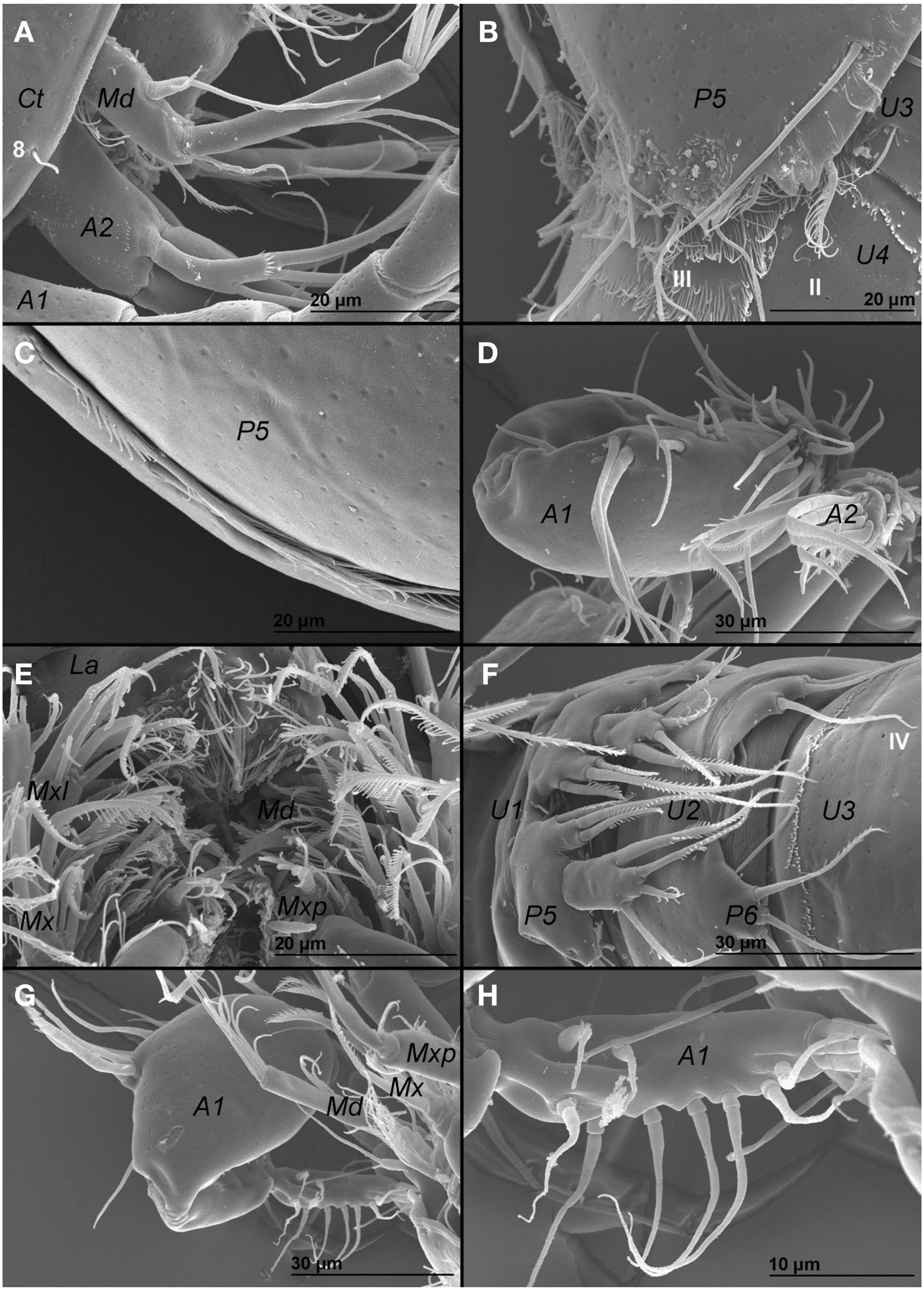

Fig. 5. *Phyllopodopsyllus kitazimai* sp. nov., A-C, paratype female 2; D and E, paratype male 2; F-H, paratype male 3, SEM photographs: A, ventral part of cephalothorax (Ct), with parts of antennula (A1), antenna (A2), and mandibula (Md), lateral; B, parts of third (U3) and fourth (U4) urosomites, with distal part of fifth leg (P5), lateral; C, median part of fifth legs (P5), lateral; D, parts of antennula (A1) and antenna (A2), ventral; E, oral cavity with distal parts of labrum (La), mandibula (Md), maxillula (Mxl), maxilla (Mx), and maxilliped (Mxp); F, first three urosomites (U1-U3), with fifth (P5) and sixth (P6) legs, ventral; G, distal parts of antennula (A1), mandibula (Md), maxillula (Mxl), and maxilliped (Mxp), ventral; H, ultimate segment of antennula (A1). Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite, and from dorsal to ventral side.

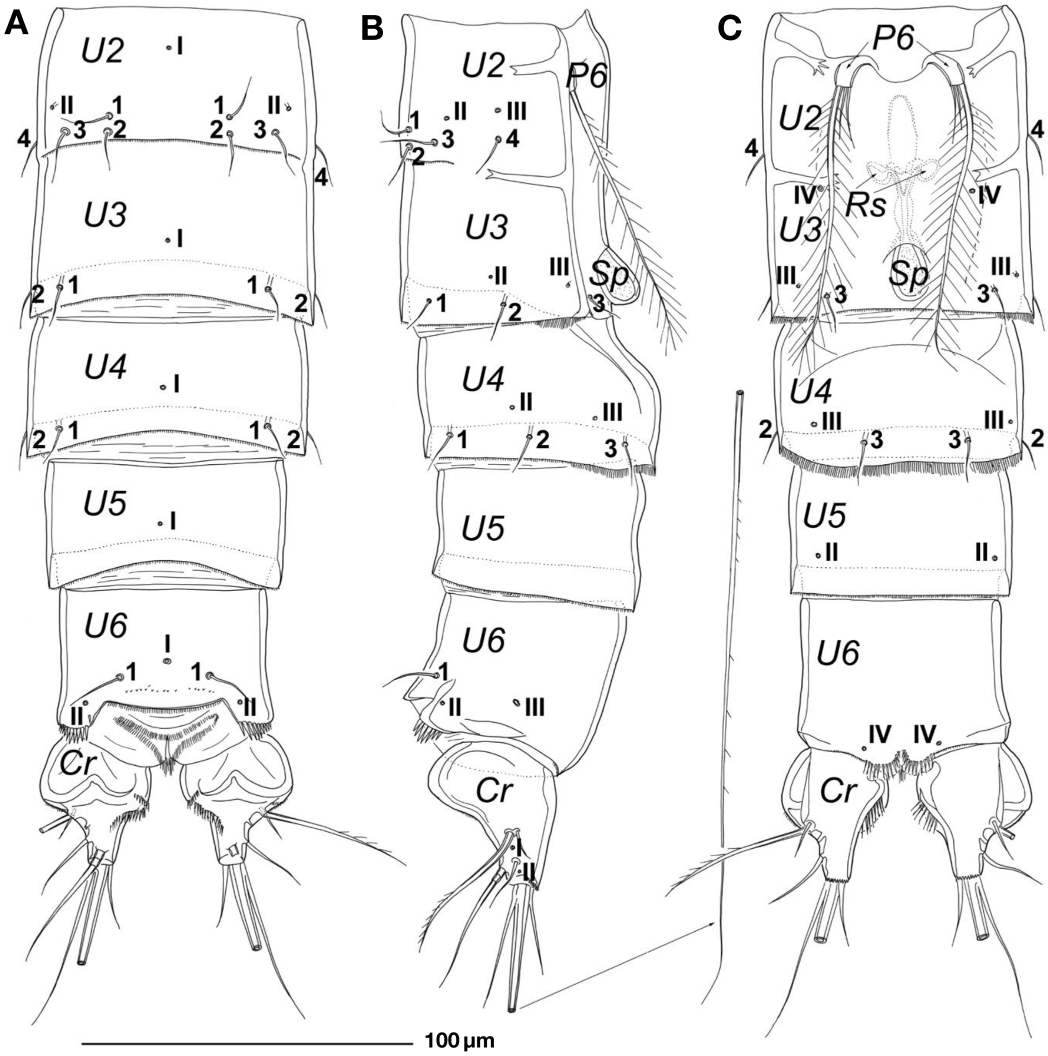

Fig. 6. *Phyllopodopsyllus kitazimai* sp. nov., holotype female, line drawings: A, second to sixth urosomites (U2-U6) and caudal rami, dorsal; B, second to sixth urosomites (U2-U6), with caudal rami (Cr), part of sixth leg (P6), and attached spermatophore (Sp), lateral; C, second to sixth urosomites (U2-U6), with caudal rami (Cr), sixth legs (P6), attached spermatophore (Sp), and internal reseptacula seminis (Rs), ventral. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side. Cuticular pits and minute surface spinules omitted for clarity.

nate setae of about same length. Exopod less than half as long as basis and twice as long as wide, ornamented with hair-like spinules along inner margin, armed with three apical bipinnate setae; outermost one about 1.5 times as long as two others and nearly 2.5 times as long as exopod.

Maxilla (Fig. 7F) composed of syncoxa, basis and two-segmented endopod. Syncoxa large, ovoid, unornamented, with four endites; endites of about same length, proximal two unornamented, distal two with arched row of minute spinules on anterior surface, armed with two, one, three, and three setae respectively from proximal side. Basis much smaller than syncoxa, elongate, with strong apical spine transformed into claw-like structure, ornamented with arched row of minute spinules on anterior surface, armed additionally with one strong apical seta and two smooth setae, one on anterior, and one on posterior surface; anterior seta half as long as posterior one. Endopod minute, with much shorter first segment than second, each armed with one strong geniculate spine and two slender setae; one slender seta on first segment minute.

Maxilliped (Fig. 7G) prehensile, three-segmented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa twice as long as wide, restricted in central part, ornamented with five short rows of long spinules (two posterior, three on anterior surface), armed with two plumose and one pinnate setae near inner-distal

Fig. 7. *Phyllopodopsyllus kitazimai* sp. nov., holotype female, line drawings: A, antennula, dorsal; B, antenna, posterior; C, mandibula, posterior; D, exopod of mandibula, posterior; E, maxillula, anterior; F, maxilla, anterior; G, maxilliped, anterior. Cuticular pits on antennula and antenna omitted for clarity.

Fig. 8. *Phyllopodopsyllus kitazimai* sp. nov., holotype female, line drawings: A, copulatory duct and receptacula seminis, compressed and slightly deformed; B, first swimming leg, anterior; C, second swimming leg, anterior; D, third swimming leg, anterior; E, fourth swimming leg, anterior; F, fifth leg, compressed and slightly deformed, anterior.

corner. Basis largest segment, nearly 4.3 times as long as wide and 1.3 times as long as syncoxa, cylindrical but wider in central part, ornamented with single longitudinal row of large spinules along inner margin in proximal half, and armed with single smooth inner seta around midlength; seta as long as larges spinules. Endopod smallest segment, 3.6 times as long as wide and 0.3 times as long as basis, cylindrical but narrower distally,

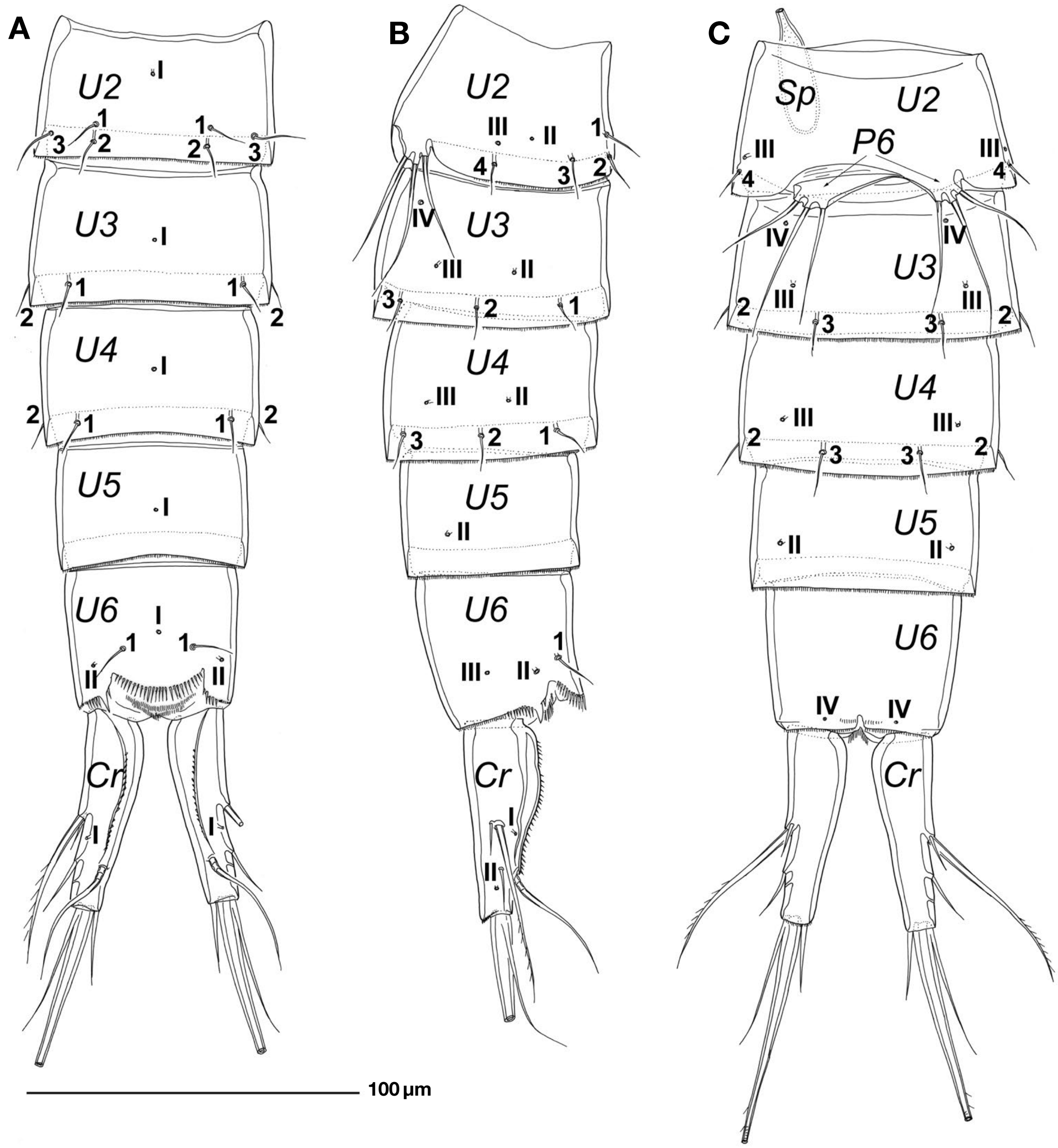

Fig. 9. *Phyllopodopsyllus kitazimai* sp. nov., allotype male, line drawings: A, second to sixth urosomites (U2-U6) and caudal rami (Cr), dorsal; B, second to sixth urosomites (U2-U6) and caudal ramus (Cr), lateral; C, second to sixth urosomites (U2-U6), with caudal rami (Cr), sixth legs (P6), and incompletely formed internal spermatophore (Sp), ventral. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side. Cuticular pits and minute surface spinules omitted for clarity.

unornamented, armed with one apical claw-like spine and one subapical slender seta; apical spine 2.3 times as long as basis and nearly 1.5 times as long as subapical seta.

All swimming legs (Fig. 8B-E) slender, short in comparison to body length and width, composed of small unarmed and unornamented triangular praecoxa, large unarmed but ornamented quadrate coxa, smaller armed basis, three-segmented armed and ornamented exopod, and two-segmented armed and ornamented endopod. Coxae in all pairs of legs connected by unornamented intercoxal sclerite, each with concave distal end and no spiniform protrusions.

First swimming leg (Fig. 8B) with widest intercox-

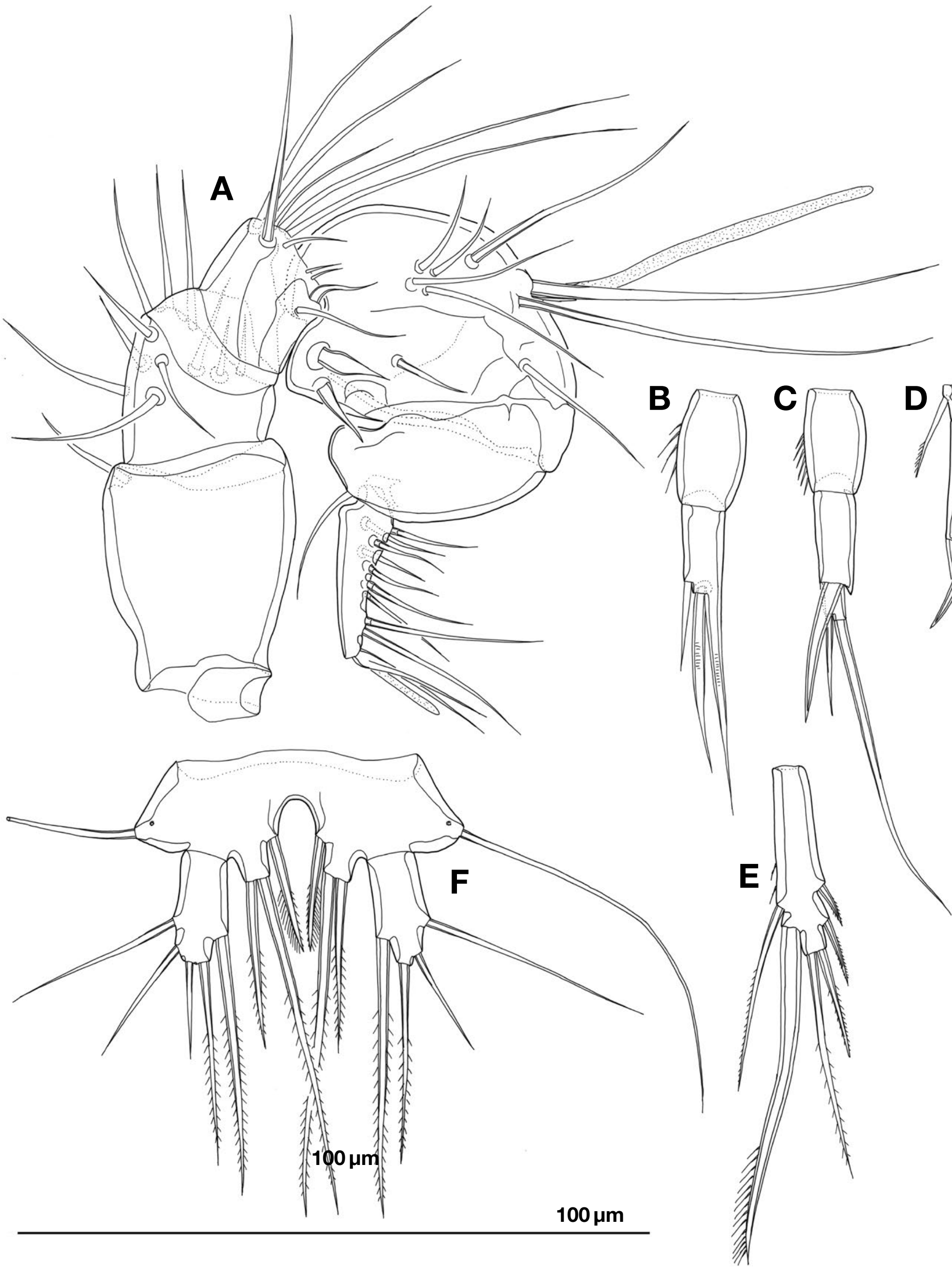

Fig. 10. *Phyllopodopsyllus kitazimai* sp. nov., allotype male, line drawings: A, antennula, dorsal; B, endopod of second swimming leg, anterior; C, endopod of third swimming leg, anterior; D, endopod of fourth swimming leg, anterior; E, third exopodal segment of fourth swimming leg, anterior; F, fifth legs, anterior. Cuticular pits on antennula omitted for clarity.

al sclerite (nearly three times as wide as long), biggest praecoxa, smallest coxa, longest basis, and longest endopod of all swimming legs. Coxa slightly longer than wide, narrower in distal part than proximal, with short outer spiniform process, ornamented with two anterior and one posterior row of spinules. Basis slightly longer than wide, with one inner and one outer strong, unipinnate spine, inner one stronger and about 1.7 times as long as outer; ornamentation consisting of row of short spinules at base of each spine on anterior surface, one row of hair-like spinules along inner margin, and single basal pore on anterior surface. Exopod with all segments of about same length, each about 2.5 times as long as wide; first and second segment armed with single strong outer spine each, third segment armed with two outer spines and two apical geniculate setae; all exopodal segments ornamented with strong spinules along outer margin and second segment additionally with hair-like spinules along inner margin; inner geniculate seta on third segment slightly longer than entire exopod and about 1.6 times as long as outer geniculate seta. Endopod geniculate and longer than exopod; first endopodal segment nearly 1.4 times as long as entire exopod, more than eight times as long as wide, and 5.6 times as long as second endopodal segment, unarmed, ornamented with hair-like spinules along inner margin; second endopodal segment about twice as long as wide, ornamented with posterior row of small spinules on anterior surface, armed with two apical elements, outer strong spine and inner long and geniculate seta; endopodal apical seta slightly shorter than exopodal outer apical seta but much stronger, and about 1.6 times as long as apical endopodal spine.

Second swimming leg (Fig. 8C) with nearly square intercoxal sclerite and much shorter praecoxa than in first leg. Coxa without spiniform process on outer margin, ornamented with three rows of spinules on anterior surface, one on posterior surface, but also with small spinules along inner margin, and strong spinules along outer margin. Basis armed only with outer spine, ornamented with only one row of spinules on posterior surface, minute spinules along inner margin (no spinules on anterior surface), and anterior basal pore. Third exopodal segment slightly longer and more slender than other two; distal inner corners of first and second exopodal segments with serrated hyaline frills and distal outer corners transformed into spiniform processes; first exopodal segment armed with inner strong seta and outer strong spine; second exopodal segment armed only with outer spine; third exopodal segment armed with two outer strong spines, strong outer apical seta, and slender inner apical seta; all exopodal segments with spinules along outer and inner margins, and third segment also with cuticular pore on anterior surface; third exopodal segment about 3.6 times as long as wide. Endopod about 0.4 times as long as exopod, both segments ornamented with spinules along inner margin only and of similar length but proximal one wider and unarmed; second segment armed with two or three apical elements: outer strong spine, central minute and slender seta (sometimes missing), and outer long and slender seta; apical edopodal spine about as long as endopod and half as long as inner apical seta.

Third swimming leg (Fig. 8D) very similar to second, except intercoxal sclerite narrower, basis with slender and long outer seta instead of spine, and third exopodal segment nearly six times as long as wide.

Fourth swimming leg (Fig. 8E) relatively similar to third leg, but with wider coxa, shorter basal seta, much shorter first endopodal segment armed with inner seta, slenderer seta on first exopodal segment, second exopodal segment armed with inner seta, and third exopodal segment with three strong inner setae; central inner seta on third exopodal segment exceptionally long and strong, about 0.8 times as along as entire exopod.

Fifth leg (Figs. 1A, 5B, C, 8F) typically foliaceous, twice as long as wide, with completely fused baseoendopod and exopod, forming brooding chamber with genital double-somite and anterior part of fourth urosomite normally containing two large eggs, ornamented with row of hair-like spinules between base and basal slender seta and two cuticular pores on anterior surface. Former baseoendopod armed with three slender and pinnte setae, most distal longest. Former exopod armed with six setae; most proximal and fifth seta smooth and slender and inserted on anterior surface, others short, plumose, and inserted on distal margin; distal margin between second and third setae and between third and fourth setae transformed into bicuspidate chitinous process, and between fifth and sixth setae transformed into finely serrated wide hyaline fringe.

Sixth leg (Fig. 6C) minute cuticular plate, about as long as wide, unornamented, armed with three apical setae; outermost seta strong and plumose, about as long as genital double-somite, 4.8 times as long as innermost slender and smooth seta, and nearly 5.6 times as long as central slender and smooth seta.

Male (based on allotype and 14 paratypes). Body length from 450 to 485 μm. Habitus shape (Fig. 1B), body proportions, and segmentation as in female, except second and third urosomites not fused (Fig. 9A-C). Ornamentation and shape of cephalothorax (Fig. 4B, C), all free prosomites (Fig. 4D), and first urosomite (Fig. 4E), as well as colour and nauplius eye (Fig. 1B), as in female.

Second urosomite (genital somite) (Figs. 4E, 5F, 9A-C) about 1.6 times as wide as long in dorsal view, with small spermatophore in right or left half, as in female with three pores (U2-I to U2-III) and four sensilla (U2-1 to U2-4), only one gonopore functional (covered by reduced sixth leg) but it could be left (Fig. 5F) or right (Fig. 9C).

Third urosomite (Figs. 4F, 5F, 9A-C) as in female with three pairs of sensilla (U3-1 to U3-3) and four pores (U3-I to U3IV), but without hair-like spinules on ventral surface and with hyaline fringe finely serrated (with minute combs) on all sides.

Fourth urosomite (Figs. 4F, 9A-C) ornamented as in female with three pairs of sensilla (U4-1 to U4-3) and three pores (U4-I to U4-III), but smaller, cylindrical, and with hyaline fringe uniformly finely serrated (no long combs on ventral side).

Fifth urosomite (Figs. 4G, 9A-C) ornamented as in female with two pores (U5-I and U5-II) but slightly slenderer.

Sixth urosomite (Figs. 4G, 9A-C) ornamented as in female with one pair of sensilla (U6-1) and four pores (U6-I to U6-IV) but much narrower and with longer spinules on anal operculum.

Caudal rami (Figs. 4H, 9A-C) much larger in comparison with anal somite than in female, almost cylindrical but with prominent dorsal ridge and tapering toward posterior end, about 3.2 times as long as wide in ventral view and 1.3 times as long as anal somite; ornamentation and all armature as in female, except no spinules along inner margin.

Antennula (Figs. 4C, 5D, G, H, 10A), strongly prehensile, robust, with almost all segments shorter than in female, with fused segments four and five, as well as seven and eighth (resulting in apparent six-segmented state); sixth segment and ancestral segments four and five highly transformed into robust pincers with several chitinous ridges along area of contact; additional armature present on second, third, and ancestral fourth somites, while sixth and ancestral fifth segments with reduced armature; position and nature of aesthetascs as in female, except apical one comparatively shorter; setal formula: 1.11.11.11.1.11; several setae on third and ancestral fourth segments very short and several of them spiniform; same six setae on ancestral seventh and eighth segments biarticulated.

Antenna (Fig. 5D), labrum (Fig. 5E), mandibula (Fig. 5E, G), maxillula (Fig. 5E), maxilla (Fig. 5E, G), maxilliped (Fig. 5E, G), exopod and endopod of first swimming leg, exopod of second swimming leg, exopod of third swimming leg, and first two endopodal segments of fourth swimming leg as in female.

Endopod of second swimming leg (Fig. 10B) also two-segmented as in female but second segment with two spiniform and strong elements (one fused basally to segment) and one short element, all of them smooth.

Endopod of third swimming leg (Fig. 10C) secondarily three-segmented, with outer spine on second segment, and two other elements on third minute segment; all three elements smooth, and outer spine curved inwards.

Fourth swimming leg (Fig. 10D, E) with only two inner setae on third exopodal segment and with both elements on second endopodal segment smooth; also outer spine on second endopodal segment curved inwards.

Fifth legs (Figs. 4E, 5F, 10F) completely different in shape from those in female, two-segmented, composed of large baseoendopod and small exopod but baseoendopods fused medially; as in female outer basal seta long and slender and endopodal lobe with three elements but central element longest; only one cuticular pore present at base of outer basal seta; exopod about twice as long as wide, unornamented, armed with four or five setae; all endopodal elements and two innermost exopodal elements bipinnate, others smooth; length ratio of endopodal armature elements, from inner side, 1 : 3 : 1.4; length ratio of exopodal armature (with five elements), from inner side, 1 : 0.8 : 0.4 : 0.5 : 0.7.

Sixth leg (Figs. 4E, F, 5F, 9C) short cuticular plate but larger than in female, unornamented, armed with three elements as in female but all smooth and central longest; length ratio of armature, from inner side, 1 : 1.2 : 0.9.

Variability. Remarkably, there is no variability in the number of sensilla and pores, although the exact position of some cuticular organs could vary between specimens (compare Figs. 4E and 9B for pores U2-II and U2-III). Another common form of obvious variability is the presence/absence of a minute central seta on the second endopodal segment of second to fourth legs in female, and in some specimens this was also a form of asymmetry; while most specimens have this element on at least one leg and at least one side, some have it on all legs and on both sides. One paratype female was observed with a deformed endopod of the right fourth leg, without seta on first segment and only apical spine on second, while the left fourth leg was normal. One paratype male was observed without inner seta on the right first exopodal segment of fourth leg, while the left fourth leg was normal. One paratype male was observed with both apical setae short on the second endopodal segment of right fourth leg, while the left fourth leg was normal. In males the spermatophore could be on the right or left side of genital segment, and accordingly left or right sixth leg could function as a genital operculum (being demarcated at base).

***Phyllopodopsyllus busanensis* sp. nov. (Figs. 1C and 11-15)**

Type locality. Korea, East Coast, Gyeongnam-do province, Busan, Songjeong Beach, intertidal sand, interstitial water from a Karaman-Chappuis hole, 35°10.741′N 129°12.317′E.

Specimens examined. Holotype female (NIBR IV 0000287280) dissected on one slide; paratype female (NIBR IV 0000287281) *in toto* on one SEM stub; both collected from the type locality, 6 May 2016, leg. T. Karanovic.

Etymology. The species is named after the type locality, the city of Busan in South Korea. The name is an adjective for place, made with the Latin suffix "-ensis".

Description. Female (based on holotype and one paratype). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae and appendages) from 405 (holotype) to 450 μm. Colour of preserved specimen light brown (Fig. 1C). Nauplius eye not visible. Segmentation as in previous species. Habitus (Figs. 1C, 11A) cylindrical but much

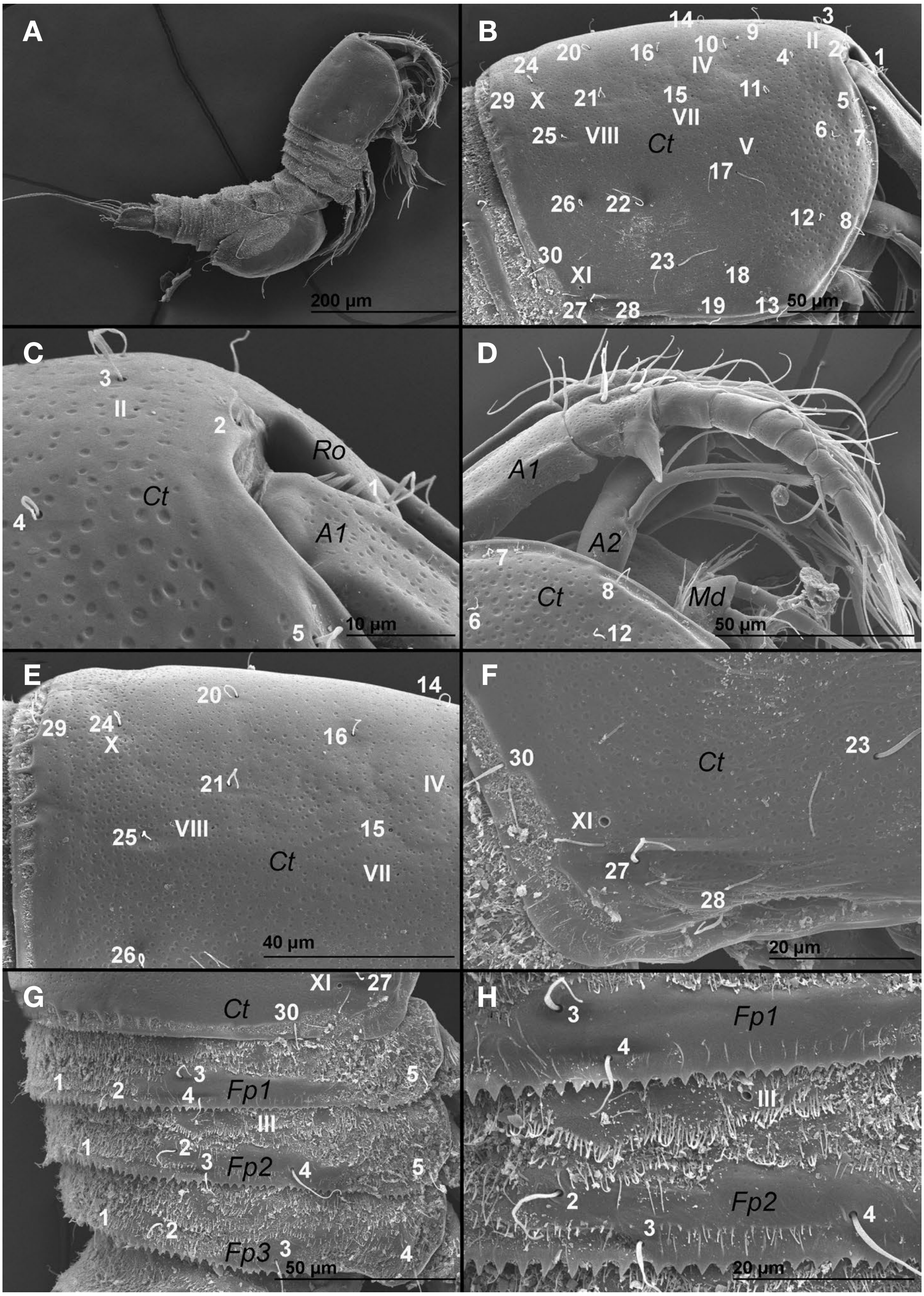

Fig. 11. *Phyllopodopsyllus busanensis* sp. nov., paratype female, SEM photographs: A, habitus, lateral; B, cephalothorax (Ct), lateral; C, anterior part of cephalothorax (Ct) with rostrum (Ro) and first segment of antennula (A1), lateral; D, ventral part of cephalothorax (Ct), with parts of antennula (A1), antenna (A2), and mandibula, lateral; E, dorso-posterior part of cephalothorax (Ct), lateral; F, ventro-posterior corner of cephalothorax (Ct), lateral; G, tergites of three free prosomites (Fp1-Fp3), lateral; H, detail of ornamentation of first (Fp1) and second (Fp2) prosomites, lateral. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side.

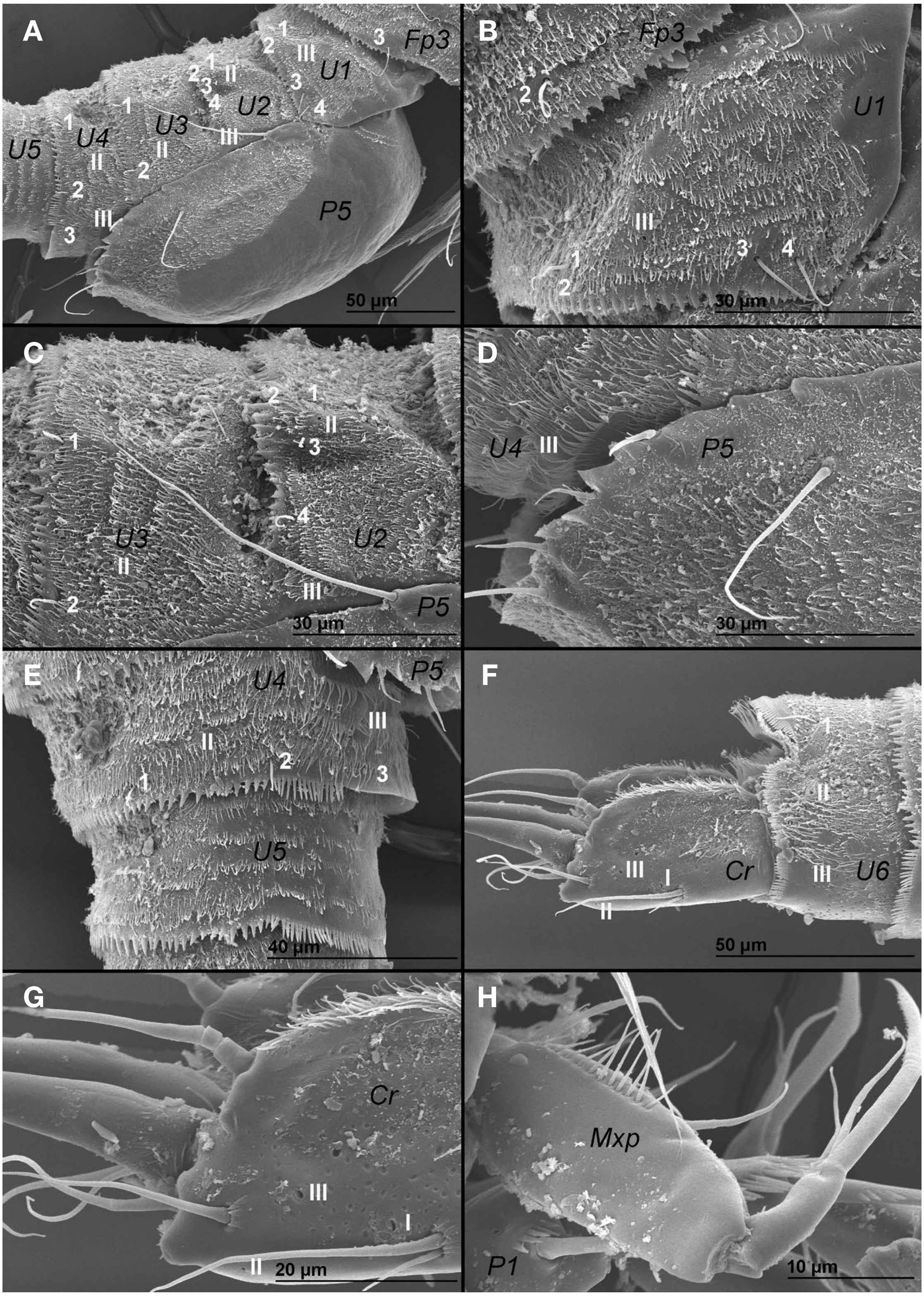

Fig. 12. *Phyllopodopsyllus busanensis* sp. nov., paratype female, SEM photographs: A, first five urosomites (U1-U5) with fifth leg (P5), lateral; B, tergite of first urosomite (U1), lateral; C, parts of fused second (U2) and third (U3) urosomites, with lateral part of fifth leg (P5), lateral; D, part of fourth urosomite (U4) and distal part of fifth leg (P5); E, fourth (U4) and fifth (U5) urosomites, lateral; F, sixth urosomite and caudal rami (Cr), lateral; G, posterior part of caudal rami (Cr), lateral; H, parts of maxilliped (Mxp) and first swimming leg (P1), lateral. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side.

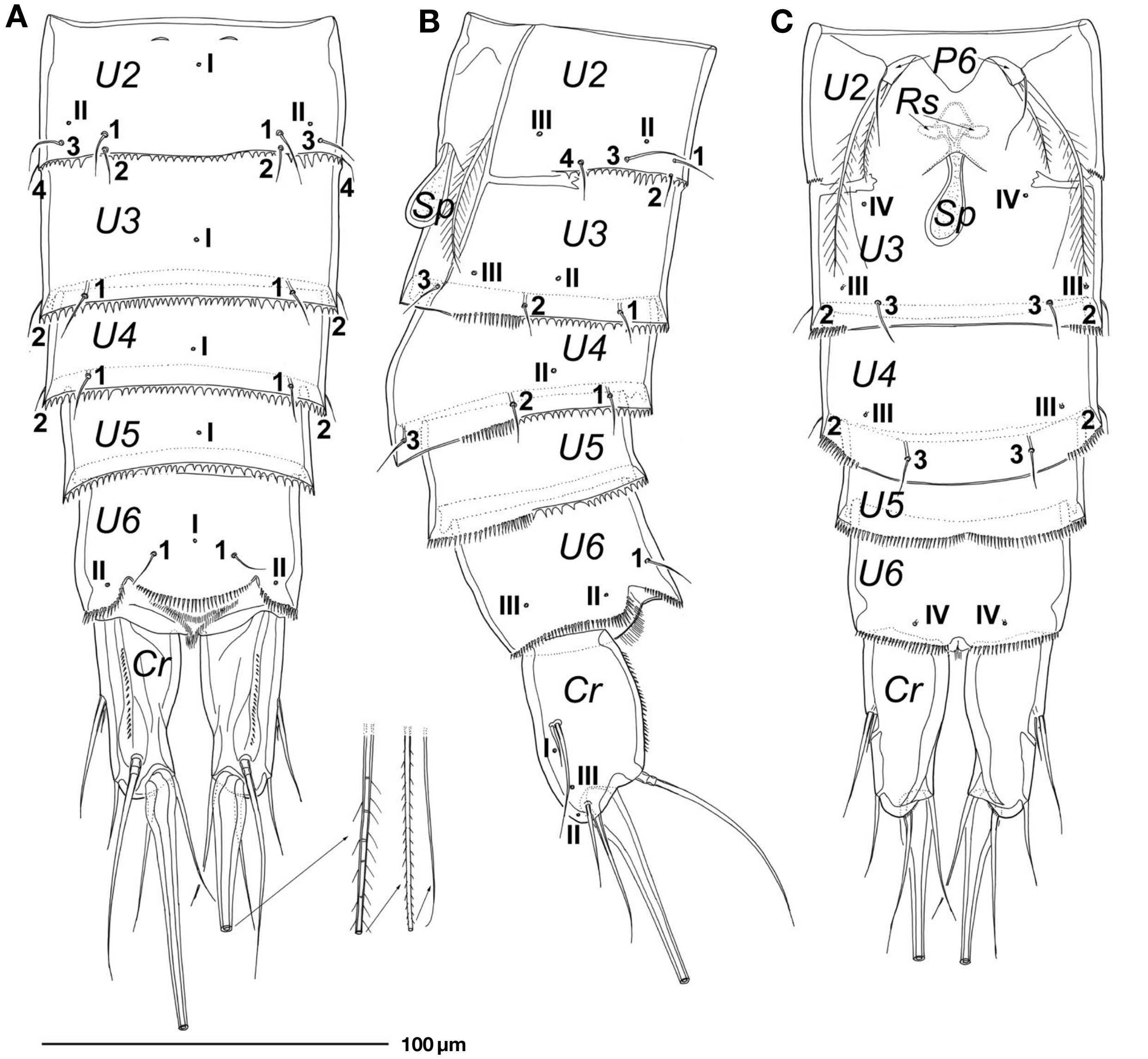

Fig. 13. *Phyllopodopsyllus busanensis* sp. nov., holotype female, line drawings: A, second to sixth urosomites (U2-U6) and caudal rami, dorsal; B, second to sixth urosomites (U2-U6), with caudal rami (Cr), and attached spermatophore (Sp), lateral; C, second to sixth urosomites (U2-U6), with caudal rami (Cr), sixth legs (P6), attached spermatophore (Sp), and internal reseptacula seminis (Rs), ventral. Arabic numerals for cuticular sensilla and Roman numerals for pores assigned consecutively from anterior to posterior end of each somite and caudal ramus, and from dorsal to ventral side. Cuticular pits and minute surface spinules omitted for clarity.

less slender than in previous species, without distinct demarcation between prosome and urosome in dorsal view, but with sharp bend in lateral view; prosome/urosome ratio about 0.9; greatest width at posterior end of cephalothorax; cephalothorax only 1.2 times as wide as genital double-somite in dorsal view. Body length/width ratio about 4.2. Free pedigerous somites without pronounced lateral or dorsal expansions. Integument of all somites relatively well sclerotized, generally smooth, covered with numerous shallow cuticular pits (see Figs. 11C, 12G); free prosomites and all urosomites additionally covered by parallel rows of minute and slender spinules; cephalothorax devoid of spinules. Hyaline fringe of all somites narrow and coarsely serrated. Surface of somites and caudal rami with total maximum of 185 cuticular organs (29 pairs of cuticular pores, 58 pairs of sensilla, one unpaired dorsal sensillum, and ten unpaired dorsal pores). All sensilla and pores homologous to those in previous species, with only small differences in their relative position; only real difference in cuticular organs visible on fifth urosomite (pore U5-II absent; see Fig. 13C) and caudal rami (additional pore Cr-III pres-

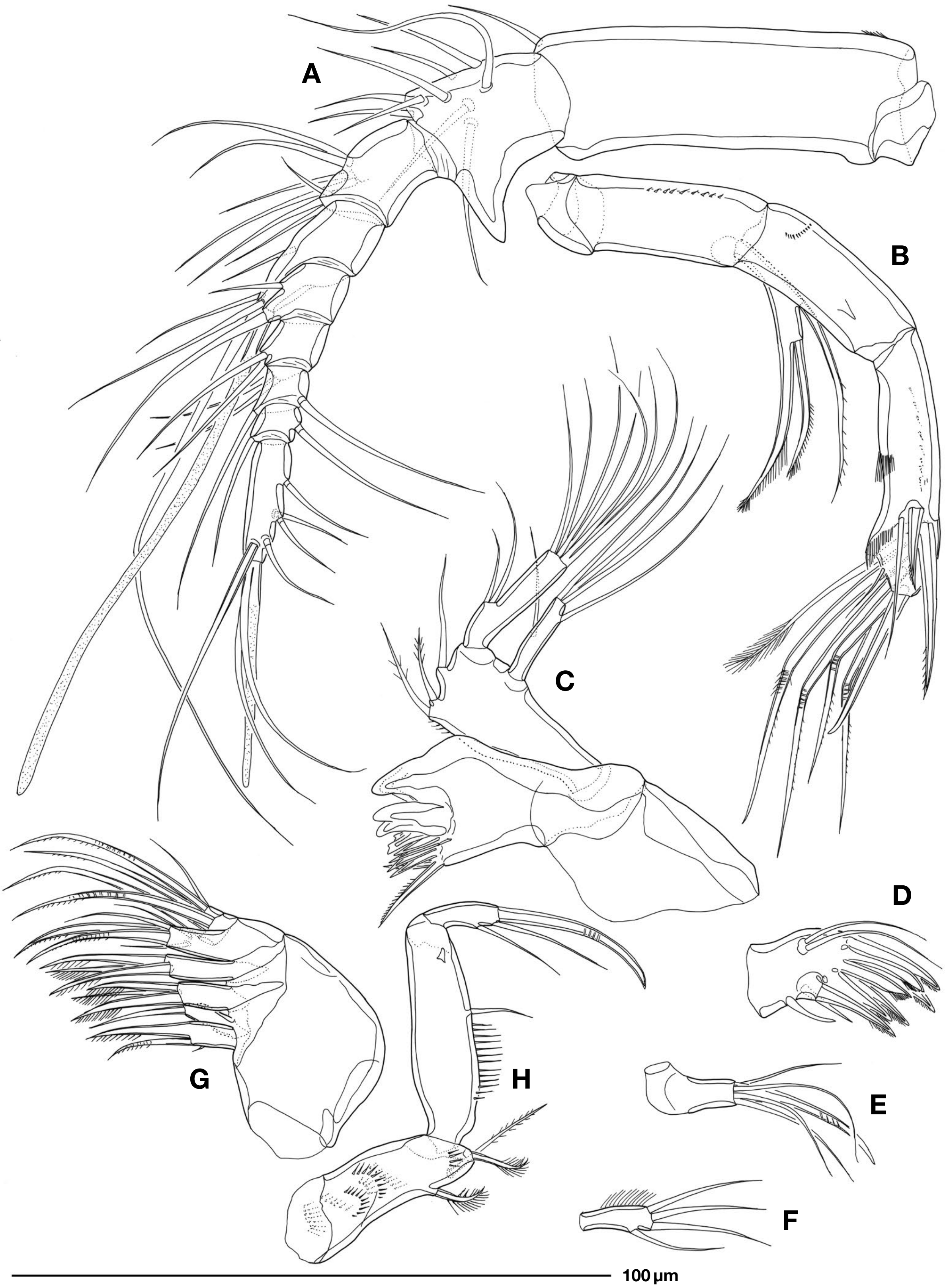

Fig. 14. *Phyllopodopsyllus busanensis* sp. nov., holotype female, line drawings: A, antennula, dorsal. B, antenna, posterior; C, mandibula, anterior; D, praecoxal arthrite of maxillula, anterior; E, coxa of maxillula, anterior; F, endopod of maxillula, anterior; G, maxilla, posterior; H, maxilliped, anterior. Cuticular pits on antennula and antenna omitted for clarity.

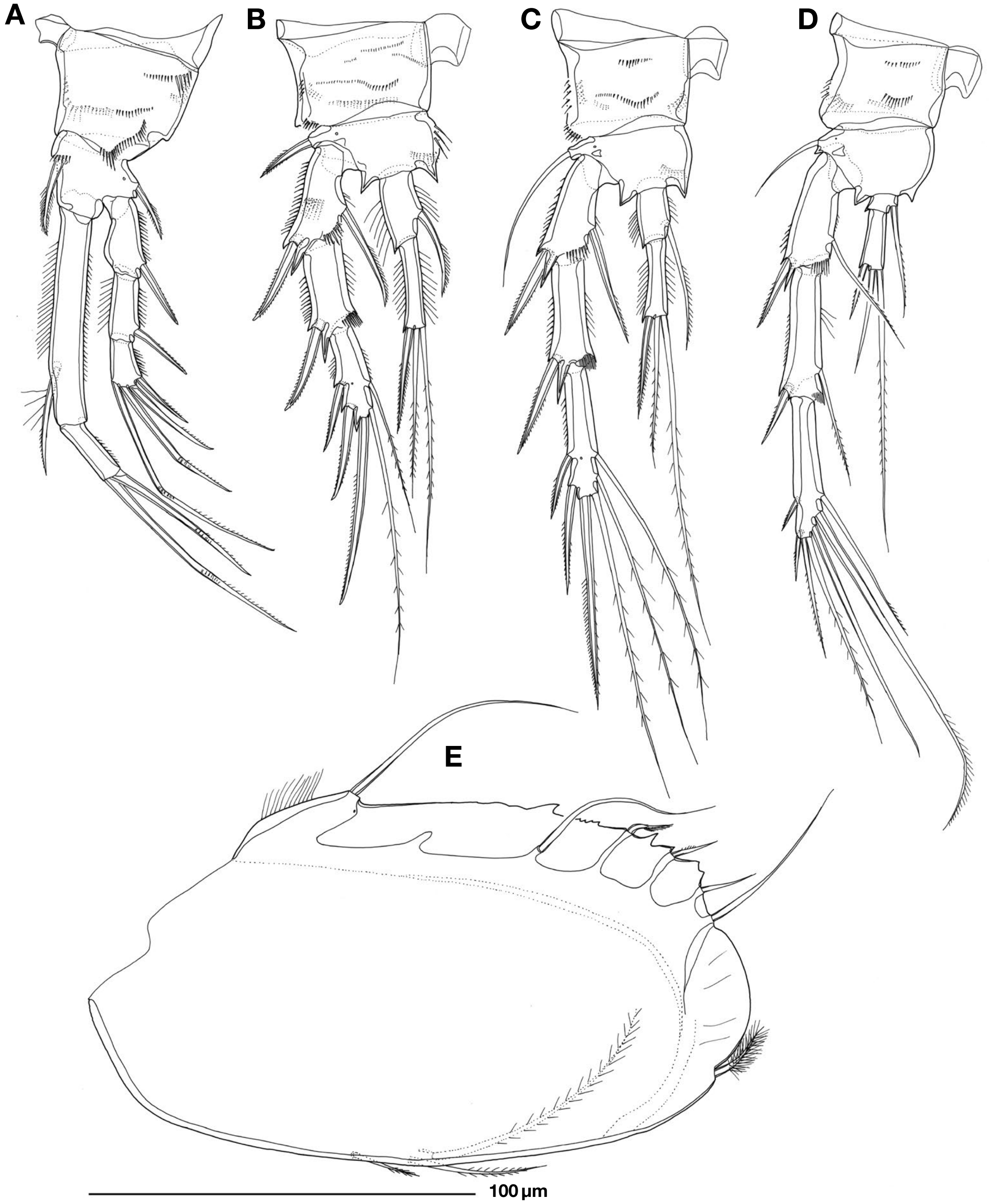

Fig. 15. *Phyllopodopsyllus busanensis* sp. nov., holotype female, line drawings: A, first swimming leg, anterior; B, second swimming leg, anterior; C, third swimming leg, anterior; D, fourth swimming leg, anterior; E, fifth leg, compressed and slightly deformed, anterior.

ent; see Figs. 12G, 13B); pore Ct-XI larger than in previous species (see Fig. 11F) and sensilla U1-3 and U1-4 closer to each other (see Fig. 12B).

Rostrum (Fig. 11C) as in previous species small, weakly demarcated at base from cephalothorax, linguiform, about as wide as long, its anterior tip hardly reaching beyond anterior margin of lateral wings of cephalothoracic shield, with single dorsal pair of sensilla (Ct-1) at about 2/3 of its length.

Cephalothorax (Fig. 11B-E) smooth, cylindrical in dorsal view, tapering towards anterior end in lateral view, about 1.5 times as long as wide in dorsal view (including rostrum); representing 33% of total body length. Hyaline fringe of cephalothoracic shield narrow, serrated dorsally, smooth laterally.

Pleurons of first free prosomites (Fig. 11G, H) shorter than in previous species and densely covered by slender spinules, with only small lateral surface free of them.

All urosomites (Fig. 12A-F) also densely covered by slender spinules, and more so on dorsal than on ventral side.

Genital double-somite (Figs. 12A, C, 13A-C) only slightly longer than wide in ventral view, with finely serrated dorsal fringe and lateral internal ridges as only evidence of ancestral segmentation. Genital complex (Fig. 13C) with single large and round copulatory pore in distal part of second urosomite, short and narrow copulatory duct, two small and ovoid seminal receptacles in central part of second urosomite, and central genital aperture in anterior part of second urosomite; aperture covered by reduced sixth legs.

Fourth urosomite (Figs. 12D, E, 13A-C) with hyaline fringe smooth ventrally.

Sixth urosomite (Figs. 12F, 13A-C) slightly narrower and significantly longer than fifth urosomite, cleft medially in posterior part, with posterior row of spinules; anal operculum broad but less so than in previous species, also longer and more convex, with finely serrated posterior margin, representing about 46% of somite's width; anal sinus as in previous species.

Caudal rami (Figs. 12F, G, 13A-C) strongly sclerotized, cylindrical but with strong dorsal ridge, with slightly inflated posterior ventro-outer corner, with slender spinules along outer-dorsal surface but without spinules along inner margin, about 1.8 times as long as greatest width in ventral view and nearly 1.7 times in lateral view, with narrow space between them; ornamented three lateral pores, two of them homologous to those in previous species (Cr-I and Cr-II); armed as in previous species with seven setae but no setae fused basally, anterior lateral setae inserted slightly more anteriorly, longer inner apical seta, and central apical seta with bulbous base; novel pore (Cr-III) situated between two other pores; doral seta marking end of dorsal ridge.

Antennula (Figs. 11C, D, 14A) nine-segmented, about as long as cephalothorax, with prominent integumental beak on second segment, with robust and long aesthetasc on fourth segment fused basally to slightly longer seta, slender and much shorter apical aesthetasc on ninth segment fused basally to two slightly longer setae, and setal formula 1.9.7.4.2.4.2.2.7. All setae slender and smooth; one lateral seta on seventh and eight segments and four lateral setae on sixth segment biarticulate. Only ornamentation short arched row of spinules at base of first segment, on dorso-median surface. Length ratio of antennular segments, from proximal end and along caudal margin, 1 : 0.4 : 0.2 : 0.2 : 0.15 : 0.15 : 0.1: 0.1: 0.4. First segment also strongest, about 2.9 times as long as wide; fourth segment with prominently protruded anterior distal corner at base of large easthetasc.

Antenna (Figs. 11D, 14B) slenderer than in previous species, but with same segmentation and armature. Coxa 0.8 times as long as wide, unornamented. Allobasis 2.5 times as long as wide and about three times as long as coxa, ornamented with longitudinal row of minute spinules along inner margin. First endopodal segment 2.4 times as long as wide and about as long as allobasis, ornamented with single transverse arched row of minute spinules in proximal part. Second endopodal segment most robust, slightly slenderer proximally but also generally cylindrical, 3.7 times as long as wide, 1.4 times as long as first endopodal segment, with two surface frills distally and row of small spinules along inner margin. Exopod slender, cylindrical but slightly curved, about 3.6 times as long as wide and half as long as allobasis, unornamented; outer apical seta strongest and spiniform, fused basally to exopod, about 1.3 times as long as inner apical seta, and 0.8 times as long as lateral seta.

Labrum as in previous species, not mounted properly for drawing.

Mandibula (Figs. 11D, 14C) segmentation, general shape, and most armature and ornamentation as in previous species, but endopod proportionately smaller and exopod much larger and armed with three apical setae. Basis twice as long as wide. Endopod 3.9 times as long as wide, 0.7 times as long as basis, and 1.4 times as long as exopod. Exopod cylindrical, very slender, 4.8 times as long as wide, unornamented, armed with one lateral and four apical slender and smooth setae.

Maxillula (Fig. 14D-F) segmentation, general shape, and most armature and ornamentation as in previous species, but praexocal arthrite armed apically only seven elements, and coxa without outer seta but with five inner elements (one strong and geniculate, four slender and smooth); endopod about 2.7 times as long as wide.

Maxilla (Fig. 14G) segmentation, general shape, armature, and ornamentation as in previous species.

Maxilliped (Figs. 12H, 14H) segmentation, general shape, and most armature and ornamentation as in previous species, but all spinules shorter and endopod armed with additional smooth and slender seta. Syncoxa 2.5 times as long as wide, cylindrical, and only slightly restricted in central part. Basis 3.4 times as long as wide and 1.1 times as long as syncoxa, cylindrical but wider in central part. Endopod nearly three times as long as wide and 0.3 times as long as basis, cylindrical but narrower in proximal half; apical spine 2.2 times as long as basis and 1.6 times as long as subapical seta.

Swimming legs (Fig. 15A-D) slightly shorter and less slender than in previous species, but with same segmentation, general shape, most ornamentation and armature.

First swimming leg (Fig. 15A) with prehensile endopod as in previous species, but coxa and basis wider, fist endopodal segment shorter and additionally armed with inner seta, and first exopodal segment with inner bulge. Coxa 0.8 times as long as wide, narrower in distal part than proximal, with short outer spiniform process, ornamented with three anterior and one posterior row of spinules. Basis about as long as wide, inner spine slightly stronger and about 1.4 times as long as outer. Exopod with first segment longest and third shortest; inner geniculate seta on third segment 1.3 times as long as entire exopod and about 1.6 times as long as outer geniculate seta. Endopod longer than exopod; first endopodal segment 1.15 times as long as entire exopod, more than six times as long as wide, and 3.1 times as long as second endopodal segment; endopodal apical seta as long as exopodal outer apical seta but slightly stronger, and about 1.4 times as long as apical endopodal spine.

Second swimming leg (Fig. 15B) with all segments shorter than in previous species, with two large spiniform processes on basis, and additionally armed with inner spiniform seta on first endopodal segment, as well as with inner slender seta on third exopodal segment. Coxa 0.7 times as long as wide, ornamented with six rows of small spinules on anterior surface and one row of spinules on posterior surface. All exopodal segments of similar length. Endopod about 0.6 times as long as exopod, first segment 0.8 times as long as second but much wider; apical edopodal spine about 0.7 times as long as endopod, 0.6 times as long as central slender seta, and less than half as long as inner apical seta.

Third swimming leg (Fig. 15C) very similar to second, except slightly slenderer and with longer inner seta on first endopodal segment; endopod 0.4 times as long as exopod; first endopodal segment 0.7 times as long as second endopodal.

Fourth swimming leg (Fig. 15D) very similar to previous species, except for spiniform processes on basis.

Fifth leg (Figs. 1A, 12A, C, D, 15E) shape, segmentation, and armature as in previous species, but covered by dense spinules in outer part, with serrate outer margin and smooth distal margin; short exopodal setae smooth or sparsely pinnate; forming brooding chamber with genital double-somite and anterior part of fourth urosomite normally containing six to seven eggs.

Sixth leg (Fig. 13C) shape and ornamentation as in previous species; also armed with three setae, but outermost seta extremely slender and shortest, while central seta longest, pinnate, not reaching posterior margin of genital double-somite, and more than twice as long as innermost pinnate seta.

Male unknown.

Variability. No obviously variable structures were observed between the two collected females, but the comparison was hindered by the fact that they were examined by different methods: the holotype was dissected and studied using light microscopy, while the paratype was permanently mounted on an SEM stub.

Discussion

The two new species differ in numerous macro-morphological characters, such as the segmentation, shape, and armature of the antennula (eight-segmented, without unguiform process, and with eight setae on third segment in *P. kitazimai* vs. nine-segmented, with unguiform process, and seven setae on third segment in *P. busanensis*); shape and armature of the mandibula (exopod minute and with only two setae in *P. kitazimai* vs. large exopod with five setae in *P. busanensis*), armature of maxillula (eight apical spines on praecoxa and three inner setae on basis in *P. kitazimai* vs. seven spines on praecoxa and five setae on basis in *P. busanensis*); armature of maxilliped (one slender seta on second endopodal segment in *P. kitazimai* vs. two slender setae in *P. busanensis*); armature of the first swimming leg (without armature on first endopodal segment in *P. kitazimai* vs. strong inner seta in *P. busanensis*), armature of the second swimming leg (third exopodal segment with four elements and first endopodal segment bare in *P. kitazimai* vs. third exopodal segment with five elements and first endopodal segment with inner seta in *P. busanensis*), armature of the third swimming leg (third exopodal with four elements and first endopodal segment bare in *P. kitazimai* vs. third exopodal segment with six elements and first endopodal segment with inner seta in *P. busanensis*), shape of the female genital field (genital pore in posterior part of genital doube-somite and long copulatory duct in *P. kitazimai* vs. genital pore central and short copulatory duct in *P. busanensis*), as well as the shape of the caudal rami (conical in *P. kitazimai* vs. cylindrical in *P. busanensis*). Other smaller differences include the presence/absence of chitinous processes on the bases of last three swimming legs, proportions of different segments and armature elements, and the exact number and placement of spinule rows. Given the number and nature of macro-morphological differences between these two new species, there is very little doubt that they are only remotely related in the genus; yet their generic placement is ensured by their very similar, and unique among copepods, foliaceous female fifth legs.

However, it was surprising to discover very few differences in the number and position of cuticular organs (pores and sensilla) on somites between the two new species; for example, fifth urosomite lacks pore U5-II and caudal rami have one additional pore (Cr-III) in *P. busanensis*. These micro-characters have not been studied in detail previously in this genus, and their use in harpacticoid taxonomy in general is a very recent development (Karanovic and Cho, 2012; Karanovic and Lee, 2012; Karanovic *et al*., 2012a; 2013b; 2015a; 2016; Karanovic and McRae, 2013; Karanovic and Kim, 2014b). As demonstrated in other harpacticoid genera and families (Karanovic and Mc Rae, 2013; Karanovic *et al*., 2013b; Karanovic and Kim, 2014a), cuticular organs in the two new species also show very little intraspecific variability and sexual dimorphism. The conservative nature of cuticular organs might prove them useful in the reconstruction of phylogenetic relationships in this group of harpacticoids, which was already suggested for a different harpacticoid family by Karanovic and Kim (2014a). Their suitability as landmarks for quantitative shape analysis was also recently demonstrated in distinguishing cryptic species of harpacticoids by Karanovic *et al*. (2016).

Both new species have their closest relatives in Japan. *Phyllopodopsyllus kitazimai* is morphologically most similar to *P. punctatus* Kitazima, 1981, but can be distinguished by much longer third exopodal segments of the third and fourth swimming legs (see Kitazima, 1981). The new species can additionally be distinguished from *P. punctatus* by shorter (wider) female genital double-somite, more posterior insertion of the dorsal seta on the caudal ramus, more widely spaced receptacula seminis, and more elongated first endopodal segment of the maxilliped. Their very close relationship is confirmed by the exact same segmentation and armature of all appendages, as well as the shape and ornamentation of the female caudal rami, which are unique in the genus.

Phyllopodopsyllus busanensis shares the largest number of morphological similarities with *P. setouchiensis* Kitazima, 1981, but can be distinguished by much shorter caudal rami, which also lack a notch in the dorsal keel in the new species. Other, smaller, differences include a longer dorsal caudal seta, absence of knees and processes on the basal part of the principal caudal seta, wider (shorter) genital double-somite, and presence of an inner bulge on the first exopodal segment of the first leg. *Phyllopodopsyllus setouchiensis* was also discovered, in addition to its type population in Japan (Kitazima, 1981), on both the Atlantic and the Pacific coasts of Costa Rica by Mielke (1992), albite with considerable morphological variation. This morphological variation probably inspired him to suggest *P. mielkei mielkei* Kunz, 1984 from Hawaii and *P. mielkei californicus* Kunz, 1984 from California as possible synonyms of *P. setouchiensis*, implying a very wide distribution for this morphologically variable species. Karanovic *et al*. (2001) added *P. crenulatus* Wells and Rao, 1987 from India to the list of potential synonyms of *P. setouchiensis*, based mostly on an unnoticed similarity of this Indian species to *P. mielkei californicus*. However, the presence of a morphologically similar, but yet distinct, species in Korea, the closest location to the type locality of *P. setouchiensis*, made me to reconsider these taxa in a new light. Although there is very little doubt that they represent a monophyletic unit in the genus, as suggested by Mielke (1992), they are probably closely related but distinct species rather than one widely distributed species. Unfortunately, members of this genus are yet to be sequenced, but experience from other studies on harpacticoid copepods where these types of morphological differences have been studied in combination with molecular data (Karanovic and Cooper, 2011; 2012; Karanovic and Kim, 2014b; Karanovic *et al*., 2015b; 2016) gives me confidence to resurrect them all. Björnberg and Kihara (2013) reported *P. setouchiensis* from Brazil, but provided only illustrations of the caudal rami; based on these the Brazilian population is more similar to *P. mielkei mielkei* than to *P. setouchiensis*, but it could be an undescribed new species. At this point it is impossible to make any other conclusions, and these specimens will have to be re-examined in detail. The only unresolved population at this point is that of *P. setouchiensis* from Costa Rica, which seems to differ from the Japanese one only by the shape of the basal inflated part of the principal caudal seta. Unfortunately, the illustrations provided by Mielke (1992) are not sufficient enough to resolve this, so this material will have to be studied again and preferably also with molecular tools. I would not be surprised if these disjunct populations prove to be conspecific, given the ease with which these animals could be subjects of anthropogenic translocation associated with shipping activities (for example in ships' ballast waters; see Grey *et al*., 2007; Zvyaginstev and Selifonova, 2008; Gregg *et al*., 2009; Karanovic and Krajicek, 2012). The fact that the population in Costa Rica is among the most abundant harpacticoids there (Mielke, 1992) is a classic signature of an introduced species (May *et al*., 2006; Ross *et al*., 2006; Lee *et al*., 2007; Winkler *et al*., 2008). Marine interstitial species have a wide range of tolerances to many environmental factors by their very nature (Brown and McLachlan, 1990; Giere, 2009; Zepelli *et al*., 2015), and are more likely to survive anthropogenic translocation than more stenoxenic elements. However, these are just speculations at this stage, and recent empirical studies provide evidence for the unusual resilience of some marine interstitial fauna (Armonies, 2017).

Below is a dichotomous key to species, which is modified from Karanovic *et al*. (2001) to include newly described Korean species, two species described from Brazil by Björnberg and Kihara (2013), and three species resurrected from the synonymy of *P. setouchiensis*. It is based on female characters, unless stated otherwise.

Key to species and subspecies of the genus *Phyllopodopsyllus*

1. Endopod of fourth leg one-segmented ··· 2
– Endopod of fourth leg two-segmented ··· 3
2. First endopodal segment of second and third legs with inner seta ··· *P. geddesi* Kunz, 1984
– First endopodal segment of second and third legs unarmed ··· *P. opisthoceratus* Geddes, 1968
3. First endopodal segment of fourth leg unarmed ··· 4
– First endopodal segment of fourth leg with inner seta ··· 8
4. Antennula nine-segmented ··· *P. xenus* (Kunz, 1951)
– Antennula eight-segmented ··· 5
5. Exopod of first leg two-segmented ··· *P. biarticulatus* (Wells, 1967)
– Exopod of first leg three-segmented ··· 6
6. Second endopodal segment of fourth leg with three setae ··· *P. longipalpatus hawaiiensis* Kunz, 1984
– Second endopodal segment of fourth leg with two setae ··· 7
7. Caudal rami with dorso-lateral cuticular process ··· *P. longipalpatus madagascarensis* Kunz, 1984
– Caudal rami without this process ··· *P. longipalpatus longipalpatus* (Chappuis, 1954)
8. Second endopodal segment of fourth leg with single seta ··· *P. hermani* Coull, 1969
– Second endopodal segment of fourth leg with more than one seta ··· 9
9. Second endopodal segment of fourth leg with two setae ··· 10
– Second endopodal segment of fourth leg with three setae ··· 14
10. Antennula nine-segmented ··· 11
– Antennula eight-segmented ··· 12
11. Antennula with unguiform process ··· *P. bahamensis* Geddes, 1968
– Antennula without unguiform process ··· *P. paraxenus* Coull, 1970
12. First endopodal segment of third leg without seta ··· *P. minutus* Lang, 1948
– First endopodal segment of third leg with inner seta 13
13. Third exopodal segment of second and third legs with four elements ··· *P. tenuis* Wells and Rao, 1985
– Third exopodal segment of second and third legs with five elements ··· *P. wellsi* Karanovic *et al*. 2001
14. First endopodal segment of third leg without seta ··· 15
– First endopodal segment of third leg with inner seta ··· 22
15. Second exopodal segment of fourth leg without inner seta ··· *P. medius* Por, 1964
– Second exopodal segment of fourth leg with inner seta ··· 16
16. Second endopodal segment of second and third legs with two setae ··· *P. hartmannorum* Kunz, 1995
– Second endopodal segment of second and third legs with three setae ··· 17
17. First endopodal segment of first leg without inner seta ··· 18
– First endopodal segment of first leg with inner seta ··· 19
18. Third exopodal segment of third leg about as long as second segment and cylindrical ··· *P. punctatus* Kitazima, 1981
– Third exopodal segment of third leg much longer than second segment and very narrow basally ··· *P. kitazimai* sp. nov.
19. Third exopodal segment of second leg with four elements ··· *P. laticauda* Por, 1964
– Third exopodal segment of second leg with five elements ··· 20
20. Antennula eight-segmented ··· *P. bermudae* Lang, 1948
– Antennula nine-segmented ··· 21
21. First endopodal segment of first leg almost as long as exopod ··· *P. angolensis* Kunz, 1984
– First endopodal segment of first leg about 1.5 times as long as exopod ··· *P. aegypticus* Nicholls, 1944
22. First endopodal segment of second leg without seta ··· 23
– First endopodal segment of second leg with inner seta ··· 33
23. Second exopodal segment of fourth leg without inner seta ··· 24
– Second exopodal segment of fourth leg with inner seta ··· 25
24. Antennula nine-segmented ··· *P. borutzkyi* Lang, 1965
– Antennula eight-segmented ··· *P. simplex* Kitazima, 1981
25. Third exopodal segment of third leg with five elements ··· *P. langi* Kunz, 1975
– Third exopodal segment of third leg with six elements ··· 26
26. Antennula nine-segmented ··· 27
– Antennula eight-segmented ··· 29
27. Caudal rami about seven times as long as wide ··· *P. longicaudatus* A. Scott, 1909
– Caudal rami less than 2.5 times as long as wide ··· 28
28. Caudal rami with large anterior inner bulge ··· *P. bradyi* (T. Scott, 1892)
– Caudal rami without anterior inner bulge ··· *P. pallaresae* Kunz, 1995

29. Antennula with additional sharp process on anterior distal corner of second segment ··· 30
− Antennula without additional sharp process (single unguiform, posteriorly directed) ··· 31
30. Dorsal seta attached close to posterior margin of caudal ramus ··· *P. parafurciger parafurciger* Geddes, 1968
− Dorsal seta attached at 2/3 of caudal ramus length ··· *P. parafurciger caroliensis* Coull, 1971
31. Caudal rami with well developed dorsal chitinous ridge. ··· *P. furciger* Sars, 1907
− Caudal rami without dorsal ridge ··· 32
32. Caudal rami more than six times as long as wide ··· *P. curtus* Marcus, 1976
− Caudal rami about four times as long as wide ··· *P. stigmosus* Wells and Rao, 1987
33. Second exopodal segment of fourth leg without inner seta ··· 34
− Second exopodal segment of fourth leg with inner seta ··· 45
34. Antennula eight-segmented ··· 35
− Antennula nine-segmented ··· 37
35. Third exopodal segment of third leg with four elements ··· 36
− Third exopodal segment of third leg with three elements ··· *P. kunzi* Mielke, 1989
36. Caudal rami in dorsal view widest in anterior third ··· *P. danielae* Bodin, 1964
− Caudal rami in dorsal view widest in posterior third ··· *P. pseudokunzi* Björnberg and Kihara, 2013
37. Antennula with strong and sharp unguiform process on second segment ··· 38
− Antennula with small and blunt process or without any processes ··· 39
38. Third exopodal segment of fourth leg with six elements ··· *P. paraborutzkyi* Kunz, 1975
− Third exopodal segment of fourth leg with seven elements ··· *P. carinatus* Mielke, 1992
39. Antennula with small and blunt process on second segment ··· 40
− Antennula without any processes ··· 41
40. Third exopodal segment of fourth leg with seven elements; caudal rami 1.5 times as long as wide ··· *P. hibernicus* (Roe, 1955)
− Third exopodal segment of fourth leg with six elements; caudal rami three times as long as wide ··· *P. hardingi* (Roe, 1955)
41. Third exopodal segment of fourth leg with six elements ··· *P. paramossmani* (Lang, 1934)
− Third exopodal segment of fourth leg with seven elements ··· 42
42. Caudal rami about 3.5 times as long as wide ··· *P. berrieri* Monard, 1936
− Caudal rami about 1.5 times as long as wide ··· 43
43. Central apical seta on caudal ramus not broadened basally ··· *P. laspalmensis* Marinov, 1973
− Central apical seta on caudal ramus broadened basally ··· 44
44. Exopod of fifth leg with five setae in male ··· *P. mossmani* T. Scott, 1912
− Exopod of fifth leg with four setae in male ··· *P. mossmani chiloensis* Mielke, 1992
45. Antennula eight-segmented ··· 46
− Antennula nine-segmented ··· 49
46. Third exopodal segment of second and third legs with four elements ··· 47
− Third exopodal segment of second leg with five, while that of third leg with six elements ··· 48
47. Central apical seta on caudal rami minute ··· *P. pauli* Crisafi, 1960
− Central apical seta on caudal rami long and strong ··· *P. ancylus* Mielke, 1992
48. Third exopodal segment of fourth leg with six elements ··· *P. chavei* Coull, 1970
− Third exopodal segment of fourth leg with seven elements ··· *P. galapagoensis* Mielke, 1989
49. Third exopodal segment of third leg with five elements ··· 50
− Third exopodal segment of third leg with six elements ··· 54
50. Antennula with unguiform process on second segment ··· 51
− Antennula without such process ··· 52
51. Caudal rami in lateral view with concave dorsal margin ··· *P. parabradyi* Lang, 1965
− Caudal rami in lateral view with convex dorsal margin ··· *P. iunamei* Björnberg and Kihara, 2013
52. Urosomites with spiniform cuticular extensions ··· *P. alatus* Fiers, 1986
− Urosomites without such extensions ··· 53
53. Exopod of fifth leg with five setae in male ··· *P. thiebaudi thiebaudi* Petkovski, 1955
− Exopod of fifth leg with four setae in male ··· *P. thiebaudi santacruzensis* Mielke, 1989
54. Antennula with strong and sharp unguiform process on second segment ··· 55
− Antennula with small and blunt process or without any processes ··· 59
55. Caudal rami in lateral view cylindrical and stout (more than half as wide as anal somite) ··· 56
− Caudal rami in lateral view conical and slender (less than half as wide as anal somite) ··· 57
56. Caudal rami in lateral view about 1.7 times as long as wide and with straight dorsal margin ··· *P. busanensis* sp. nov.
− Caudal rami in lateral view about 2.5 times as long as wide and with notch in dorsal keel ··· *P. setouchiensis* Kitazima, 1981

57. Caudal rami in lateral view without notch in dorsal keel ······································· *P. mielkei* Kunz, 1984
 – Caudal rami in lateral view with notch in dorsal keel ··· 58
58. Caudal rami in dorsal view widest at base ················ ···························· *P. crenulatus* Wells and Rao, 1987
 – Caudal rami in dorsal view widest at first third ········ ························· *P. californicus* Kunz, 1984 stat. nov.
59. Antennula without any processes on second segment ···························· *P. gracilipes* Wells and Rao, 1987
 – Antennula with small blunt process ····················· 60
60. First endopodal segment of first leg about as long as exopod ··················· *P. briani briani* Petkovski, 1955
 – First endopodal segment of first leg longer than exopod ························· *P. briani petkovskii* Kunz, 1984

Acknowledgements

This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the ministry of Environment (MOE) of the Republic of Korea (NIBR201704101). The scanning electron microscope was made available through the courtesy of Prof. Jin Hyun Jun (Eulji University, Seoul), and I also want to thank Mr. Junho Kim (Eulji University, Seoul) for the technical help provided. Two anonymous reviewers are acknowledged for many constructive remarks.

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Submitted: October 27, 2017
Revised: November 13, 2017
Accepted: November 13, 2017