

# Five new subterranean amphipods of the genus *Pseudocrangonyx* from Korea (Crustacea, Amphipoda, Pseudocrangonyctidae)

Tae Won Jung<sup>1</sup>, Jong Guk Kim<sup>2</sup>, Min-Seop Kim<sup>3</sup>, Seong Myeong Yoon<sup>4</sup>

**1** National Institute of Ecology, Yeongyang 36531, South Korea **2** Korea Institute of Ocean Science & Technology, Busan 49111, South Korea **3** National Marine Biodiversity Institute of Korea, Seocheon 33662, South Korea **4** Department of Biology, Chosun University, Gwangju 61452, South Korea

Corresponding author: Seong Myeong Yoon ([smyun@chosun.ac.kr](mailto:smyun@chosun.ac.kr))

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## Abstract

Although the majority of the species belonging to the genus *Pseudocrangonyx* Akatsuka & Komai, 1922 are found among the subterranean fauna of eastern Asia, the taxonomic knowledge is very poor and only four species have been recorded in Korea. In this study, the morphology of the stygobitic pseudocrangonyctid amphipods from Korean subterranean waters was examined and five new species were identified: *Pseudocrangonyx concavus* **sp. nov.** has a characteristic emarginated posteroventral margin of epimeral plate 3; *Pseudocrangonyx gracilipes* **sp. nov.** differs from other pseudocrangonyctids by the slender and elongated pereopods and more produced posterodistal corner of epimeral plate 3. *Pseudocrangonyx crassus* **sp. nov.** shows the expanded peduncular articles and a reduced flagellum of antenna 2. *Pseudocrangonyx minutus* **sp. nov.** is distinguished by more reduced pleopod articles compare to other pseudocrangonyctids. *Pseudocrangonyx villosus* **sp. nov.** has the more setose bases of pereopods 3 and 4. Detailed descriptions and illustrations are presented for these five new species.

## Keywords

Korea, new species, pseudocrangonyctid, stygobiotic amphipods, taxonomy

## Introduction

Stygobitic amphipods of the genus *Pseudocrangonyx* are the dominant crangonyctoids in subterranean waters and springs of the east Asia region including the Far East of Russia, eastern China, Japan, and the Korean peninsula (Labay 2001, Sidorov and Gontcharov 2013, Tomikawa et al. 2016, Zhao and Hou 2017, Lee et al. 2018, 2020, Tomikawa and Nakano 2018).

To date, 27 described species of the genus *Pseudocrangonyx* have been reported in the east Asia region (Horton et al. 2020). Thirteen species have been described from the Far East of Russia, including *P. bohaensis* (Derzhavin, 1927), *P. levanidovi* Birstein, 1955, *P. camtschaticus* Birstein, 1955, *P. birsteini* Labay, 1999, *P. relictus* Labay, 1999, *P. susanaensis* Labay, 1999, *P. korkishkorum* Sidorov, 2006, *P. febras* Sidorov, 2009, *P. elenae* Sidorov, 2011, *P. kseniae* Sidorov, 2012, *P. holsingeri* Sidorov & Gontcharov, 2013, *P. sympatricus* Sidorov & Gontcharov, 2013, and *P. tiunovi* Sidorov & Gontcharov, 2013 (Derzhavin 1927, Birstein 1955, Labay 1999, Sidorov 2006, 2009, 2011, 2012, Sidorov and Gontcharov 2013). The seven species known in Japan are *P. kyotonis* Akatsuka & Komai, 1922, *P. shikokunis* Akatsuka & Komai, 1922, *P. yezonis* Akatsuka & Komai, 1922, *P. gudariensis* Tomikawa & Sato, 2016, *P. akatsukai* Tomikawa & Nakano, 2018, *P. komaii* Tomikawa & Nakano, 2018, and *P. uenoi* Tomikawa, Abe & Nakano, 2019 (Akatsuka and Komai 1922, Tomikawa and Sato 2016, Tomikawa and Nakano 2018, Tomikawa et al. 2019). The four species known in China are *P. manchuricus* Oguro, 1938, *P. asiaticus* Uéno, 1934, *P. cavernarius* Hou & Li, 2003, and *P. elegantulus* Hou, 2017 (Uéno 1934, Oguro 1938, Hou and Li 2003, Hou 2017). In Korea, only four species have been reported: *P. asiaticus* Uéno, 1934, *P. coreanus* Uéno, 1966, *P. daejeonensis* Lee, Tomikawa, Nakano & Min, 2018, and *P. joolaei* Lee, Tomikawa, Nakano & Min, 2020 (Uéno 1934, 1966, Lee et al. 2018, 2020).

The first record of Korean pseudocrangonyctid amphipods was *P. asiaticus* from Dongryonggul Cave in North Korea (Uéno 1940). Later, Uéno (1966) examined other specimens collected from several caves in central South Korea and reported that *P. asiaticus* and *P. coreanus* were both present with variations in the character states of the several appendages such as maxilla 1, antennal flagellum, uropod 3, and telson.

Recently, several morphological and molecular phylogenetic studies of this genus have shown a high species diversity of the genus *Pseudocrangonyx* and considered *P. asiaticus* and *P. coreanus* to be a species complex (Sidorov and Gontcharov 2013, Tomikawa et al. 2016, Lee et al. 2018, 2020, Tomikawa and Nakano 2018). In this respect, the authors carefully examined the morphologies of the Korean pseudocrangonyctid specimens and found five new species: *Pseudocrangonyx concavus* sp. nov., *Pseudocrangonyx gracilipes* sp. nov., *Pseudocrangonyx crassus* sp. nov., *Pseudocrangonyx minutus* sp. nov., and *Pseudocrangonyx villosus* sp. nov. This paper presents the detailed descriptions and illustrations of these species.



## Materials and methods

The collected specimens were initially fixed in 80% ethyl alcohol in the field and then preserved in 95% ethyl alcohol after sorting in the laboratory. Specimens were stained with lignin pink before dissection. Appendages were dissected in petri dishes or excavated microscopic slides filled with a mixed solution of glycerol-ethanol using dissecting forceps and needles under a stereomicroscope (Discovery V8; ZEISS, Oberkochen, Germany) and mounted onto temporary slides using glycerol. To prepare illustrations, pencil drawings were made under a light microscope (ECLIPSE 80i; Nikon, Tokyo, Japan) with the aid of a drawing tube. These drawings were then scanned, digitally inked, and arranged on digital plates using the methods described by Coleman (2003, 2009). All dissected appendages and remaining bodies of type specimens were preserved in 95% ethanol. Once examined, specimens were deposited in the collection of the National Institute of Biological Resources (NIBR) of Korea.

## Systematic accounts

**Order Amphipoda** Latreille, 1816

**Suborder Senticaudata** Lowry & Myers, 2013

**Superfamily Crangonyctoidea** Bousfield, 1973

**Family Pseudocrangonyctidae** Holsinger, 1989

**Genus *Pseudocrangonyx*** Akatsuka & Komai, 1922

*Pseudocrangonyx concavus* sp. nov.

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Figs 1–4

**Korean name.** O-mok-nal-gae-dong-gul-yeop-sae-u, new

**Type locality.** Hwansangul Cave, Samcheok-si, Gangwon-do, South Korea; 37°20'55"N, 129°04'45"E.

**Material examined.** Type material. *Holotype*: 1 female, 9.2 mm, NIBRIV0000862807. *Paratypes*: 4 specimens, NIBRIV0000872407. All type materials were collected from the type locality on 19 Jan 2001 by YG Choi.

Additional material. 1 female, 8.9 mm, NIBRIV0000872408; 1 male, 5.5 mm, NIBRIV0000872409, collected from the type locality on 13 Jan 2010 by YG Choi.

**Etymology.** The specific name originates from the Latin word *concavus* meaning concave, hollow. This name refers to the shape of posteriorly emarginated ventral margin of epimeral plate 3.

**Diagnosis.** Maxilla 1 inner lobe with five plumose setae on apical margin; 2<sup>nd</sup> palp article with eight robust setae along distomedial and apical margins. Maxilla 2 inner lobe with one oblique row of seven plumose setae on surface; outer lobe apical margin with three

plumose setae medially. Pereopod 5 coxa anterior lobe expanded ventrally ( $1.00 \times$  longer than wide), margin lined with seven simple setae; basis expanded and subrectangular ( $0.55 \times$  wider than long). Pereopod 6 coxa anterior lobe  $0.62 \times$  as long as that of pereopod 5, with one seta only on ventral margin; basis expanded. Sternal gills present from pereonites 2–5 (1+2+1+1 in formulae). Epimeral plate 2 ventral margin with two submarginal setae anteriorly, posterodistal corner slightly notched bearing one elongate setae. Epimeral plate 3 posterodistal corner without notch, rounded, ventral margin with three submarginal setae anteriorly, posteriorly emarginated. Uropod 1 inner ramus with one elongate seta on ventral margin subproximally. Uropod 2 peduncle  $0.62 \times$  as long as that of uropod 1.

**Description.** Holotype female: Body (Fig. 1A) approximately 9.2 mm long.

Head (Fig. 1B) as long as pereonite 1; rostrum reduced, without minute setae; lateral cephalic lobe anteriorly expanded, apex rounded, slightly dilated anteroventrally; antennal sinus not deep; eye absent.

Antenna 1 (Fig. 1C)  $0.51 \times$  as long as body; peduncle 1<sup>st</sup>–3<sup>rd</sup> articles length ratio of 1.00 : 0.76 : 0.40; 1<sup>st</sup> article stout, with one pair of robust setae on posterior margin; accessory flagellum bi-articulate, last article very reduced, with one pair of aesthetascs distally; flagellum  $1.15 \times$  as long as peduncles, composed of 16 articles, calceoli absent, aesthetascs present on the 9<sup>th</sup>–11<sup>th</sup>, 13<sup>th</sup>, 14<sup>th</sup>, and last articles.

Antenna 2 (Fig. 1D, E)  $0.59 \times$  as long as antenna 1; antennal cone developed, apex rounded; peduncle 4<sup>th</sup> and 5<sup>th</sup> articles length ratio of 1.00 : 0.89; 4<sup>th</sup> article margins parallel,  $0.27 \times$  wider than long, posterior margin with one row of setae at the middle and one elongate seta subdistally, 5<sup>th</sup> article  $0.75 \times$  wider than 4<sup>th</sup> article, two calceoli present on medial surface; flagellum composed of eight articles,  $1.21 \times$  as long as peduncle 5<sup>th</sup> article, single calceoli present on 1<sup>st</sup>, 4<sup>th</sup>, and 5<sup>th</sup> articles medially, aesthetascs absent.

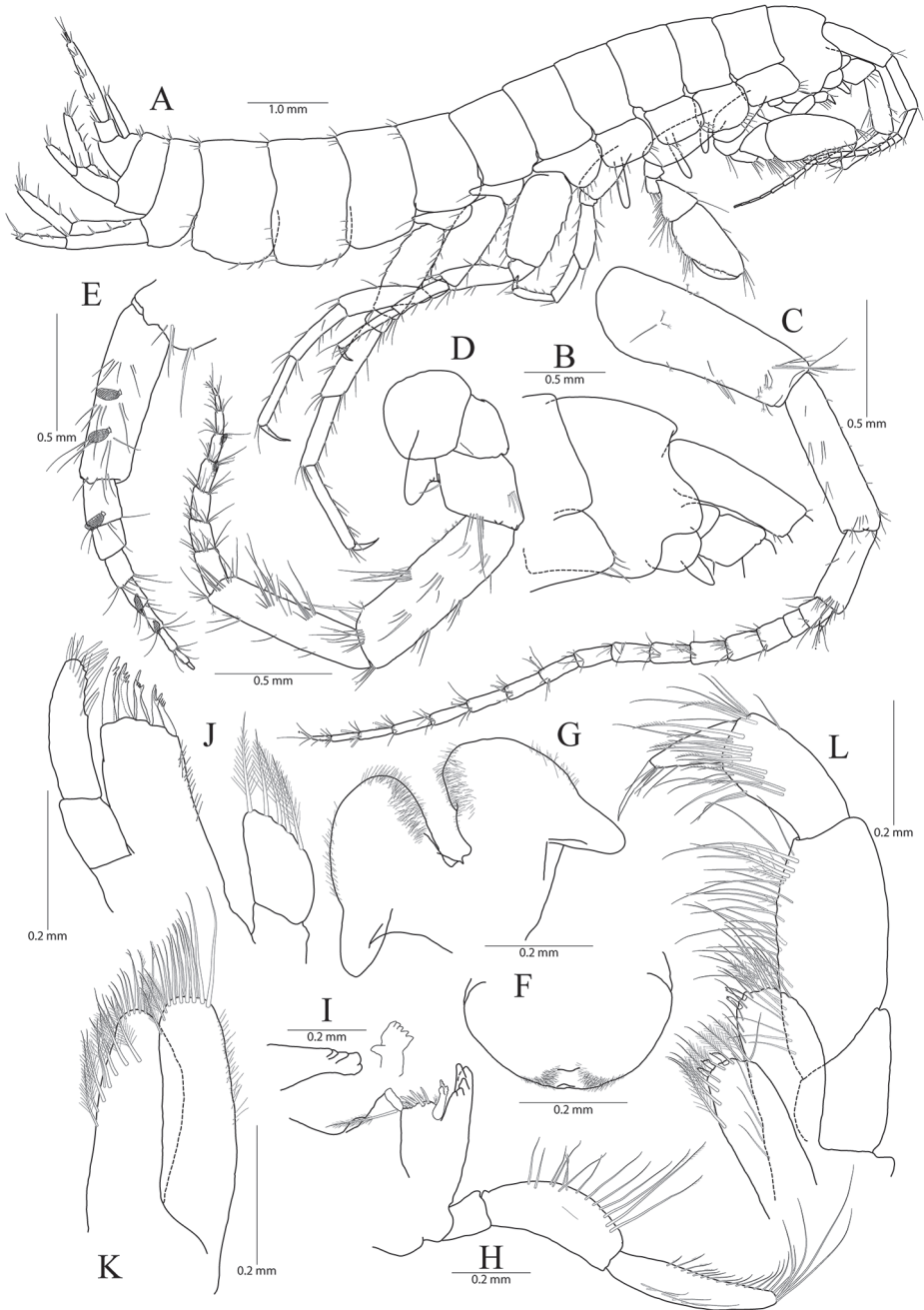
Upper lip (Fig. 1F) anteriorly rounded, apex covered with minute setae, slightly notched.

Lower lip (Fig. 1G) inner lobes indistinct; outer lobes covered with minute setae; mandibular processes developed.

Mandibles (Fig. 1H, I) incisor 5-dentate on both sides; lacinia mobilis tri-cuspidate (each finely dentate) on right side and bi-furcate (one 5-dentate and the other not dentate) on left side; four raker setae present on both sides; molar process columnar, triturative, with one plumose seta on right side only; palp tri-articulate; 2<sup>nd</sup> article convex and with 14 setae medially; 3<sup>rd</sup> article subfalcate,  $1.31 \times$  as long as 2<sup>nd</sup> article, lined with 19 setae from medial margin to apex.

Maxilla 1 (Fig. 1J) inner lobe subrhomboid, with five plumose setae on apical margin; outer lobe with seven dentate robust setae; palp bi-articulate, 2<sup>nd</sup> article apex slightly exceeding apical setae of outer plate, with eight robust setae along distomedial and apical margins, with one oblique row of seven setae subdistally.

Maxilla 2 (Fig. 1K) inner lobe slightly shorter but wider than outer lobe, with one oblique row of seven plumose setae on surface and two rows of simple setae on apical margin; outer lobe apical margin with three plumose setae medially, also with two rows of simple setae.



**Figure 1.** *Pseudocrangonyx concavus* sp. nov. Holotype: female, NIBRV0000862807, 9.2 mm, from Hwansangul Cave, South Korea. **A** habitus **B** head **C** antenna 1 **D, E** antenna 2, lateral (**D**) and medial (**E**) **F** upper lip **G** lower lip **H** right mandible **I** incisor and lacinia mobilis of left mandible **J** maxilla 1 **K** maxilla 2 **L** maxilliped.

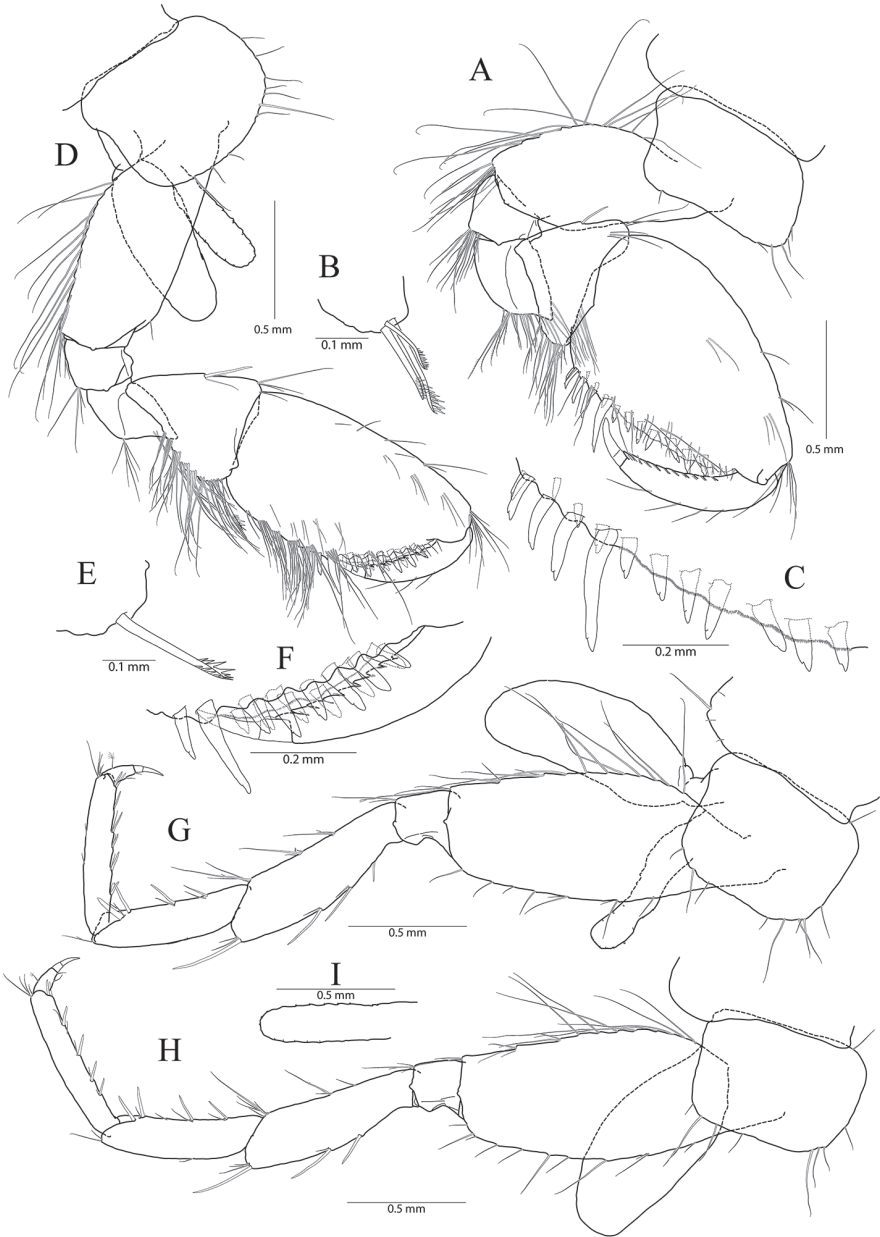
Maxilliped (Fig. 1L) inner lobe subrectangular, with three dentate robust setae on apex and eight plumose setae subapically; outer lobe elongate semicircular,  $0.89 \times$  as long as palp 2<sup>nd</sup> article, with two dentate robust setae and six plumose setae apically; palp composed of four articles; 2<sup>nd</sup> article with many setae on medial margin; 3<sup>rd</sup> article slightly dilated distally,  $0.60 \times$  as long as 2<sup>nd</sup> article; 4<sup>th</sup> article falcate,  $0.67 \times$  as long as 3<sup>rd</sup> article, apical setae  $0.67 \times$  as long as 4<sup>th</sup> article.

Gnathopod 1 (Fig. 2A–C) coxa subrectangular,  $1.52 \times$  wider than long, slightly produced anterodistal corner with five setae marginally, ventral margin slightly convex, with one seta posteriorly, posterior margin humped proximally; basis obtuse trapezoidal, posteriorly expanded,  $0.49 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin obliquely truncated distally, without setae; ischium  $0.30 \times$  as long as basis, with small anterior lobe; carpus  $0.51 \times$  as long as basis, with one robust seta on anterior margin, carpal lobe not developed, apex rounded with three rastellate setae and many simple or serrate setae; propodus subovate,  $1.30 \times$  as long and  $1.65 \times$  as wide as basis, with five robust setae laterally along posterior margin distally and ten robust setae medially along posterior margin and palm (all medial setae small, but lateral setae larger and successively increasing distally), palm irregular, finely serrated, defined by largest lateral seta of posterior margin; dactylus as long as palm, inner margin toothed, outer margin with four setae, unguis developed.

Gnathopod 2 (Fig. 1D–F) as long as gnathopod 1; coxa  $1.28 \times$  as long as that of gnathopod 1,  $1.19 \times$  wider than long, anterior and ventral margins not produced, rounded, lined with seven setae anteriorly and three setae posteriorly, posterior margin humped proximally; coxal gill present, subovate; oostegite present, narrow, shorter than coxal gill, without marginal setae; basis subtrapezoidal, posteriorly expanded,  $0.37 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin with one seta subdistally; ischium  $0.19 \times$  as long as basis, with small anterior lobe; carpus  $0.42 \times$  as long as basis, with one pair of robust seta and simple seta on anterior margin, carpal lobe not developed, apex rounded with one rastellate seta and many simple or serrate setae; propodus trapezoidal,  $0.98 \times$  as long and  $1.42 \times$  as wide as basis, anterior margin slightly convex, posterior margin  $0.49 \times$  as long as anterior margin, lined with five clusters of elongate setae, palm irregular, finely serrated, lined with six medial and eight lateral robust setae (palm defined by two unequal setae distally among lateral setae); dactylus as long as palm, inner margin toothed, outer margin with three setae, unguis developed.

Pereopod 3 (Fig. 2G) coxa rectangular,  $1.24 \times$  wider than long, ventral margin with six anterior and three posterior setae, posterior margin slightly humped proximally; coxal gill present, subovate; oostegite present, narrow, shorter than coxal gill, without marginal setae; basis expanded,  $0.80 \times$  as wide and  $2.60 \times$  as long as coxa, width longest at proximal 1/3 and gradually diminished distally, anterior margin slightly convex, lined with simple setae, posterior margin lined with elongate setae; ischium  $0.15 \times$  as long as basis; merus anterodistally expanded,  $0.31 \times$  wider than long,  $0.58 \times$  as long as basis, anterodistal corner produced, apex blunt; carpus not expanded,  $0.46 \times$  as long as basis; propodus  $0.49 \times$  as long as basis, linear; dactylus  $0.38 \times$  as long as propodus, unguis developed.

Pereopod 4 (Fig. 2H, I) similar to pereopod 3 except that merus  $0.92 \times$  as long as that of pereopod 3; different number or position of several setae.



**Figure 2.** *Pseudocrangonyx concavus* sp. nov. Holotype: female, NIBRV0000862807, 9.2 mm, from Hwansangul Cave, South Korea. **A** gnathopod 1 **B** rastellate seta of gnathopod 1 **C** palm of gnathopod 1 **D** gnathopod 2 **E** rastellate setae of gnathopod 2 **F** palm of gnathopod 2 **G** pereopod 3 **H** pereopod 4 **I** oostergite of pereopod 4.

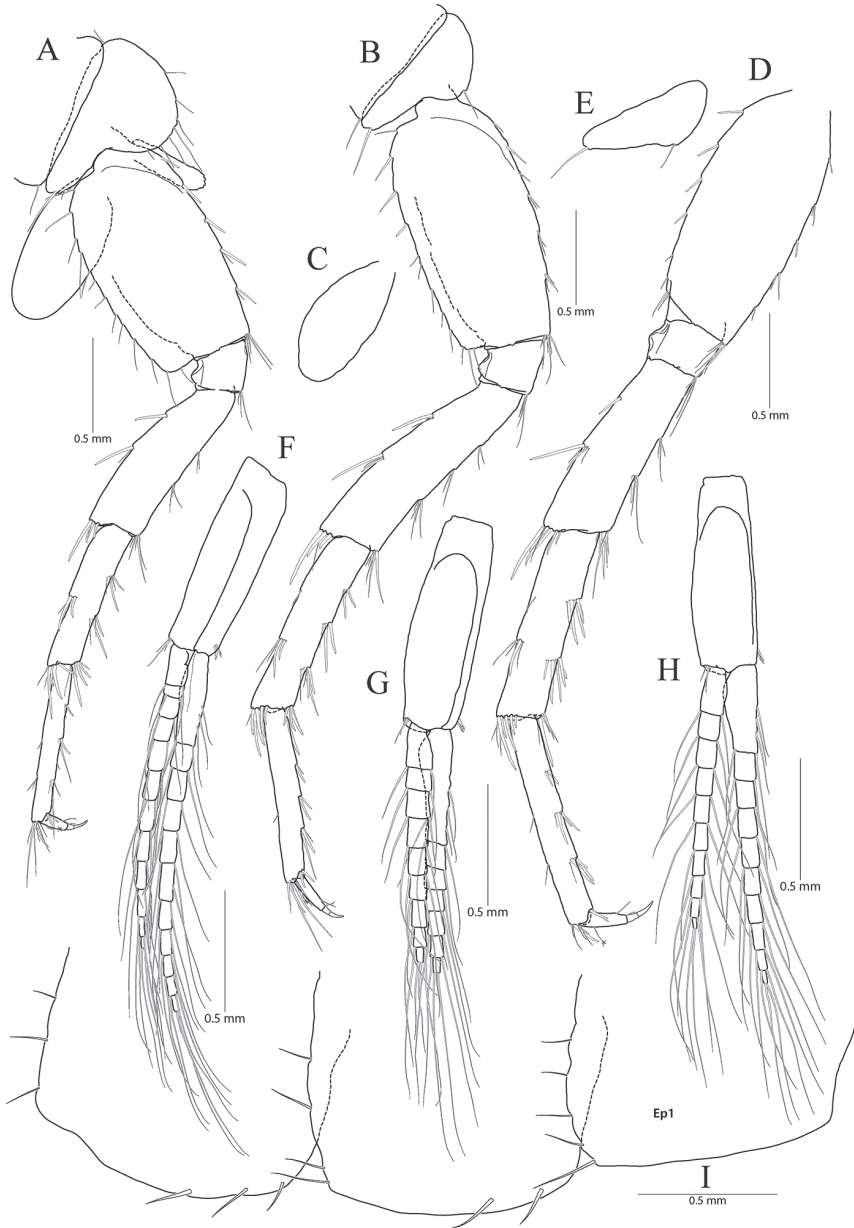
Pereopod 5 (Fig. 3A) coxa bilobate, anterior lobe larger than posterior lobe, expanded ventrally (1.00 × longer than wide), margin rounded, lined with seven simple setae; posterior lobe with two setae at posterior corner (ventral one very short); coxal

gill present, subovate; oostegite present, narrow, shortest, without marginal setae; basis expanded, subrectangular,  $0.55 \times$  wider than long, anterior margin slightly convex, lined with three single robust setae and two pairs of robust and simple setae, with one cluster of elongate simple setae at distal corner, posterior margin lined with twelve elongate simple setae, distal corner produced forming an angle; merus posterodistally expanded,  $0.42 \times$  as wide and  $0.80 \times$  as long as basis, anterior margin with two clusters of simple setae marginally and one cluster of simple setae distally, posterior margin with one single robust seta and one pair of unequal setae marginally and one cluster of robust setae distally; carpus not expanded,  $0.69 \times$  as long as basis, anterior margin with two marginal clusters and one distal cluster of setae, posterior margin with one marginal and one distal clusters of setae; propodus linear,  $1.03 \times$  as long as carpus, anterior margin with three setal clusters (longest seta of distal cluster slightly exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with one single and one pair of marginal short seta and one distal cluster of elongate setae; dactylus  $0.31 \times$  as long as propodus, unguis developed.

Pereopod 6 (Fig. 3B, C)  $1.14 \times$  as long as pereopod 5; coxa bilobate, anterior lobe  $0.62 \times$  as long as that of pereopod 5, with one seta only on ventral margin, posterior lobe expanded backward, with one seta at posterior corner; coxal gill present, subovate; oostegite absent; basis expanded, subrectangular,  $1.16 \times$  as long and  $1.00 \times$  as wide as that of pereopod 5,  $0.46 \times$  wider than long, anterior margin slightly convex, lined with three single robust setae and three clusters of robust and simple setae, with one cluster of elongate simple setae at distal corner, posterior margin lined with twelve setae, distal corner produced forming an angle; merus posterodistally expanded,  $1.22 \times$  as long as that of pereopod 5,  $0.50 \times$  as wide and  $0.84 \times$  as long as basis, anterior margin with three marginal clusters and one distal cluster of simple setae, posterior margin with two marginal clusters and one distal cluster of simple and robust setae; carpus not expanded,  $0.73 \times$  as long as basis, anterior margin with three marginal clusters and one distal cluster of simple and robust setae, posterior margin with one simple seta and one cluster of simple and robust setae marginally and one cluster of setae distally; propodus linear,  $0.92 \times$  as long as carpus, anterior margin with three setal clusters (longest seta of distal cluster not exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with one marginal short seta and one distal cluster of elongate setae; dactylus  $0.37 \times$  as long as propodus, unguis developed.

Pereopod 7 (Fig. 3D, E)  $1.06 \times$  as long as pereopod 6; coxa unilobed, subtriangular,  $0.77 \times$  as long as that of pereopod 6, with one seta on ventral margin, posteriorly expanded with one seta at posterior corner; ); coxal gill and oostegite absent; basis expanded, subrectangular,  $1.00 \times$  as long and  $0.92 \times$  as wide as that of pereopod 6,  $0.42 \times$  wider than long, anterior margin slightly convex, lined with three single setae and two clusters of setae, with one cluster of elongate simple setae at distal corner, posterior margin lined with eight setae, distal corner slightly produced but angle smaller than those of pereopods 6 and 7; merus posterodistally expanded,  $0.80 \times$  as long as that of pereopod 6,  $0.54 \times$  as wide and  $0.67 \times$  as long as basis, anterior margin with two marginal clusters and one distal cluster of simple setae, posterior margin with one single robust seta and one cluster of simple and robust setae marginally, and one cluster of





**Figure 3.** *Pseudocrangonyx concavus* sp. nov. Holotype: female, NIBRV0000862807, 9.2 mm, from Hwansangul Cave, South Korea. **A** pereopod 5 **B** pereopod 6 **C** coxal gill of pereopod 6 **D** pereopod 7 **E** coxa of pereopod 7 **F** pleopod 1 **G** pleopod 2 **H** pleopod 3 **I** epimeral plates 1–3. Abbreviation: Ep, epimeral plate.

simple and robust setae distally; carpus not expanded, rectangular,  $0.24 \times$  as wide as long,  $1.09 \times$  as long as merus, anterior margin with three marginal clusters and one distal cluster of simple and robust setae, posterior margin with one simple seta and



one cluster of simple and robust setae marginally, and one cluster of simple and robust setae distally; propodus linear,  $1.11 \times$  as long as carpus, anterior margin with three setal clusters (longest seta of distal cluster not exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with two marginal short setae and one distal cluster of setae posteriorly (shorter than those of pereopods 6 and 7); dactylus  $0.38 \times$  as long as propodus, unguis developed.

Sternal gills (Fig. 4A) present in pereonites 2 to 5 (1+2+1+1 in formulae), narrower than oostegites, shortest in that of pereonite 5.

Epimeral plate 1 subquadrate, a little produced posteroventrally, ventral margin without setae, posterior margin with four setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 2 subquadrate, larger than plate 1, ventral margin with two submarginal setae anteriorly, posterior margin with three setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 3 posterior margin with three setae, posterodistal corner without notch, rounded, ventral margin with three submarginal setae anteriorly, posteriorly emarginated. (Fig. 3I).

Pleopod 1 (Fig. 3F) peduncle with one pair of retinaculae mediodistally and one cluster of three simple setae laterodistally; outer ramus  $1.55 \times$  as long as peduncle, composed of twelve articles; inner ramus  $1.85 \times$  as long as peduncle, composed of eleven articles (coalesced 1<sup>st</sup> article as long as proximal four articles of outer ramus combined).

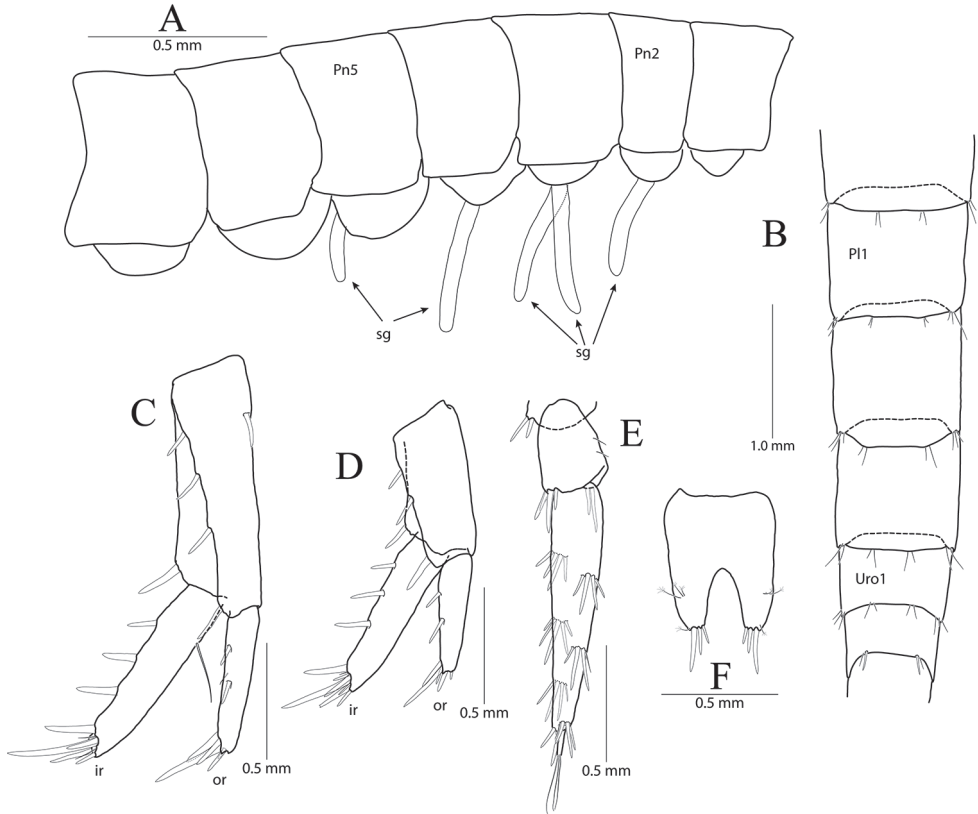
Pleopod 2 (Fig. 3G) peduncle  $1.08 \times$  as long as that of pleopod 1, with one pair of retinaculae mediodistally and one pair of simple setae laterodistally; outer ramus as long as peduncle, composed of nine articles; inner ramus as long as outer ramus, composed of seven articles (coalesced 1<sup>st</sup> article as long as proximal four articles of outer ramus combined).

Pleopod 3 (Fig. 3H)  $1.11 \times$  as long as pleopod 2; peduncle  $0.91 \times$  as long as that of pleopod 2, with one pair of retinaculae mediodistally and one pair of simple setae laterodistally; outer ramus  $1.36 \times$  as long as peduncle, composed of ten articles; inner ramus  $1.21 \times$  as long as outer ramus, composed of ten articles (coalesced 1<sup>st</sup> article  $1.20 \times$  as long as proximal two articles of outer ramus combined).

Uropod 1 (Fig. 4C) peduncle with one basofacial seta, with three marginal robust setae and one distal robust seta dorsolaterally, with one distal robust seta dorsomedially; outer ramus  $0.59 \times$  as long as peduncle, with one simple seta dorsomedially and two robust setae dorsolaterally, apical cluster composed of five robust setae; inner ramus  $1.32 \times$  as long as outer ramus, with three robust setae dorsomedially, apical cluster composed of five robust and two simple setae, with one elongate seta on ventral margin subproximally.

Uropod 2 (Fig. 4D)  $0.70 \times$  as long as uropod 1; peduncle  $0.62 \times$  as long as that of uropod 1, with one marginal seta and one distal seta on both lateral and medial margins; outer ramus  $0.77 \times$  as long as peduncle, with two robust setae dorsolaterally, apical cluster composed of five robust setae; inner ramus  $1.35 \times$  as long as outer ramus, with three robust setae dorsomedially, apical cluster composed of one simple seta and six robust setae (apex of one robust seta abnormal).

Uropod 3 (Fig. 4E) uniramous,  $0.91 \times$  as long as uropod 1; peduncle short,  $0.58 \times$  as long as that of uropod 2, with two minute setae on medial margin, with two setal



**Figure 4.** *Pseudocrangonyx concavus* sp. nov. Holotype: female, NIBRV0000862807, 9.2 mm, from Hwan-sangul Cave, South Korea. **A** sternal gills **B** pleonites and urosomites, dorsal **C** uropod 1 **D** uropod 2 **E** uropod 3 **F** telson. Abbreviations: Pl, pleonite; Uro, urosomite; sg, sternal gill; ir, inner ramus; and or, outer ramus.

clusters on mediobasal and laterobasal corners; ramus  $3.1 \times$  as long as peduncle, bi-articulate, proximal article gradually diminished in width, with three lateral and four medial clusters of setae (longest one of distal cluster exceeding distal article of ramus), distal article  $0.13 \times$  as long as proximal article, with three simple setae apically.

Telson (Fig. 4F)  $0.78 \times$  as wide as long, cleft for 43% of length, each lobe with one cluster of two or three penicillate setae dorsally, and one penicillate seta and three robust setae on apex.

**Remarks.** *Pseudocrangonyx concavus* sp. nov. resembles *Pseudocrangonyx asiaticus* sensu Uéno (1934), but differs in the absence of calceoli in the flagellum of antenna 1 (compared to the slender calceoli present in that of *P. asiaticus*), in the presence of seven dentate setae on the apical margin of outer plate (compared to five in *P. asiaticus*) and eight setae apically on the palp of maxilla 1 (compared to four in *P. asiaticus*), by the more expanded basis of pereopods 5–7, by bearing sternal gills from pereonites 2 to 5 of 1+2+1+1 in formulae, by the presence of three and four setae on posterior margins of epimeral plates 2 and 3, respectively (compared to six and seven setae in *P. asiaticus*),

by the emarginated posteroventral margin of epimeral plate 3 (not emarginated in *P. asiaticus*), by the presence of only one subproximal elongate seta on the ventral margin of the inner ramus on uropod 1 (compared to four in *P. asiaticus*), and by the longer peduncle of uropod 2 than that of *P. asiaticus* (Uéno 1934).

***Pseudocrangonyx gracilipes* sp. nov.**

<http://zoobank.org/57FD3300-7429-4122-9A63-828E0F4C75C4>

Figs 5–8

**Korean name.** Ga-neun-da-ri-dong-gul-yeop-sae-u, new

**Type locality.** Gosugul Cave, Danyang-gun, Chungcheongbuk-do, South Korea; 36°59'12"N, 128°22'52"E.

**Material examined.** Type material. **Holotype:** 1 female, 9.9 mm, NIBRIV0000862808, 19 Jan 2001. **Paratype:** 1 male, 1.4 mm, NIBRIV0000872410, 11 Nov 1973; 1 male and 1 female, NIBRIV0000872411, 27 Sep 1975. All type materials were collected by YG Choi.

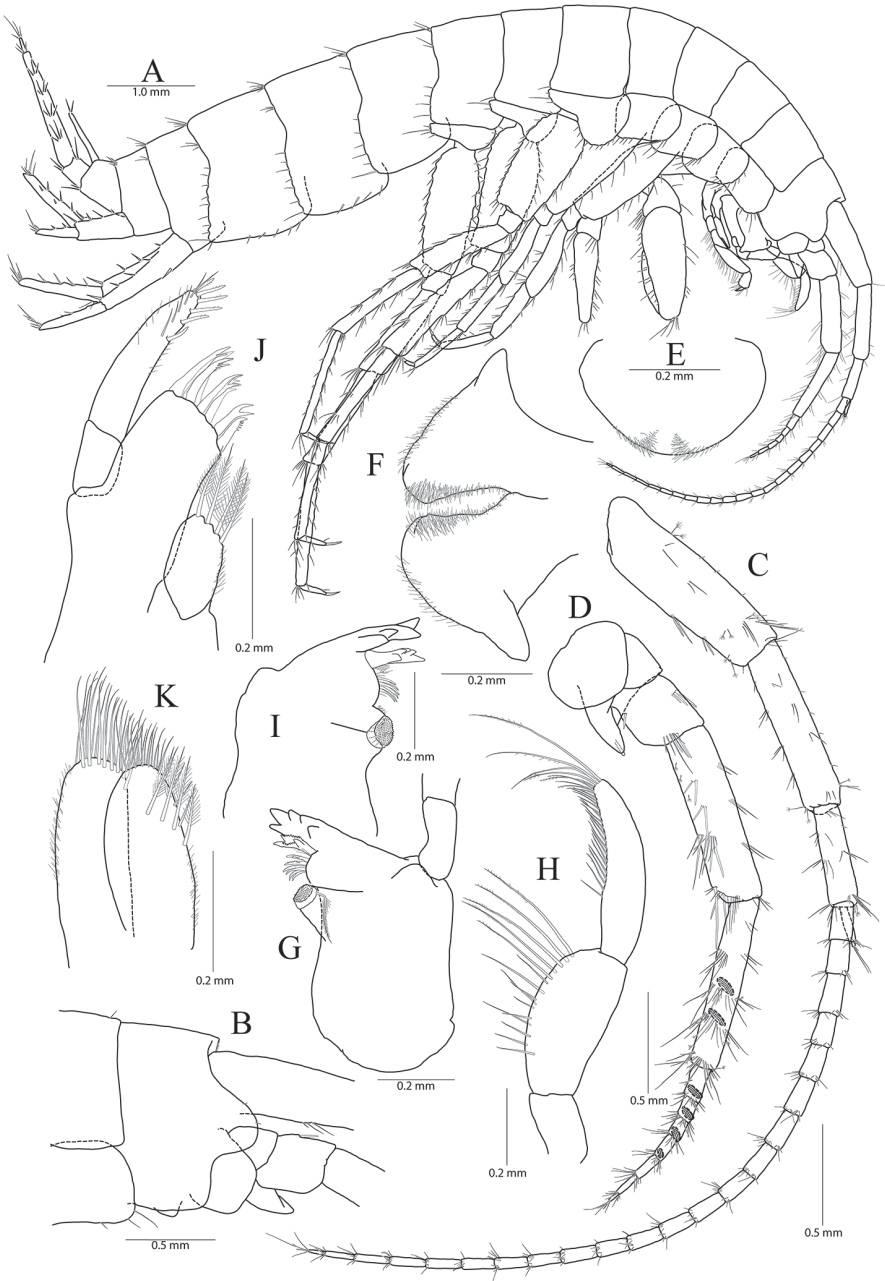
**Etymology.** The specific name originates from the combination of the Latin word *gracilis*, meaning slender, thin and *pes*, meaning foot. This name refers to the shape of the elongate pereopods that are more evident than those of other pseudocrangonyctids.

**Diagnosis.** Maxilla 1 inner lobe with four plumose setae on apical margin; 2<sup>nd</sup> palp article apex with six robust setae (weakly dentate). Maxilla 2 inner lobe with one oblique row of four plumose setae on surface; outer lobe apical margin without plumose setae. Maxilliped inner lobe with three dentate robust setae on apex. Gnathopod 1 carpus 0.55 × as long as basis, with one pair of robust setae marginally on anterior margin, carpal lobe with three rastellate setae. Gnathopod 2 as long as gnathopod 1, carpal lobe with one cluster of three rastellate setae subdistally. Pereopods 5–7 articles slightly slender and elongate. Sternal gills present from pereonites 2–5 (1+1+1+1 in formulae). Epimeral plate 2 ventral margin with four submarginal setae anteriorly, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 3 posterior margin with eight setae, posterodistal corner produced backward, with weak notch, bearing one elongate seta, ventral margin with five submarginal setae anteriorly, not concave. Pleopods 1–3 peduncles with robust setae laterally. Uropod 1 inner ramus with two elongate setae subproximally on ventral margin. Telson 0.63 × as wide as long, cleft for 47% of length.

**Description.** Holotype female: Body (Fig. 5A) approximately 9.9 mm long.

Head (Fig. 5B) 0.76 × as long as pereonite 1; rostrum reduced, with minute setae; lateral cephalic lobe anteriorly expanded, apex rounded, slightly dilated anteroventrally; antennal sinus not deep; eye absent.

Antenna 1 (Fig. 5C) 0.53 × as long as body; 1<sup>st</sup>–3<sup>rd</sup> peduncular articles length ratio of 1.00 : 0.86 : 0.48; 1<sup>st</sup> article stout, with two pairs of robust setae on posterior margin; accessory flagellum bi-articulate, last article very reduced, with one cluster of simple setae distally; flagellum 1.45 × as long as peduncles, composed of 22 articles, calceoli absent, aesthetascs present from 16<sup>th</sup>–20<sup>th</sup> and last articles.



**Figure 5.** *Pseudocrangonyx gracilipes* sp. nov. Holotype: female, NIBRV0000862808, 9.9 mm, from Gosugul Cave, South Korea. **A** habitus **B** head **C** antenna 1 **D** antenna 2 **E** upper lip **F** lower lip **G, H** right mandible **I** left mandible **J** maxilla 1 **K** maxilla 2.

Antenna 2 (Fig. 5D)  $0.51 \times$  as long as antenna 1; antennal cone developed, apex rounded; 4<sup>th</sup> peduncular article  $0.97 \times$  as long as 2<sup>nd</sup> peduncular article of antenna 1, margins parallel,  $0.25 \times$  wider than long, densely setose with several rows or clusters

of various setae; 5<sup>th</sup> article  $1.00 \times$  as long and  $0.67 \times$  as wide as 4<sup>th</sup> article, two calceoli present on medial surface, also densely setose with several rows or clusters of various setae; flagellum composed of seven articles,  $0.91 \times$  as long as 5<sup>th</sup> peduncular article, single calceoli present from 1<sup>st</sup>–4<sup>th</sup> articles medially, aesthetascs absent.

Upper lip (Fig. 5E) anteriorly rounded, apex covered with minute setae, not notched.

Lower lip (Fig. 5F) inner lobes indistinct; outer lobes covered with minute setae; mandibular processes developed.

Mandible (Fig. 5G–I) incisor 5-dentate on right side and 4-dentate on left side; lacinia mobilis tri-cuspidate (two finely dentate and one not dentate) on right side and bi-furcate (one 4-dentate and the other not dentate) on left side; six raker setae present on both sides; molar process columnar, triturative, with one plumose seta on right side only; palp tri-articulate; 2<sup>nd</sup> article convex and with 15 setae medially; 3<sup>rd</sup> article sub-falcate,  $1.16 \times$  as long as 2<sup>nd</sup> article, lined with 27 setae from medial margin to apex..

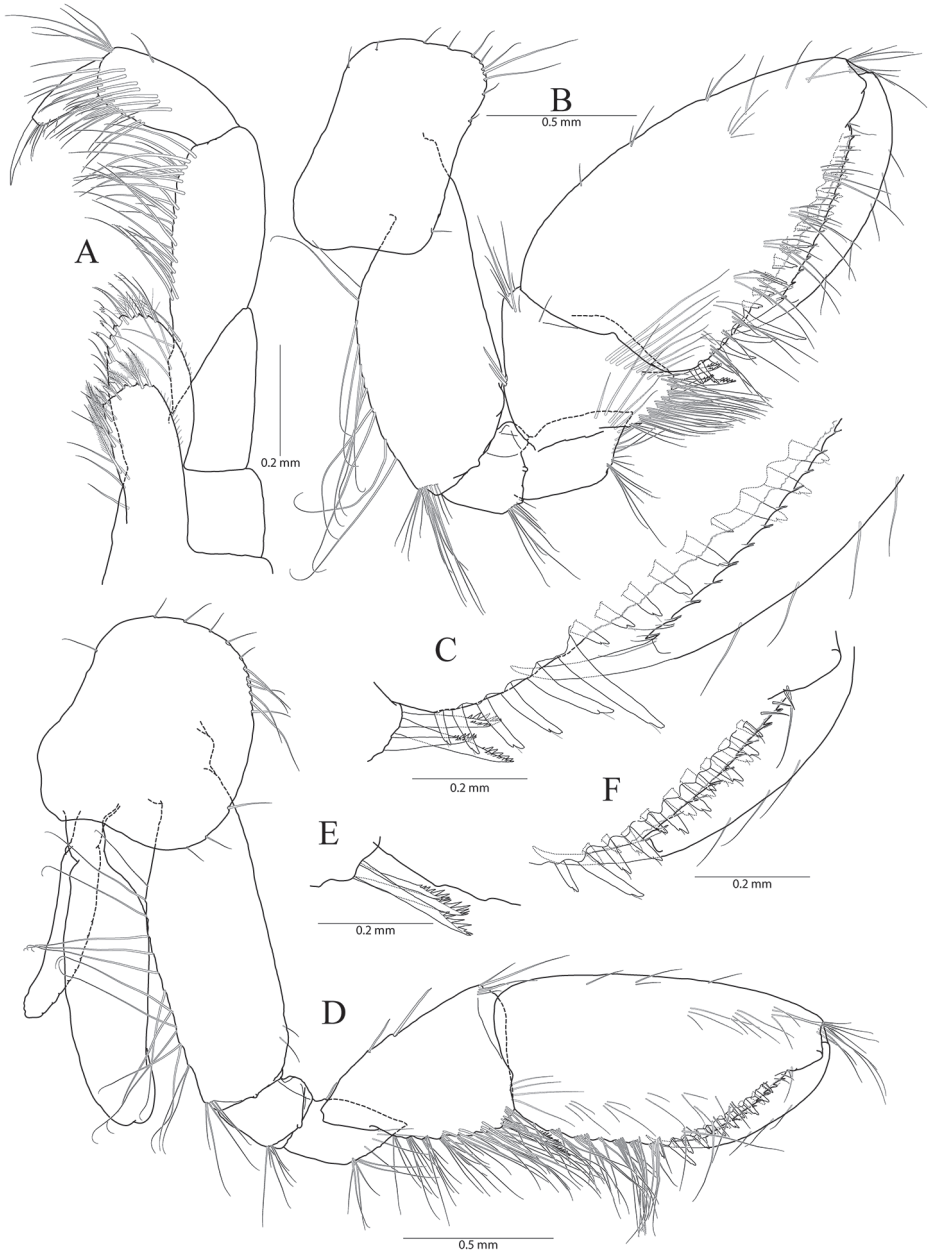
Maxilla 1 (Fig. 5J) inner lobe subrhomboid, with four plumose setae on apical margin; outer lobe with seven dentate robust setae; palp bi-articulate, 2<sup>nd</sup> article apex obviously exceeding apical setae of outer plate, with six robust setae (weakly dentate) along distomedial to apical margins, with one oblique row of six setae subdistally.

Maxilla 2 (Fig. 5K) inner lobe slightly shorter but wider than outer lobe, with one oblique row of four plumose setae on surface and two rows of simple setae on apical margin; outer lobe apical margin also with two rows of simple setae (without plumose setae).

Maxilliped (Fig. 6A) inner lobe subrectangular with three dentate robust setae on apex and eleven plumose setae mediodistally and subapically; outer lobe elongate semicircular,  $0.62 \times$  as long as 2<sup>nd</sup> palp article, lined with four dentate robust setae (one distal seta smallest) and four plumose setae apically; palp composed of four articles; 2<sup>nd</sup> article with many setae on medial margin; 3<sup>rd</sup> article slightly dilated distally,  $0.56 \times$  as long as 2<sup>nd</sup> article; 4<sup>th</sup> article falcate,  $0.61 \times$  as long as 3<sup>rd</sup> article, apical setae  $0.76 \times$  as long as 4<sup>th</sup> article.

Gnathopod 1 (Fig. 6B, C) coxa subrectangular,  $1.52 \times$  wider than long, anter-oventral corner slightly produced with nine setae marginally, ventral margin a little concaved, with one seta posteriorly, posterior margin humped proximally; basis obtuse trapezoidal, posteriorly expanded,  $0.45 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin obliquely truncated distally, without setae; ischium  $0.27 \times$  as long as basis, with small anterior lobe; carpus  $0.55 \times$  as long as basis, with one pair of robust setae marginally and one cluster of simple setae on anterior margin, carpal lobe not developed, apex rounded with three rastellate setae and many simple or serrate setae; propodus subtriangular,  $1.38 \times$  as long and  $1.64 \times$  as wide as basis, with six robust setae laterally along posterior margin (successively increasing distally), palm irregular, finely serrated, lined with nine robust setae medially, defined by largest lateral seta of posterior margin; dactylus exceeding largest lateral seta of posterior margin, inner margin toothed, outer margin with four setae, unguis developed.

Gnathopod 2 (Fig. 6D–F) as long as gnathopod 1; coxa  $1.37 \times$  as long as that of gnathopod 1,  $1.14 \times$  wider than long, anterior and ventral margins not produced, rounded, lined with eleven setae, ventral margin with three setae posteriorly, posterior



**Figure 6.** *Pseudocrangonyx gracilipes* sp. nov. Holotype: female, NIBRV0000862808, 9.9 mm, from Gosugul Cave, South Korea. **A** maxilliped **B** gnathopod 1 **C** rastellate setae and palm of gnathopod 1 **D** gnathopod 2 **E** rastellate setae of gnathopod 2 **F** palm of gnathopod 2.

margin humped proximally; coxal gill present, subovate; oostegite present, narrow, shorter than that of coxal gill, without marginal setae; basis subtrapezoidal, posteriorly expanded,  $0.33 \times$  wider than long, lined with elongate simple setae posteriorly, anterior



margin with two setae subdistally; ischium  $0.21 \times$  as long as basis, with small anterior lobe; carpus  $0.63 \times$  as long as basis, with two robust setae on anterior margin, carpal lobe not developed, broad, with seven clusters of many simple or serrate setae, with one cluster of three rastellate setae subdistally; propodus trapezoidal,  $0.93 \times$  as long and  $1.41 \times$  as wide as basis, anterior margin slightly convex, posterior margin  $0.48 \times$  as long as anterior margin, lined with six clusters of elongate setae, palm irregular, finely serrated, lined with nine medial and eleven lateral robust setae (palm defined by two unequal setae distally among lateral setae); dactylus exceeding palm, inner margin toothed, outer margin with three setae, unguis developed.

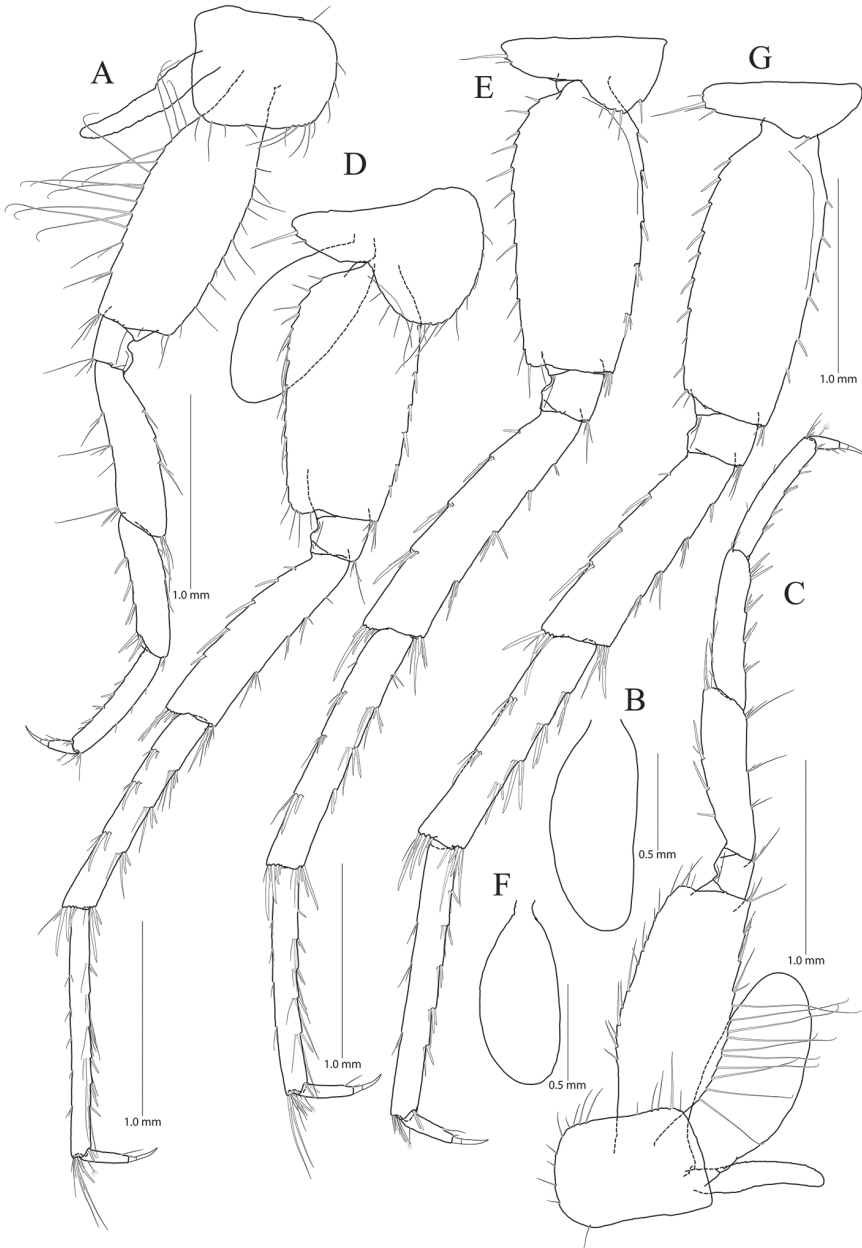
Pereopod 3 (Fig. 7A, B) coxa subrectangular,  $1.27 \times$  wider than long, anteriorly convex, with ten setae anteriorly, ventral margin a little concave, with four setae posteriorly; coxal gill present, subovate; oostegite present, narrow, shorter than that of coxal gill, without marginal setae; basis expanded,  $0.70 \times$  as wide and  $2.55 \times$  as long as coxa, width longest at proximal  $1/3$  and slightly diminished distally, anterior margin lined with simple setae, posterior margin lined with elongate setae; ischium  $0.16 \times$  as long as basis; merus anterodistally expanded,  $0.30 \times$  wider than long,  $0.60 \times$  as long as basis, anterodistal corner produced, apex blunt; carpus not expanded,  $0.48 \times$  as long as basis; propodus linear,  $0.93 \times$  as long as carpus; dactylus  $0.44 \times$  as long as propodus, unguis developed.

Pereopod 4 (Fig. 7C) similar to pereopod 3 except that carpus and propodus  $1.11 \times$  as long as those of pereopod 3; different number or position of several setae.

Pereopod 5 (Fig. 7D) coxa bilobate, anterior lobe larger than posterior lobe, expanded ventrally ( $1.14 \times$  longer than wide), margin rounded, lined with 13 simple setae; posterior lobe with two setae at posterior corner (ventral one short); coxal gill present, subovate; oostegite present, narrow, shorter than that of coxal gill, length shortest, without marginal setae; basis expanded, subrectangular,  $0.46 \times$  wider than long, anterior margin slightly convex, lined with five single robust setae and one pair of robust setae, posterior margin lined with 18 simple setae, distal corner produced and forming angle; merus posterodistally expanded,  $0.40 \times$  as wide and  $0.86 \times$  as long as basis, anterior margin with one simple seta and three clusters of simple setae marginally, and one cluster of setae distally, posterior margin with five single robust setae marginally, and one cluster of robust and simple setae distally; carpus not expanded  $1.00 \times$  as long as basis, anterior and posterior margins with three marginal clusters and one distal cluster of setae, respectively; propodus linear,  $1.11 \times$  as long as carpus, anterior margin with six setal clusters (longest seta of distal cluster not exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with five pairs of short setae marginally and one cluster of elongate setae distally; dactylus slender,  $0.32 \times$  as long as propodus, unguis developed.

Pereopod 6 (Fig. 7E, F)  $1.12 \times$  as long as pereopod 5; coxa bilobate, anterior lobe  $0.60 \times$  as long as that of pereopod 5, with four setae on ventral margin, posterior lobe expanded backward, with two setae at posterior corner (ventral one very short); coxal gill present, subovate; oostegite absent; basis expanded, subrectangular,  $1.13 \times$  as long and  $1.08 \times$  as wide as that of pereopod 5,  $0.46 \times$  wider than long, anterior margin slightly convex, lined with three single robust setae and two clusters of robust setae, with one cluster of robust setae at distal corner, posterior margin lined with 14 se-





**Figure 7.** *Pseudocrangonyx gracilipes* sp. nov. Holotype: female, NIBRV0000862808, 9.9 mm, from Gosugul Cave, South Korea. **A** pereopod 3 **B** coxal gill of pereopod 3 **C** pereopod 4 **D** pereopod 5 **E** pereopod 6 **F** coxal gill of pereopod 6 **G** pereopod 7.

tae, posterodistal corner produced forming an angle; merus posterodistally expanded,  $1.24 \times$  as long as that of pereopod 5,  $0.44 \times$  as wide and  $0.95 \times$  as long as basis, anterior and posterior margins with four single setae or clusters of setae marginally and

one cluster of setae distally, respectively; carpus not expanded,  $0.73 \times$  as long as basis, anterior margin with four clusters of setae marginally and one cluster of setae distally, posterior margin with one simple seta and three clusters of simple and robust setae marginally, and one cluster of setae distally; propodus linear,  $0.88 \times$  as long as carpus, anterior margin with one robust seta and four clusters of setae marginally (longest seta of distal cluster not exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with four pairs of short setae marginally and one cluster of elongate setae distally; dactylus  $0.39 \times$  as long as propodus, unguis developed.

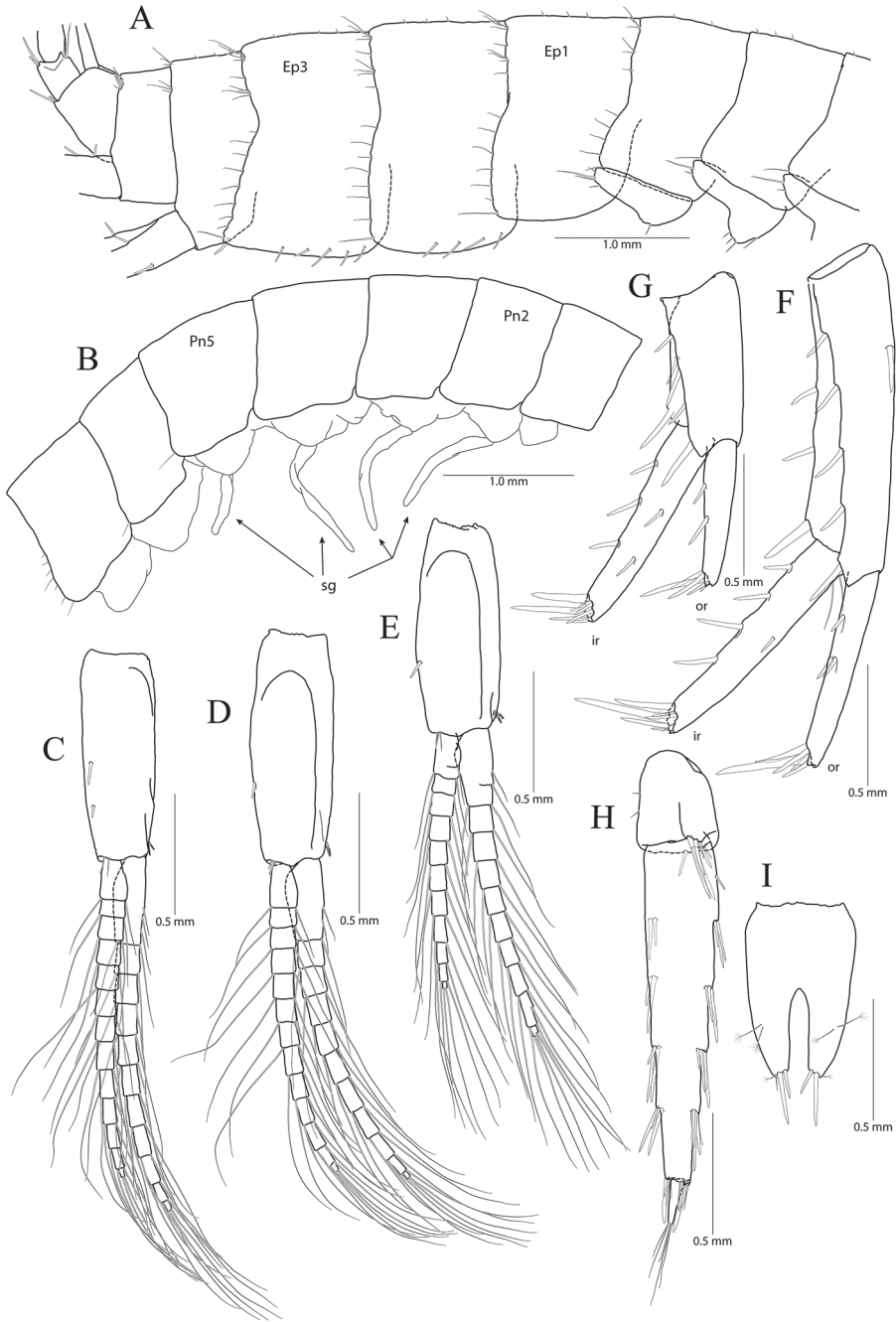
Pereopod 7 (Fig. 7G)  $0.97 \times$  as long as pereopod 6; coxa unilobed, subtriangular,  $0.73 \times$  as long as that of pereopod 6, with one seta on ventral margin, posteriorly expanded with four setae at posterior corner; coxal and oostegite absent; basis expanded, subrectangular,  $1.01 \times$  as long and  $0.87 \times$  as wide as that of pereopod 6,  $0.39 \times$  wider than long, anterior margin slightly convex, lined with six robust setae, with one cluster of setae at distal corner, posterior margin lined with eleven setae, distal corner slightly produced but angle smaller than in pereopods 6 and 7; merus posterodistally expanded,  $0.82 \times$  as long as that of pereopod 6,  $0.57 \times$  as wide and  $0.77 \times$  as long as basis, anterior margin with four marginal clusters and one distal cluster of setae, posterior margin with one single robust seta and three clusters of simple and robust setae marginally, and one cluster of simple and robust setae distally; carpus not expanded, rectangular,  $1.11 \times$  as long as merus, anterior margin with four clusters of setae marginally and one cluster of setae distally, posterior margin with two clusters of setae marginally and one cluster of setae distally; propodus linear,  $1.22 \times$  as long as carpus, anterior margin with five clusters of setae (without elongate setae) and one pair of locking robust setae distally; posterior margin with three pairs of short setae marginally and one cluster of setae distally (shorter than those of pereopods 6 and 7); dactylus  $0.36 \times$  as long as propodus, unguis developed.

Sternal gills (Fig. 8B) present from pereonites 2–5 (1+1+1+1 in formulae), narrower than oostegites, shortest in that of pereonite 5.

Epimeral plate 1 subquadrate, slightly produced posteroventrally, ventral margin without setae, posterior margin with six setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 2 subquadrate, larger than epimeron 1, ventral margin with four submarginal setae anteriorly, posterior margin with seven setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 3 posterior margin with eight setae, posterodistal corner produced backward, with weak notch, bearing one elongate seta, ventral margin with five submarginal setae anteriorly, not emarginated (Fig. 8A).

Pleopod 1 (Fig. 8C) peduncle with one pair of retinaculae mediodistally and one pair of simple setae laterodistally, with two robust setae laterally; outer ramus  $1.55 \times$  as long as peduncle, composed of 13 articles; inner ramus  $1.75 \times$  as long as peduncle, composed of eleven articles (coalesced 1<sup>st</sup> article as long as proximal three articles of outer ramus combined).

Pleopod 2 (Fig. 8D) peduncle  $1.11 \times$  as long as that of pleopod 1, with one pair of retinaculae mediodistally and one pair of simple setae laterodistally, with one robust



**Figure 8.** *Pseudocrangonyx gracilipes* sp. nov. Holotype: female, NIBRV0000862808, 9.9 mm, from Gosugul Cave, South Korea. **A** epimeral plates 1–3 **B** sternal gills **C** pleopod 1 **D** pleopod 2 **E** pleopod 3 **F** uropod 1 **G** uropod 2 **H** uropod 3 **I** telson. Abbreviations: Ep, epimeral plate; Pn, pereonite; sg, sternal gill; ir, inner ramus; and or, outer ramus.

seta laterally; outer ramus  $1.42 \times$  as long as peduncle, composed of 13 articles; inner ramus  $1.48 \times$  as long as peduncle, composed of eleven articles (coalesced 1<sup>st</sup> article  $0.90 \times$  as long as proximal three articles of outer ramus combined).

Pleopod 3 (Fig. 8E)  $0.91 \times$  as long as pleopod 2; peduncle  $0.92 \times$  as long as that of pleopod 2, with one pair of retinaculæ mediodistally and one pair of simple setae laterodistally, with one robust seta laterally; outer ramus  $1.20 \times$  as long as peduncle, composed of eleven articles, 1<sup>st</sup> article not fully coalesced and with trace; inner ramus  $1.46 \times$  as long as outer ramus, composed of ten articles, 1<sup>st</sup> article not fully coalesced and with trace, 9<sup>th</sup> and 10<sup>th</sup> articles coalesced.

Uropod 1 (Fig. 8F) peduncle with one basofacial seta, with four marginal setae and one distal seta dorsolaterally, with two marginal setae and one distal seta dorsomedially; outer ramus  $0.63 \times$  as long as peduncle, with one robust seta dorsomedially and two robust setae dorsolaterally, apical cluster composed of five robust setae; inner ramus  $1.15 \times$  as long as outer ramus, with one robust seta dorsolaterally and four robust setae dorsomedially, apical cluster composed of five robust setae and one simple and one penicillate seta, with two elongate setae subproximally on ventral margin.

Uropod 2 (Fig. 8G)  $0.59 \times$  as long as uropod 1; peduncle  $0.52 \times$  as long as that of uropod 1, with three marginal setae and one distal seta dorsolaterally, with one marginal seta and one distal seta dorsomedially; outer ramus  $0.84 \times$  as long as peduncle, with two robust setae dorsolaterally, apical cluster composed of five robust setae; inner ramus  $1.50 \times$  as long as outer ramus, with two robust setae dorsolaterally and three robust setae dorsomedially, apical cluster composed of seven robust setae and one penicillate seta.

Uropod 3 (Fig. 8H) uniramous,  $0.83 \times$  as long as uropod 1; peduncle short,  $0.55 \times$  as long as uropod 2, with two minute setae on medial margin, with one dorsal and one ventral cluster of robust setae laterodistally; ramus  $4.17 \times$  as long as peduncle, bi-articulate, proximal article gradually diminished distally, with five lateral and five medial clusters of setae (longest seta of each distal cluster exceeding end of last article), distal article  $0.13 \times$  as long as proximal article, with five simple setae apically.

Telson (Fig. 8I)  $0.63 \times$  as wide as long, cleft for 47% of length, each lobe with one pair of penicillate setae dorsally, and one penicillate seta and two robust setae on apex.

**Remarks.** *Pseudocrangonyx gracilipes* sp. nov. resembles with its several congeners including *P. bohaensis* (Derzhavin, 1927), *P. yezonis* Akatsuka & Komai, 1992, *P. relicta* Labay, 1999, and *P. camtschaticus* Birstein, 1955 in having the notched posterodistal corners of epimeral plates 2 and 3. However, this new species is distinguished from these species by the more produced posterodistal corner of epimeral plate 3 (Birstein 1955, Akatsuka and Komai 1992, Labay 1999).

This character state of the epimeral plates is also observed in *P. villosus* sp. nov., but *P. gracilipes* sp. nov. has four plumose setae on the inner plate of maxilla 1 (compared to seven in *P. villosus* sp. nov.), four plumose setae on inner plate of maxilla 2 (compared to ten in *P. villosus* sp. nov.), both three rastellate setae on gnathopods 1 and 2 (compared to two rastellate setae in *P. villosus* sp. nov.), and the presence of the more slender and elongated pereopods 5–7.

***Pseudocrangonyx crassus* sp. nov.**

<http://zoobank.org/BE3227BA-231F-4FA5-B280-B814B7C4C95E>

Figs 9–12

**Korean name.** Keun-deo-deum-i-dong-gul-yeop-sae-u, new

**Type locality.** Gossigul Cave, Yeongwol-gun, Gangwon-do, South Korea; 37°08'00"N, 128°31'21"E.

**Material examined.** Type material. **Holotype:** 1 male, 10.6 mm, NI-BRIV0000862809, collected from the type locality on 19 Jan 2001 by YG Choi.

**Etymology.** The specific name originates from the Latin word *crassus* meaning thick. This name refers to the shape of the 4<sup>th</sup> and 5<sup>th</sup> articles of antenna 2.

**Diagnosis.** Antenna 2, 4<sup>th</sup> and 5<sup>th</sup> peduncular articles expanded, plump medially, calceoli and aesthetascs absent. Maxilla 1 inner lobe with five plumose setae on apical margin; 2<sup>nd</sup> palp article with six robust setae along distomedial to apical margins. Maxilla 2 inner lobe with one oblique row of five plumose setae on surface; outer lobe without plumose setae. Gnathopods 1 and 2 each possessing carpus with three rastellate setae, respectively. Pereopods 3 and 4 basis bearing elongate setae on posterior margins. Sternal gills present on pereonites 2, 3, and 5 (1+1+0+1 in formulae). Epimeral plate 3 posteroventral corner slightly produced. Telson cleft for 39% of length.

**Description.** Holotype male: Body (Fig. 9A) approximately 10.6 mm long.

Head (Fig. 9B) 1.30 × as long as pereonite 1; rostrum reduced, with one minute seta; lateral cephalic lobe anteriorly expanded, apex rounded, slightly dilated anteroventrally; antennal sinus not deep; eye absent.

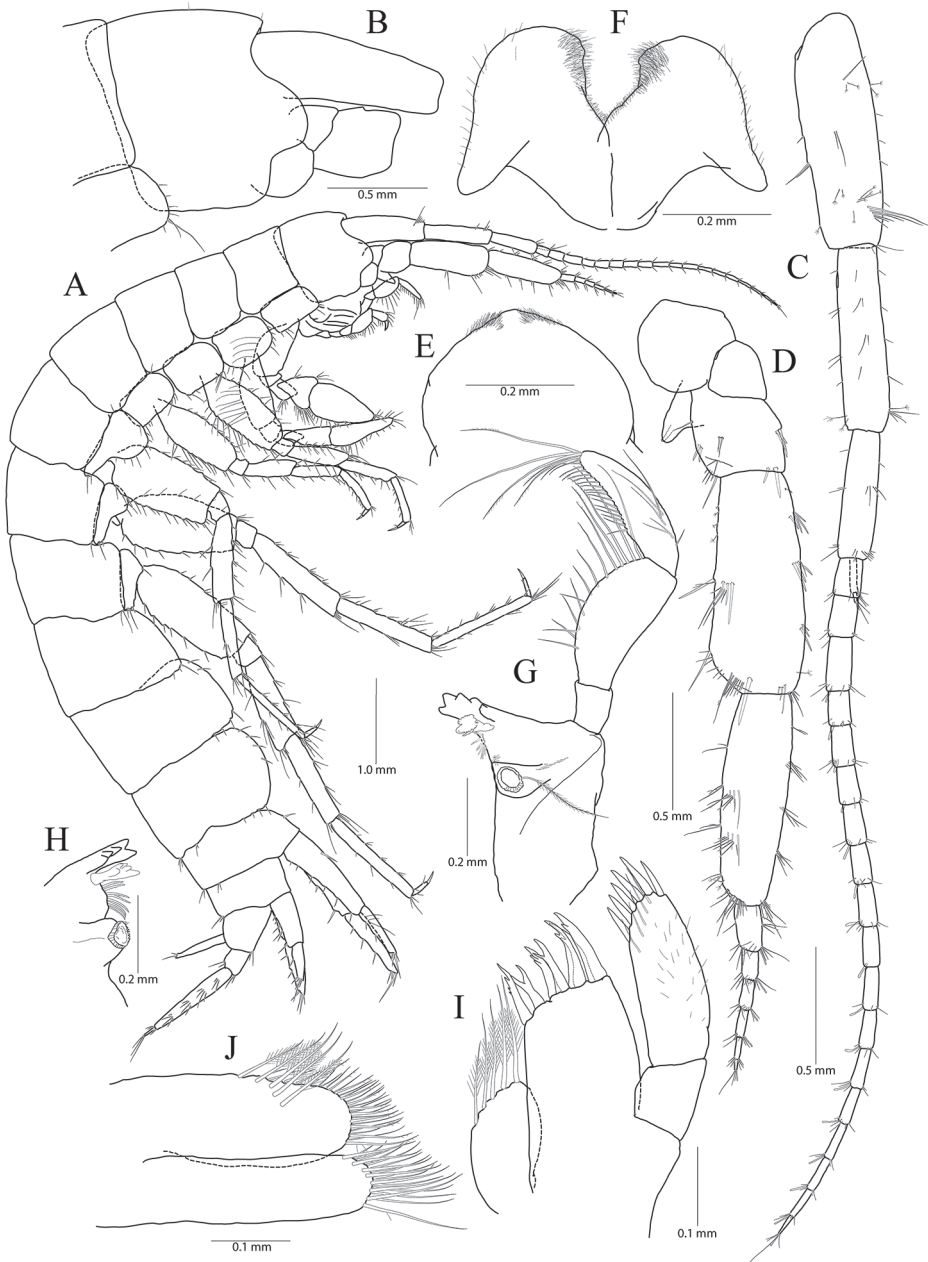
Antenna 1 (Fig. 9C) 0.50 × as long as body; 1<sup>st</sup>–3<sup>rd</sup> peduncular articles length ratio of 1.00 : 0.80 : 0.56; 1<sup>st</sup> article stouter than 2<sup>nd</sup> and 3<sup>rd</sup> articles, without robust setae on posterior margin; accessory flagellum bi-articulate, last article very reduced; flagellum 1.28 × as long as peduncles, composed of 18 articles, calceoli absent, aesthetascs present from proximal 3<sup>rd</sup> to last articles.

Antenna 2 (Fig. 9D) 0.62 × as long as antenna 1; antennal cone developed, apex rounded; 4<sup>th</sup> and 5<sup>th</sup> peduncular articles expanded, plump medially; 4<sup>th</sup> article 0.93 × as long as 1<sup>st</sup> peduncular article of antenna 1, anterior margin convex, with three clusters of robust setae, posterior margin distally expanded, rounded posterodistally; 5<sup>th</sup> article expanded at the middle, 0.98 × as long and 0.69 × as wide as 4<sup>th</sup> article, calceoli absent; flagellum composed of six articles, 0.77 × as long as 5<sup>th</sup> peduncular article; calceoli and aesthetascs absent.

Upper lip (Fig. 9E) anteriorly rounded, apex covered with minute setae, not notched.

Lower lip (Fig. 9F) inner lobes indistinct; outer lobes covered with minute setae; mandibular processes developed.

Mandible (Fig. 9G, H) incisor 5-dentate on both sides; lacinia mobilis tri-cuspidate (two finely dentate and one not dentate) on right and bi-furcate (one 4-dentate and the other not dentate) on left side; seven and eight raker setae present on right and left sides; molar process columnar, triturative, with one plumose seta on right side only; palp tri-articulate; 2<sup>nd</sup> article convex and with 14 setae medially; 3<sup>rd</sup> article subfalcate, 1.2 × as long as 2<sup>nd</sup> article, medial margin lined with 23 setae from medial margin to apex.



**Figure 9.** *Pseudocrangonyx crassus* sp. nov. Holotype: male, NIBRV0000862809, 10.6 mm, from Gosugul Cave, South Korea. **A** habitus **B** head **C** antenna 1 **D** antenna 2 **E** upper lip **F** lower lip **G** right mandible **H** left mandible **I** maxilla 1 **J** maxilla 2.

Maxilla 1 (Fig. 9I) inner lobe subrhomboid, with five plumose setae on apical margin; outer lobe with seven dentate robust setae; palp bi-articulate, 2<sup>nd</sup> article apex



slightly exceeding apical setae of outer plate, with six robust setae along distomedial to apical margins, with one oblique row of five setae subdistally.

Maxilla 2 (Fig. 9J) inner lobe slightly shorter but wider than outer lobe, with one oblique row of five plumose setae on surface and two rows of simple setae on apical margin; outer lobe apical margin also with two rows of simple setae (without plumose setae).

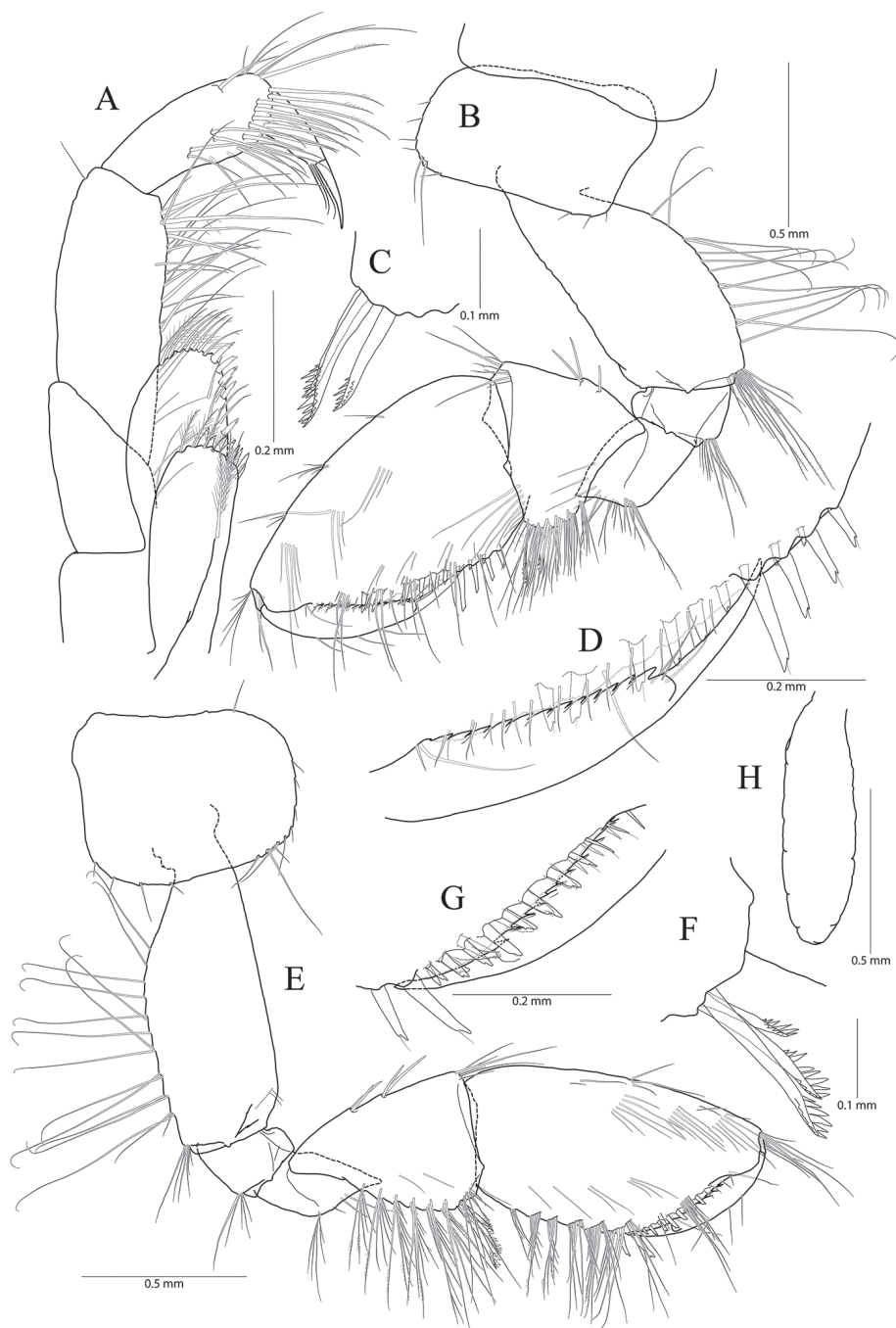
Maxilliped (Fig. 10A) inner lobe subrectangular, with eight dentate robust setae on apex and eight plumose setae mediodistally and subapically; outer lobe elongate semicircular,  $0.70 \times$  as long as  $2^{\text{nd}}$  palp article, with five dentate robust setae and seven weakly plumose setae apically; palp composed of four articles;  $2^{\text{nd}}$  article with many setae on medial margin;  $3^{\text{rd}}$  article slightly dilated distally,  $0.70 \times$  as long as  $2^{\text{nd}}$  article;  $4^{\text{th}}$  article falcate,  $0.49 \times$  as long as  $3^{\text{rd}}$  article, apical setae  $0.76 \times$  as long as  $4^{\text{th}}$  article.

Gnathopod 1 (Fig. 10B-D) coxa subrectangular,  $1.63 \times$  wider than long, anteroventral corner not produced, rounded, with seven setae marginally, ventral margin slightly concave, with three setae posteriorly, posterior margin humped proximally; basis obtuse trapezoidal, posteriorly expanded,  $0.49 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin without setae; ischium  $0.28 \times$  as long as basis, with small anterior lobe; carpus  $0.62 \times$  as long as basis, with one single seta and one pair of robust setae on anterior margin, carpal lobe not developed, apex rounded with three rastellate setae and many simple or serrate setae; propodus subovate,  $1.24 \times$  as long and  $1.39 \times$  as wide as basis, posterior margin short,  $0.24 \times$  as long as anterior margin, with four robust setae laterally along posterior margin distally and nine robust setae medially along posterior margin and palm (all medial setae small, but lateral setae larger and successively increasing distally), palm irregular, finely serrated, defined by largest lateral seta of posterior margin; dactylus as long as palm, apex reaching largest lateral seta of posterior margin, inner margin toothed, outer margin with four setae, unguis developed.

Gnathopod 2 (Fig. 10E-H)  $1.07 \times$  as long as gnathopod 1; coxa  $1.29 \times$  as long as that of gnathopod 1,  $1.29 \times$  wider than long, anterior and ventral margins not produced, rounded, lined with eight setae, ventral margin with four setae posteriorly, posterior margin humped proximally; coxal gill present, subovate; basis subtrapezoidal, posteriorly expanded,  $0.92 \times$  as wide as that of gnathopod 1,  $0.36 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin with two setae subdistally; ischium  $0.23 \times$  as long as basis, with small anterior lobe; carpus  $0.60 \times$  as long as basis, with two pairs of robust setae on anterior margin, carpal lobe not developed, broad, with seven clusters of many simple or serrate setae, with three rastellate setae distally; propodus trapezoidal,  $0.93 \times$  as long and  $1.31 \times$  as wide as basis, anterior margin slightly convex, posterior margin  $0.52 \times$  as long as anterior margin, lined with six clusters of elongate setae, palm irregular, finely serrated, lined with six medial and nine lateral robust setae (palm defined by two unequal setae distally among lateral setae); dactylus as long as palm, inner margin toothed, outer margin with three setae, unguis developed.

Pereopod 3 (Fig. 11A) coxa rectangular,  $1.35 \times$  wider than long, with ten setae anteriorly and three setae posteroventrally, ventral margin a little concave; coxal gill present, subovate; basis expanded,  $0.78 \times$  as wide and  $2.65 \times$  as long as coxa, width longest at proximal  $1/3$  and slightly diminished distally, anterior margin slightly convex, lined with nine simple setae, posterior margin lined with 18 elongate setae; ischium  $0.16 \times$  as long as basis;





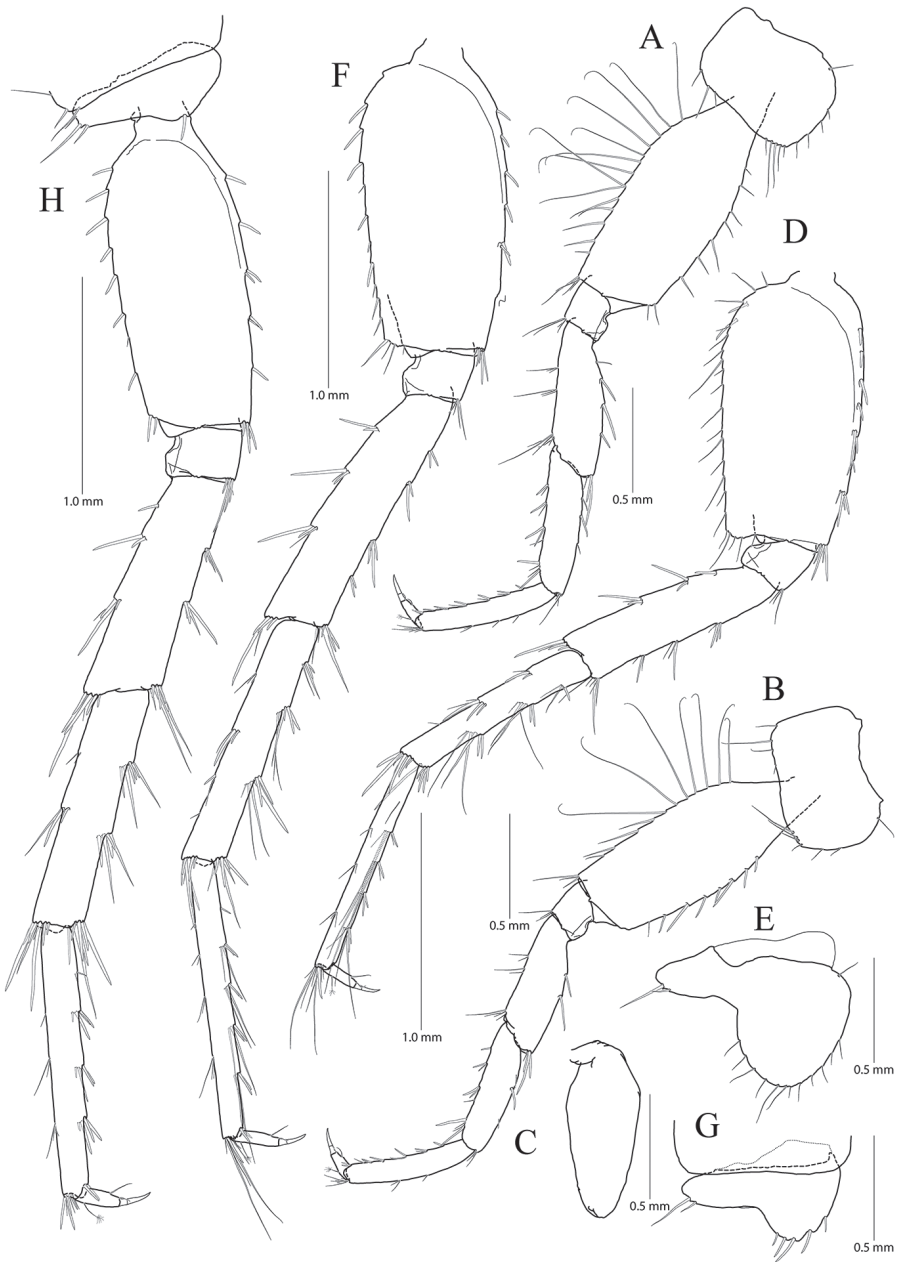
**Figure 10.** *Pseudocrangonyx crassus* sp. nov. Holotype: male, NIBRV0000862809, 10.6 mm, from Gos-sigul Cave, South Korea. **A** maxilliped **B** gnathopod 1 **C** rastellate setae gnathopod 1 **D** and palm of gnathopod 1 **E** gnathopod 2 **F** rastellate setae of gnathopod 2 **G** palm of gnathopod 2 **H** coxal gill of gnathopod 2.

merus anterodistally expanded,  $0.36 \times$  wider than long,  $0.51 \times$  as long as basis, anterodistal corner produced, apex blunt; carpus not expanded,  $1.00 \times$  as long as merus; propodus linear,  $1.06 \times$  as long as carpus; dactylus  $0.43 \times$  as long as propodus, unguis developed.

Pereopod 4 (Fig. 11B, C) each article similar to but slightly shorter than those of pereopod 3, except for the number and positions of several setae.

Pereopod 5 (Fig. 11D, E) coxa with additional tumid lobe proximally, bilobate, anterior lobe larger than posterior lobe, expanded ventrally ( $1.09 \times$  longer than wide), margin rounded, lined with twelve simple setae; posterior lobe with two setae at posterior corner (ventral one very short); coxal gill present, subovate; basis expanded, subrectangular,  $0.52 \times$  wider than long, anterior margin slightly convex, lined with five single robust setae and two clusters of robust setae, with one cluster of elongate setae at distal corner, posterior margin lined with 21 simple setae, with two submarginal robust setae proximally, distal corner produced forming an angle; merus posterodistally expanded,  $0.38 \times$  as wide and  $0.78 \times$  as long as basis, anterior margin with three clusters of setae marginally and one cluster of setae distally, posterior margin with one single robust seta and two clusters of setae marginally, and one cluster of setae distally; carpus not expanded,  $0.92 \times$  as long as merus, anterior margin with two clusters of setae and one single seta marginally, and one cluster of setae distally, posterior margin with three clusters bearing elongate simple setae marginally and one cluster of setae distally; propodus linear,  $1.17 \times$  as long as carpus, anterior margin with six setal clusters (all clusters with elongate setae and those of distal cluster exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with three marginal clusters of short setae and one cluster of elongate setae distally; dactylus slender,  $0.29 \times$  as long as propodus, unguis developed.

Pereopod 6 (Fig. 11F, G)  $1.21 \times$  as long as pereopod 5; coxa with additional tumid lobe proximally, bilobate, anterior lobe  $0.80 \times$  as long as that of pereopod 5, with five robust setae on ventral margin, posterior lobe expanded backward, with two setae at posterior corner (ventral one short); coxal gill present, subovate; basis expanded, subrectangular,  $1.12 \times$  as long and  $1.02 \times$  as wide as that of pereopod 5,  $0.47 \times$  wider than long, anterior margin slightly convex, lined with more than four single robust setae and one clusters of robust setae, with one cluster of setae at distal corner, posterior margin lined with 14 setae, distal corner produced forming an angle; merus posterodistally expanded,  $1.28 \times$  as long as that of pereopod 5,  $0.41 \times$  as wide and  $0.89 \times$  as long as basis, anterior margin with four clusters of setae marginally and one cluster of setae distally, posterior margin with three clusters of setae marginally and one cluster of setae distally; carpus not expanded,  $0.85 \times$  as long as basis, anterior margin with three clusters of setae marginally and one cluster of simple and robust setae distally, posterior margin with one simple seta and three clusters of simple or robust setae marginally, and one cluster of setae distally; propodus linear,  $1.08 \times$  as long as carpus, anterior margin with one single seta and four clusters of setae marginally (longest seta of distal cluster exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with one single seta, four pairs of short setae marginally and one distal cluster of elongate setae distally; dactylus  $0.28 \times$  as long as propodus, unguis developed.



**Figure 11.** *Pseudocrangonyx crassus* sp. nov. Holotype: male, NIBRV0000862809, 10.6 mm, from Gos-sigul Cave, South Korea. **A** pereopod 3 **B** pereopod 4 **C** coxal gill of pereopod 4 **D** pereopod 5 **E** coxa of pereopod 5 **F** pereopod 6 **G** coxal gill of pereopod 7 **H** pereopod 7.

Pereopod 7 (Fig. 11H)  $0.98 \times$  as long as pereopod 6; coxa unilobed, subtriangular,  $0.65 \times$  as long as that of pereopod 6, with one seta on ventral margin, posteriorly expanded with three setae at posterior corner; basis expanded, subrectangular,  $1.17 \times$

as long and  $0.92 \times$  as wide as that of pereopod 6,  $0.41 \times$  wider than long, anterior margin slightly convex, lined with three single robust setae and two clusters of robust setae, with one cluster of setae at distal corner, posterior margin lined with ten setae, distal corner slightly produced but angle smaller than those of pereopods 6 and 7; merus posterodistally expanded,  $0.82 \times$  as long as that of pereopod 6,  $0.55 \times$  as wide and  $0.68 \times$  as long as basis, anterior margin with two clusters of setae marginally and one cluster of setae distally, posterior margin with one single seta and two clusters of setae marginally and one cluster of setae distally; carpus not expanded, rectangular,  $0.22 \times$  as wide as long,  $1.13 \times$  as long as merus, anterior margin with two marginal clusters and one distal cluster of simple and robust setae, posterior margin with two clusters of setae marginally and one cluster of simple and robust setae distally; propodus linear,  $1.10 \times$  as long as carpus, anterior margin with four setal clusters (without elongate setae) marginally and one pair of locking robust setae distally, posterior margin with one single seta and two pairs of short setae marginally, and one cluster of setae distally (shorter than those of pereopods 6 and 7), dactylus  $0.29 \times$  as long as propodus, unguis developed.

Sternal gills (Fig. 12A) present on pereonites 2, 3, and 5 ( $1+1+0+1$  in formulae), narrow, not short in pereonite 5.

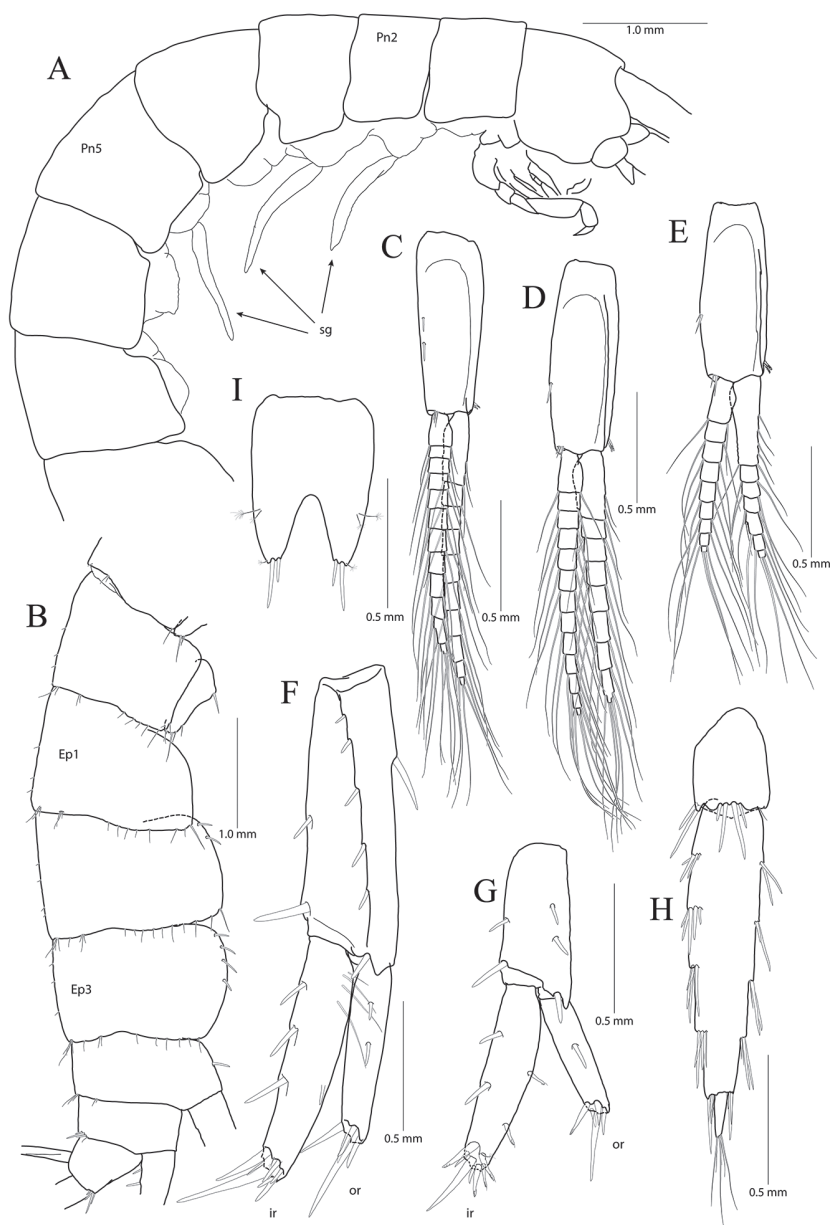
Epimeral plate 1 subquadrate, slightly produced posteroventrally, ventral margin without setae, posterior margin with seven setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 2 subquadrate, larger than epimeron 1, ventral margin with two submarginal setae anteriorly, posterior margin with nine setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 3 posterior margin with six setae, posterodistal corner a little produced and without notch, ventral margin with four submarginal setae anteriorly, not emarginated (Fig. 12B).

Pleopod 1 (Fig. 12C) peduncle with one pair of retinaculae mediodistally and three simple setae laterodistally, with two robust setae laterally; outer ramus  $1.40 \times$  as long as peduncle, composed of twelve articles, 11<sup>th</sup> and 12<sup>th</sup> articles coalesced; inner ramus  $1.54 \times$  as long as peduncle, composed of ten articles (1<sup>st</sup> coalesced article exceeding three proximal articles of outer ramus combined).

Pleopod 2 (Fig. 12D) peduncle  $1.06 \times$  as long as that of pleopod 1, with one pair of retinaculae mediodistally and one cluster of three simple setae laterodistally, with one robust seta laterally; outer ramus  $1.43 \times$  as long as peduncle, composed of 13 articles; inner ramus  $0.92 \times$  as long as outer ramus, composed of eight articles (1<sup>st</sup> coalesced article exceeding two proximal articles of outer ramus combined, last articles coalesced).

Pleopod 3 (Fig. 12E)  $0.78 \times$  as long as pleopod 2; peduncle  $0.95 \times$  as long as that of pleopod 2, with one pair of retinaculae mediodistally and one pair of simple setae laterodistally, with one pair of setae laterally; outer ramus  $1.00 \times$  as long as peduncle, composed of nine articles, 1<sup>st</sup> article not fully coalesced and with trace; inner ramus  $1.06 \times$  as long as outer ramus, composed of seven articles, 1<sup>st</sup> article not fully coalesced and with trace, 5<sup>th</sup> article coalesced.

Uropod 1 (Fig. 12F) peduncle with one basofacial seta, with five marginal setae and one distal seta dorsolaterally, with one marginal seta and one distal seta dorsomedially; outer ramus  $0.60 \times$  as long as peduncle, with two robust setae dorsolaterally, apical cluster com-



**Figure 12.** *Pseudocrangonyx crassus* sp. nov. Holotype: male, NIBRV0000862809, 10.6 mm, from Gos-sigul Cave, South Korea. **A** sternal gills **B** epimeral plates 1–3 **C** pleopod 1 **D** pleopod 2 **E** pleopod 3 **F** uropod 1 **G** uropod 2 **H** uropod 3 **I** telson. Abbreviations: Ep, epimeral plate; Pn, pereonite; sg, sternal gill; ir, inner ramus; and or, outer ramus.

posed of five robust setae; inner ramus  $1.31 \times$  as long as outer ramus, with one robust seta dorsolaterally and three robust setae dorsomedially, apical cluster composed of seven robust setae and one penicillate seta, with four elongate setae on ventral margin subproximally.

Uropod 2 (Fig. 12G)  $0.63 \times$  as long as uropod 1; peduncle  $0.55 \times$  as long as that of uropod 1, with two marginal setae and one distal seta dorsolaterally, with one distal seta and one marginal seta dorsomedially; outer ramus  $0.76 \times$  as long as peduncle, with one robust seta dorsolaterally, apical cluster composed of five robust setae (one of them with abnormal apex); inner ramus  $1.52 \times$  as long as outer ramus, with two robust setae (bearing abnormal apices) dorsolaterally and two robust setae dorsomedially, apical cluster composed of seven robust setae (three of them with abnormal apices) and one penicillate seta.

Uropod 3 (Fig. 12H) uniramous,  $0.85 \times$  as long as uropod 1; peduncle short,  $0.61 \times$  as long as uropod 2, distal margin with one dorsal and one medial clusters of robust setae; ramus  $3.25 \times$  as long as peduncle, bi-articulate, proximal article gradually diminished in width, with five lateral and five medial clusters of setae (longest seta of each distal cluster exceeding end of last article), distal article  $0.16 \times$  as long as proximal article, with six simple setae apically.

Telson (Fig. 12I)  $0.73 \times$  as wide as long, cleft for 39% of length, each lobe with one pair of penicillate setae dorsally, and one penicillate seta and two robust setae on apex.

**Remarks.** *Pseudocrangonyx crassus* sp. nov. is very similar to *P. tiunovi* Sidorov & Gontcharov, 2013 in having expanded peduncular articles and a reduced flagellum of antenna 2, in addition to bearing similarities in the general shape and length ratio of the articles in the gnathopods and pereopods. However, this new species differs from *P. tiunovi* by possessing more expanded 4<sup>th</sup> and 5<sup>th</sup> peduncular articles of antenna 2, longer palp articles of maxilla 1 bearing more robust setae (six in *P. crassus* sp. nov. compared to four in *P. tiunovi*), a longer 3<sup>rd</sup> palp article on the maxilliped compared to *P. tiunovi*, three rastellate setae in both gnathopods 1 and 2 (one and two on gnathopods 1 and 2, respectively, in *P. tiunovi*), more elongate setae on the basis posterior margins on pereopods 3 and 4, a more expanded anterior lobe of coxa 5, a slightly produced poster-ventral corner of epimeral plate 3 (more produced in *P. tiunovi*), and a telson cleft for 39% of length (cleft for 20% of length in *P. tiunovi*) (Sidorov and Gontcharov 2013).

***Pseudocrangonyx minutus* sp. nov.**

<http://zoobank.org/697E91AE-9C90-4F6C-BEB4-F3CC80DA777A>

Figs 13–16

**Korean name.** Jak-eun-dong-gul-yeop-sae-u, new

**Type locality.** Gageodo-ri, Heuksan-myeon, Sinan-gun, Jeollanam-do, South Korea;  $34^{\circ}03'52.2''\text{N}$ ,  $125^{\circ}06'55.7''\text{E}$ ; an old tube well for using groundwater.

**Material examined.** Type material. **Holotype:** 1 adult female, 9.1 mm, NIBRIV0000862810. **Paratypes:** 2 males and 2 females, NIBRIV0000872412. All type materials collected on 7 Oct 2009 by Dr. M-S Kim.

**Etymology.** The specific name originates from the Latin word *minutus* meaning small, petty. This name refers to more reduced pleopod articles compare to other pseudocrangonyctids.

**Diagnosis.** Antenna 1,  $0.33 \times$  as long as body; flagellum composed of 15 articles. Antenna 2 flagellum composed of seven articles. Both mandibles bearing



five raker setae. Maxilla 1 inner lobe with four plumose setae on apical margin; 2<sup>nd</sup> palp article with six robust setae along distomedial to apical margins, with one oblique row of three setae subdistally. Maxilla 2 inner lobe with one oblique row of ten plumose setae on surface. Gnathopods 1 and 2 each possessing carpus with one and two rastellate setae, respectively. Pereopod 6,  $1.33 \times$  as long as pereopod 5; coxa anterior lobe with one seta on ventral margin. Sternal gills absent. Epimeral plate 2 ventral margin with two submarginal setae anteriorly, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 3 ventral margin with three submarginal setae anteriorly, slightly concaved at the middle, posterodistal corner slightly notched bearing one elongate seta. Pleopods rami reduced. Telson cleft for 0.14% of length.

**Description.** Holotype female: Body approximately 9.1 mm long. Sternal gills absent (Fig. 13A).

Head (Fig. 13B)  $1.26 \times$  as long as pereonite 1; rostrum reduced, with minute setae apically; lateral cephalic lobe anteriorly expanded, apex rounded, slightly dilated anteroventrally; antennal sinus not deep; eye absent.

Antenna 1 (Fig. 13C)  $0.33 \times$  as long as body; 1<sup>st</sup>–3<sup>rd</sup> peduncular articles length ratio of  $1.00 : 0.66 : 0.37$ ; 1<sup>st</sup> article stout, posterior margin with one pair of robust setae and one single robust seta; accessory flagellum bi-articulate, last article very reduced; flagellum  $1.14 \times$  as long as peduncles, composed of 15 articles, calceoli absent, aesthetascs present from 3<sup>rd</sup> to 14<sup>th</sup> articles.

Antenna 2 (Fig. 13D)  $0.59 \times$  as long and more setose than antenna 1; antennal cone well developed, apex rounded; 4<sup>th</sup> peduncular article margins subparallel,  $0.34 \times$  wider than long, posterior margin slightly widening distally and notched at distal corner, 5<sup>th</sup> article  $1.07 \times$  as long as 4<sup>th</sup> article, three calceoli present on medial surface; flagellum composed of seven articles,  $1.13 \times$  as long as 5<sup>th</sup> peduncular article, single calceoli present from 1<sup>st</sup> to 3<sup>rd</sup> articles, aesthetascs absent.

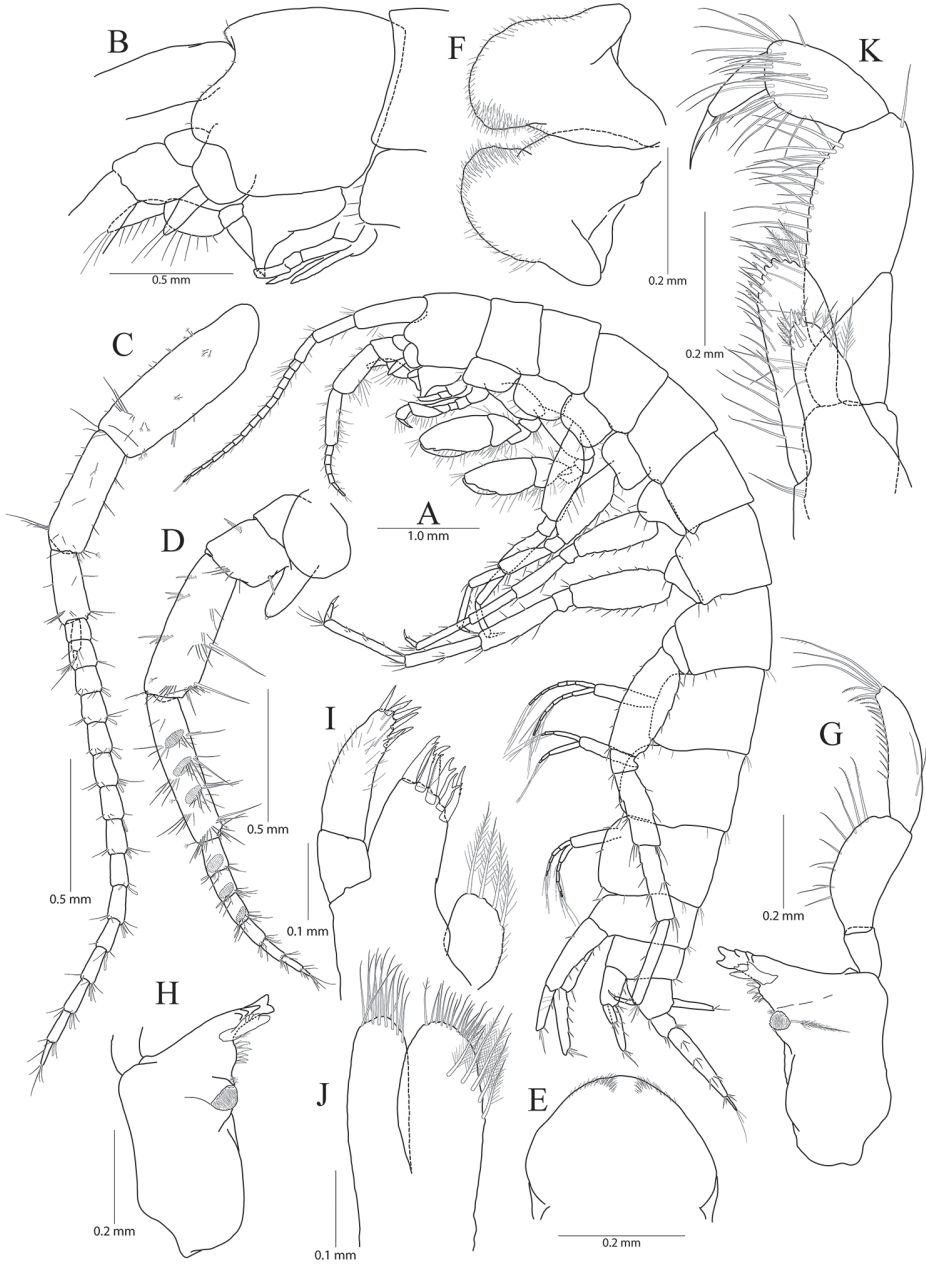
Upper lip (Fig. 13E) rounded, apex slightly produced apically, covered with minute setae, not notched.

Lower lip (Fig. 13F) inner lobes indistinct; outer lobes covered with minute setae; mandibular processes developed.

Mandible (Fig. 13G, H) incisor 5-dentate on both sides; lacinia mobilis tri-cuspidate (two of them finely dentate and one small, produced upwards) on right and 5-dentate on left side; five raker setae present on both sides; molar process columnar, triturative, with one plumose seta on right side only; palp tri-articulate; 2<sup>nd</sup> article convex and with ten setae medially; 3<sup>rd</sup> article subfalcate, as long as 2<sup>nd</sup> article, lined with 18 setae from medial margin to apex.

Maxilla 1 (Fig. 13I) inner lobe subrhomboid, with four plumose setae on apical margin; outer lobe with seven dentate robust setae; palp bi-articulate, 2<sup>nd</sup> article apex exceeding apical setae of outer plate, with six robust setae along distomedial to apical margins, with one oblique row of three setae subdistally.

Maxilla 2 (Fig. 13J) inner lobe slightly shorter but wider than outer lobe, with one oblique row of ten plumose setae on surface and two rows of simple setae on apical margin; outer lobe apical margin with two rows of simple setae.



**Figure 13.** *Pseudocrangonyx minutus* sp. nov. Holotype: female, NIBRV0000862810, 9.1 mm, from Gageo Is., South Korea. **A** habitus **B** head **C** antenna 1 **D** antenna 2 **E** upper lip **F** lower lip **G** right mandible **H** left mandible **I** maxilla 1 **J** maxilla 2 **K** maxilliped.

Maxilliped (Fig. 13K) inner lobe subrectangular, apex rounded, with six subdentate robust setae mediolaterally and with seven plumose setae subapically; outer lobe elongate semicircular,  $1.13 \times$  as long as 2<sup>nd</sup> palp article, with five robust setae and nine

plumose setae apical or subapically; inner lobe apex not exceeding middle of 2<sup>nd</sup> article of palp, with three plumose setae and five dentate robust setae apically; palp composed of four articles; 2<sup>nd</sup> article with many setae on medial margin; 3<sup>rd</sup> article slightly dilated distally,  $0.5 \times$  as long as 2<sup>nd</sup> article; 4<sup>th</sup> article falcate,  $0.76 \times$  as long as 3<sup>rd</sup> article, apical setae  $0.75 \times$  as long as 4<sup>th</sup> article.

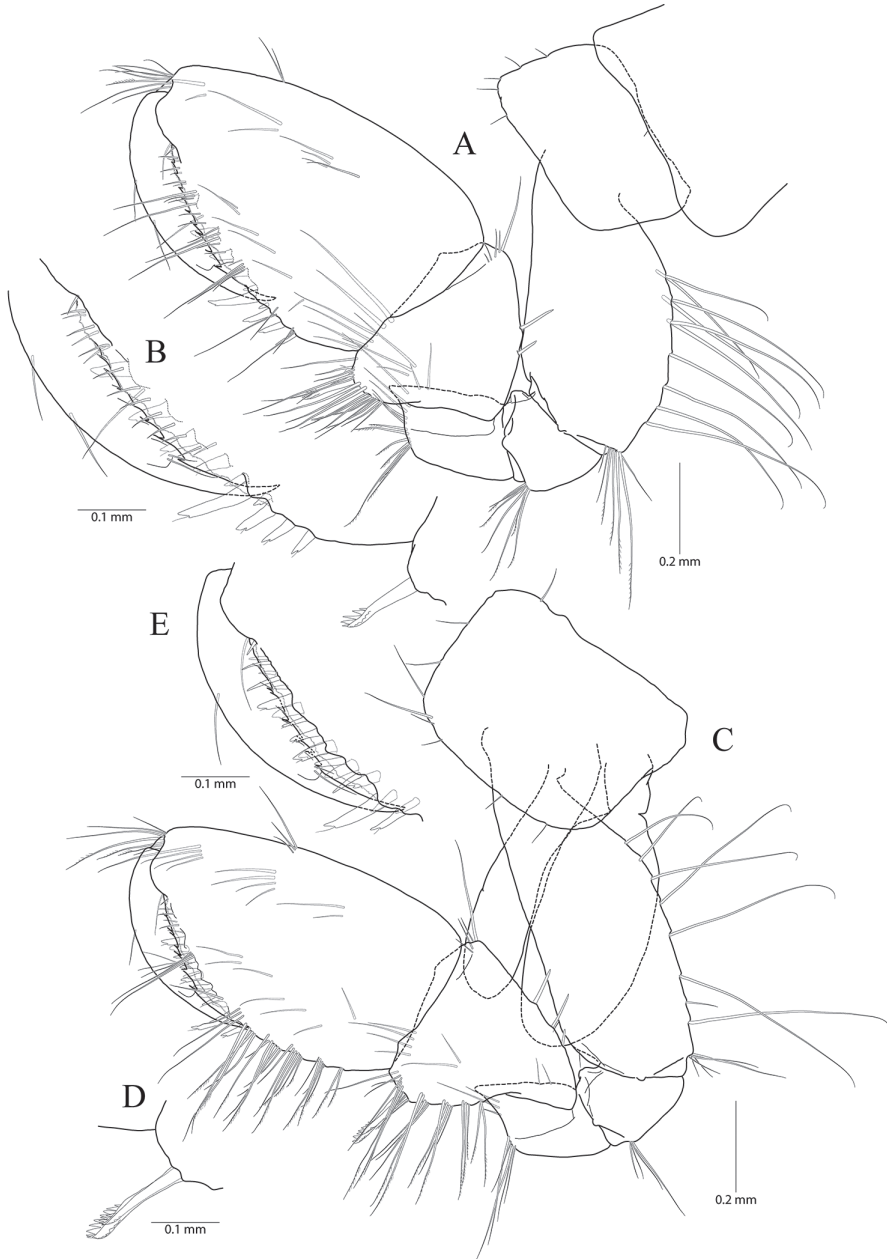
Gnathopod 1 (Fig. 14A, B) coxa subrectangular,  $1.43 \times$  wider than long, antero-distal corner somewhat produced, with five setae marginally, ventral margin a little convex; basis obtuse trapezoidal, posteriorly expanded,  $0.51 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin without setae; ischium  $0.16 \times$  as long as basis, with small anterior lobe; carpus  $0.58 \times$  as long as basis, with two robust seta on anterior margin, carpal lobe not developed, apex rounded with one rastellate seta and many simple or serrate setae; propodus subovate,  $1.32 \times$  as long and  $1.48 \times$  as wide as basis, posterior margin distal half with four robust setae successively increasing distally, palm irregular, defined by largest lateral seta of posterior margin, finely serrated, lined with six robust setae medially; dactylus as long as palm, inner margin toothed, outer margin with two setae, unguis developed.

Gnathopod 2 (Fig. 14C–E) as long as gnathopod 1; coxa  $1.32 \times$  as long as that of gnathopod 1,  $1.22 \times$  wider than long, , anterior and ventral margins not produced, rounded, lined with 15 setae, posterior margin slightly humped proximally; basis posteroproximally expanded,  $0.34 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin without setae; ischium  $0.14 \times$  as long as basis, with small anterior lobe; carpus  $0.56 \times$  as long as basis, with two pairs of robust and simple setae on anterior margin, carpal lobe not developed, broader than that of gnathopod 1, margin weakly crenulate, with two rastellate setae and many simple or serrate setae; propodus trapezoidal,  $1.00 \times$  as long and  $1.54 \times$  as wide as basis, anterior margin slightly convex, posterior margin  $0.57 \times$  as long as anterior margin, lined with five clusters of elongate setae, with two defining robust setae distally; palm irregular, finely serrated, lined with nine medial and eleven lateral robust setae (two defining setae stouter than others); dactylus as long as palm, inner margin toothed, outer margin with one seta, unguis developed.

Pereopod 3 (Fig. 15A, B) coxa subrectangular,  $1.53 \times$  wider than long, slightly expanded posteroventrally, with six setae anteriorly, ventral margin concave, with three posterior setae; basis expanded,  $0.63 \times$  as wider than long, width longest at proximal  $1/3$ , anterior margin lined with minute setae, with one sensory seta, posterior margin with seven elongate setae; merus anterodistally expanded,  $0.32 \times$  wider than long,  $0.62 \times$  as long as basis, anterodistal corner produced, apex blunt; carpus not expanded,  $0.50 \times$  as long as basis; propodus linear, as long as carpus; dactylus  $0.40 \times$  as long as propodus, unguis developed.

Pereopod 4 (Fig. 15C, D) similar to pereopod 3 except that merus  $0.88 \times$  as long as that of pereopod 3; different number or position of several setae.

Pereopod 5 (Fig. 15E) coxa bilobate, anterior lobe larger than posterior lobe, expanded ventrally ( $0.81 \times$  longer than wide), margin rounded, lined with five simple setae ventrally; posterior lobe with one seta at posterior corner; basis expanded, subrectangular,  $0.53 \times$  wider than long, anterior margin slightly convex, lined with five single robust setae, posterior margin more expanded, lined with eleven simple setae, distal corner produced forming an angle; merus posterodistally expanded,  $0.42 \times$  as wide and



**Figure 14.** *Pseudocrangonyx minutus* sp. nov. Holotype: female, NIBRV0000862810, 9.1 mm, from Gageo Is., South Korea. **A** gnathopod 1 **B** rastellate setae and palm of gnathopod 1 **C** gnathopod 2 **D** rastellate setae of gnathopod 2 **E** palm of gnathopod 2.

0.73 × as long as basis, with three pairs of simple setae on anterior margin and two robust setae on posterior margin; carpus subrectangular, posterodistal corner slightly produced, 0.25 × wider than long, 0.61 × as long as basis, with two anterior and one pos-

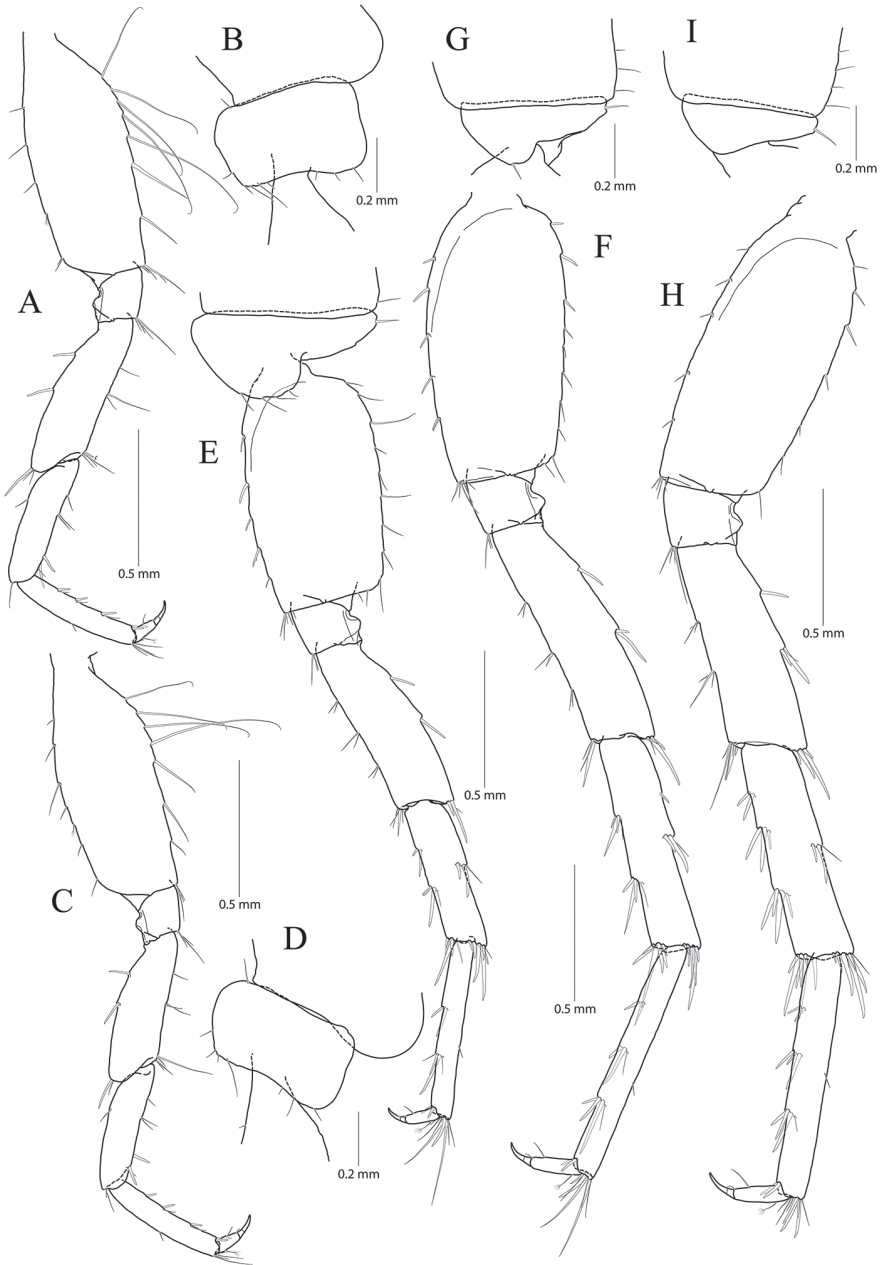
terior clusters of simple and robust setae, with well-developed distal clusters of setae at both anterior and posterior corners (longest seta  $0.31\times$  as long as propodus); propodus linear,  $1.17\times$  as long as carpus, anterior margin with two clusters of simple and robust setae (longest seta of distal cluster slightly not exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with one marginal short seta and one distal cluster of elongate setae; dactylus  $0.31\times$  as long as propodus, unguis developed.

Pereopod 6 (Fig. 15F, G)  $1.33\times$  as long as pereopod 5; coxa bilobate, anterior lobe  $0.71\times$  as long as that of pereopod 5, ventral margin with one seta only, posterior lobe expanded backward, with one seta at posterior corner; basis expanded, subrectangular,  $1.12\times$  as long and  $1.00\times$  as wide as that of pereopod 5,  $0.49\times$  wider than long, posterodistal corner produced forming an angle; merus posterodistally expanded,  $0.44\times$  as wide and  $0.85\times$  as long as basis, with three anterior and two posterior setal clusters; carpus rectangular,  $0.23\times$  wider than long,  $0.80\times$  as long as basis, with two setal clusters on anterior and posterior margins, respectively, with well-developed antero- and posterodistal setal clusters (longest seta  $0.25\times$  as long as propodus); propodus linear,  $1.09\times$  as long as carpus, anterior margin with three setal clusters (longest seta of distal cluster not exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with one marginal short seta and one distal cluster of elongate setae; dactylus  $0.33\times$  as long as propodus, unguis developed.

Pereopod 7 (Fig. 15H, I)  $1.01\times$  as long as pereopod 6; coxa unilobed, subtriangular,  $0.83\times$  as long as that of pereopod 6, posteriorly expanded with one seta at posterior corner, with one seta on ventral margin; basis expanded, subrectangular,  $1.09\times$  as long and  $0.93\times$  as wide as that of pereopod 6,  $0.42\times$  wider than long, posterodistal corner slightly produced but weaker than those of pereopods 6 and 7; merus posterodistally expanded,  $0.60\times$  as wide and  $0.70\times$  as long as basis, with two setal clusters on anterior and posterior margins, respectively; carpus rectangular,  $0.26\times$  wider than long,  $0.70\times$  as long as basis, with one cluster and three clusters of setae on anterior and posterior margins, respectively, with well-developed antero- and posterodistal setal clusters (longest seta  $0.25\times$  as long as propodus); propodus linear,  $1.09\times$  as long as carpus, anterior margin with three setal clusters (longest seta of distal cluster shorter than that of pereopod 6) and one pair of locking robust setae distally, posterior margin with one marginal short seta and one distal cluster of elongate setae (those shorter than that of pereopod 6); dactylus  $0.42\times$  as long as propodus, unguis developed.

Epimeral plate 1 subquadrate, ventral margin without setae, posterior margin convex, lined with four setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 2 subquadrate, larger than plate 1, ventral margin with two submarginal setae anteriorly, posterior margin convex, with four setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 3 larger than plate 2, ventral margin with three submarginal setae anteriorly, slightly concaved at the middle, posterodistal corner slightly notched bearing one elongate seta (Fig. 16A).

Pleopod 1 (Fig. 16B) peduncle with one pair of retinaculæ medioidistally, one simple seta laterodistally; outer ramus  $1.23\times$  as long as peduncle, composed of eight articles; inner ramus  $1.49\times$  as long as peduncle, composed of seven articles (coalesced 1<sup>st</sup> article exceeding proximal two articles of outer ramus combined).



**Figure 15.** *Pseudocrangonyx minutus* sp. nov. Holotype: female, NIBRV0000862810, 9.1 mm, from Gageo Is., South Korea. **A** pereopod 3 **B** coxal gill of pereopod 3 **C** pereopod 4 **D** coxal gill of pereopod 4 **E** pereopod 5 **F** pereopod 6 **G** coxal gill of pereopod 6 **H** pereopod 7 **I** coxal gill of pereopod 7.

Pleopod 2 (Fig. 16C, D) peduncle  $1.10 \times$  as long as that of pleopod 1, with one pair of retinaculæ mediodistally and one simple seta laterodistally; reduction of rami different from right and right sides; in left side, outer ramus  $0.66 \times$  as long as peduncle,



composed of four articles; inner ramus  $1.16 \times$  as long as peduncle, composed of six articles (coalesced 1<sup>st</sup> articles on inner and outer rami equal each other); in right side, both rami more reduced or coalesced.

Pleopod 3 (Fig. 16E)  $0.80 \times$  as long as pleopod 2; peduncle  $0.84 \times$  as long as that of pleopod 2, with one pair of retinaculae mediodistally and one seta laterodistally; outer ramus  $0.84 \times$  as long as peduncle, composed of six articles; inner ramus  $1.06 \times$  as long as peduncle, composed of five articles (coalesced 1<sup>st</sup> article  $1.40 \times$  as long as proximal two articles of outer ramus combined).

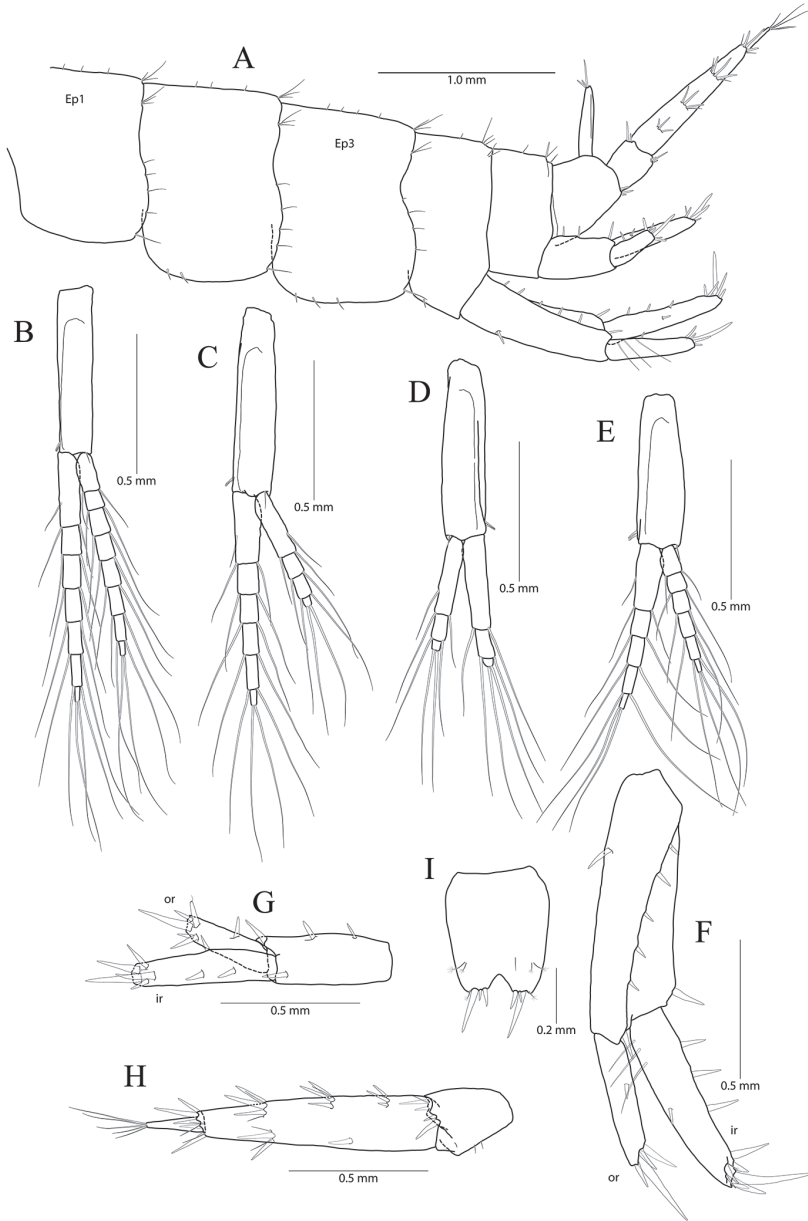
Uropod 1 (Fig. 16F) peduncle with one basofacial seta, with five margin robust setae and one distal seta dorsolaterally, with one distal robust seta dorsomedially; outer ramus  $0.51 \times$  as long as peduncle, with one distal robust seta dorsomedially, apical cluster composed of five robust setae (longest seta  $0.59 \times$  as long as outer ramus); inner ramus  $0.70 \times$  as long as peduncle, with three robust setae dorsomedially and one robust seta dorsolaterally, with three elongate setae on ventral margin subproximally, apical cluster of setae composed of seven robust setae and one sensory seta (longest seta  $0.45 \times$  as long as inner ramus).

Uropod 2 (Fig. 16G)  $0.57 \times$  as long as uropod 1; peduncle  $0.46 \times$  as long as that of uropod 1, with two marginal robust setae and one distal robust seta dorsolaterally, with one distal robust seta dorsomedially; outer ramus  $0.73 \times$  as long as peduncle, with one distal robust seta dorsolaterally, apical cluster composed of five robust setae (longest seta  $0.61 \times$  as long as outer ramus, one of those with abnormal apex); inner ramus  $1.15 \times$  as long as peduncle, with two robust setae dorsomedially and one robust seta dorsolaterally, apical cluster composed of five robust setae and one sensory seta (longest seta  $0.38 \times$  as long as inner ramus).

Uropod 3 (Fig. 16H) uniramous,  $0.76 \times$  as long as uropod 1; peduncle short,  $0.62 \times$  as long as uropod 2, with two minute setae on medial margin, with two setal clusters laterodistally; ramus  $3.75 \times$  as long as peduncle, bi-articulate, proximal article gradually diminished in width, with four clusters of setae laterally, with two clusters of setae and one single robust seta medially, (longest seta of distal cluster not exceeding distal article ramus), distal article  $0.24 \times$  as long as proximal article, with five elongate simple setae apically.

Telson (Fig. 16I)  $0.81 \times$  as wide as long, cleft for 14% of length, each lobe with one pair of penicillate setae dorsally, and one penicillate seta and three robust setae on apex.

**Remarks.** *Pseudocrangonyx minutus* sp. nov. is very similar to *P. daejeonensis* Lee, Tomikawa, Nakano & Min, 2018 in that the telson is concave (less than 15%) at the apex. However, the lateral cephalic lobe is more produced anteriorly and the antennal sinus is deeper in *P. minutus* compared to *P. daejeonensis* (Lee et al. 2018). In addition, the 2<sup>nd</sup> peduncular article of antenna 1 is  $0.66$  times as long as 1<sup>st</sup> article (compared to  $0.5$  times in *P. daejeonensis*), the flagellum of antenna 1 is composed of 15 articles (compared to ten articles in *P. daejeonensis*), antenna 2 has calceoli on the medial surface of the 5<sup>th</sup> peduncular article and the 1<sup>st</sup>–3<sup>rd</sup> flagellum articles (which are absent in *P. daejeonensis*), the flagellum of antenna 1 is composed of seven articles (compared to four articles in *P. daejeonensis*), eight raker setae are present on each mandible (compared to three on left and two on right in *P. daejeonensis*), the mandibular palp is more



**Figure 16.** *Pseudocrangonyx minutus* sp. nov. Holotype: female, NIBRV0000862810, 9.1 mm, from Gageo Is., South Korea. **A** epimeral plates and urosomites **B** pleopod 1, left **C** pleopod 2, left **D** pleopod 2, right **E** pleopod 3, left **F** uropod 1 **G** uropod 2 **H** uropod 3 **I** telson. Abbreviations: Ep, epimeral plate; ir, inner ramus; and or, outer ramus.

setose, the inner lobe of maxilla 1 has four plumose setae on the apical margin (compared to two plumose setae in *P. daejeonensis*), the 2<sup>nd</sup> article of palp maxilla 1 shows six dentate robust setae apically (two dentate robust setae in *P. daejeonensis*), and the outer

plate of the maxilliped is larger (Lee et al. 2018). Moreover, in *P. minutus*, each basis of gnathopods 1 and 2 is more setose posteriorly and each propodus is less expanded posteriorly, pereopods 3 and 4 are also more setose, each propodus of pereopods 5–7 is slender and has more robust setae than that of *P. daejeonensis*, each posterior margin of the bases in pereopods 5–7 has a smooth or smaller angle at the distal corner, each propodus of pereopods 5–7 is more slender and elongate. Lastly, in *P. minutus* sp. nov., the peduncle of uropod 1 has five robust setae marginally on the dorsolateral margin (compared to two robust setae in *P. daejeonensis*) and the inner ramus of uropod 1 has three elongate simple setae proximally on the ventral margin (compared to one seta in *P. daejeonensis*) (Lee et al. 2018).

*Pseudocrangonyx minutus* sp. nov. is also similar to *P. komaii* Tomikawa & Nakano, 2018 from Japan with regard to general shape and length ratio of the articles in the gnathopods and pereopods, the reduced number of the articles of rami in the pleopods, and the slightly concave shape of the telson (less than 15%) at the apex. On the other hand, *P. minutus* sp. nov. can be readily distinguished from *P. komaii* by the slender and elongate peduncular articles of antennae 1 and 2, the six apical robust setae in the palp of maxilla 1 (compared to four in *P. komaii*), by one and two rastellate setae in gnathopods 1 and 2, respectively (which are absent in *P. komaii*), by a more setose posterior margin of the basis in each gnathopod, by the presence of five setae ventrally on the anterior lobe of coxa 5 (compared to one in *P. komaii*), and by the more expanded basis of pereopod 5 (Tomikawa and Nakano 2018).

***Pseudocrangonyx villosus* sp. nov.**

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Figs 17–21

**Korean name.** Teol-son-dong-gul-yeop-sae-u, new

**Type locality.** Ansanangul Cave, Beolcheon-ri, Danseong-myeon, Danyang-gun, Chungcheongbuk-do, South Korea; 36°52'10"N, 128°17'00"E.

**Material examined.** Type material. **Holotype:** 1 female, 12.4 mm, NIBRIV0000862811. **Paratypes:** 2 specimens, NIBRIV0000872413. All type materials were collected on 17 Mar 2002 by YG Choi.

**Etymology.** The specific name originates from the Latin word *villosus* meaning hairy. This name refers to the more setose bases of pereopods 3 and 4 compared to other pseudocrangonyctids.

**Diagnosis.** Antenna 1,  $1.61 \times$  as long as body; 1<sup>st</sup>–3<sup>rd</sup> peduncular articles length ratio of 1.00 : 0.86 : 0.64. Antenna 2 peduncles moderate. Mandibles eight raker setae present on both sides. Maxilla 1 inner lobe with seven plumose setae on apical margin; palp with nine robust setae along distomedial to apical margins, with one oblique row of seven setae subdistally. Maxilla 2 with one oblique row of ten plumose setae on surface. Gnathopods 1 and 2 each possessing carpus with two rastellate setae, respectively. Pereopods 3 and 4 basis more setose on both margins. Pereopods 5–7 basis slightly

elongate. Pereopod 5 carpus and propodus with rows of elongate setae medially. Pereopod 6,  $1.24 \times$  as long as pereopod 5. Pereopod 7 merus, carpus and propodus stout. Sternal gills present from pereonites 2 to 5 (1+1+1+1 in formulae). Epimeral plates 2 ventral margin with three setae anteriorly, posterodistal corner slightly notched bearing one elongate seta. Epimeral plates 3 posterior margin with eight setae, posterodistal corner slightly notched bearing one elongate seta, ventral margin with four submarginal setae anteriorly. Uropod 1 inner ramus with three elongate simple setae on ventral margin subproximally. Telson  $0.71 \times$  as wide as long, cleft for 35% of length.

**Description.** Holotype female: Body (Fig. 17A) approximately 12.4 mm long.

Head (Fig. 17B) as long as pereonite 1; rostrum reduced, with three minute setae; lateral cephalic lobe anteriorly expanded, apex rounded, slightly dilated anteroventrally; antennal sinus not deep; eye absent.

Antenna 1 (Fig. 17C)  $0.61 \times$  as long as body; 1<sup>st</sup>–3<sup>rd</sup> peduncular articles length ratio of 1.00 : 0.86 : 0.64; 1<sup>st</sup> article stout, posterior margin with simple setae only; accessory flagellum bi-articulate, last article very reduced; flagellum  $1.32 \times$  as long as peduncles, composed of 23 articles, calceoli absent, aesthetascs present from 16<sup>th</sup> to last articles.

Antenna 2 (Fig. 17D)  $0.59 \times$  as long as antenna 1; antennal cone developed, apex rounded; 4<sup>th</sup> peduncular article margins parallel,  $0.25 \times$  wider than long, posterior margin with one row of setae in the middle and one elongate seta subdistally, 5<sup>th</sup> article  $0.95 \times$  as long and  $0.61 \times$  as wide as 4<sup>th</sup> article, three calceoli present on medial surface; flagellum composed of nine articles,  $1.05 \times$  as long as 5<sup>th</sup> peduncular article, single calceoli present from 1<sup>st</sup> to 5<sup>th</sup> articles medially, aesthetascs absent.

Upper lip (Fig. 17E) rounded, apex slightly produced apically, covered with minute setae, not notched.

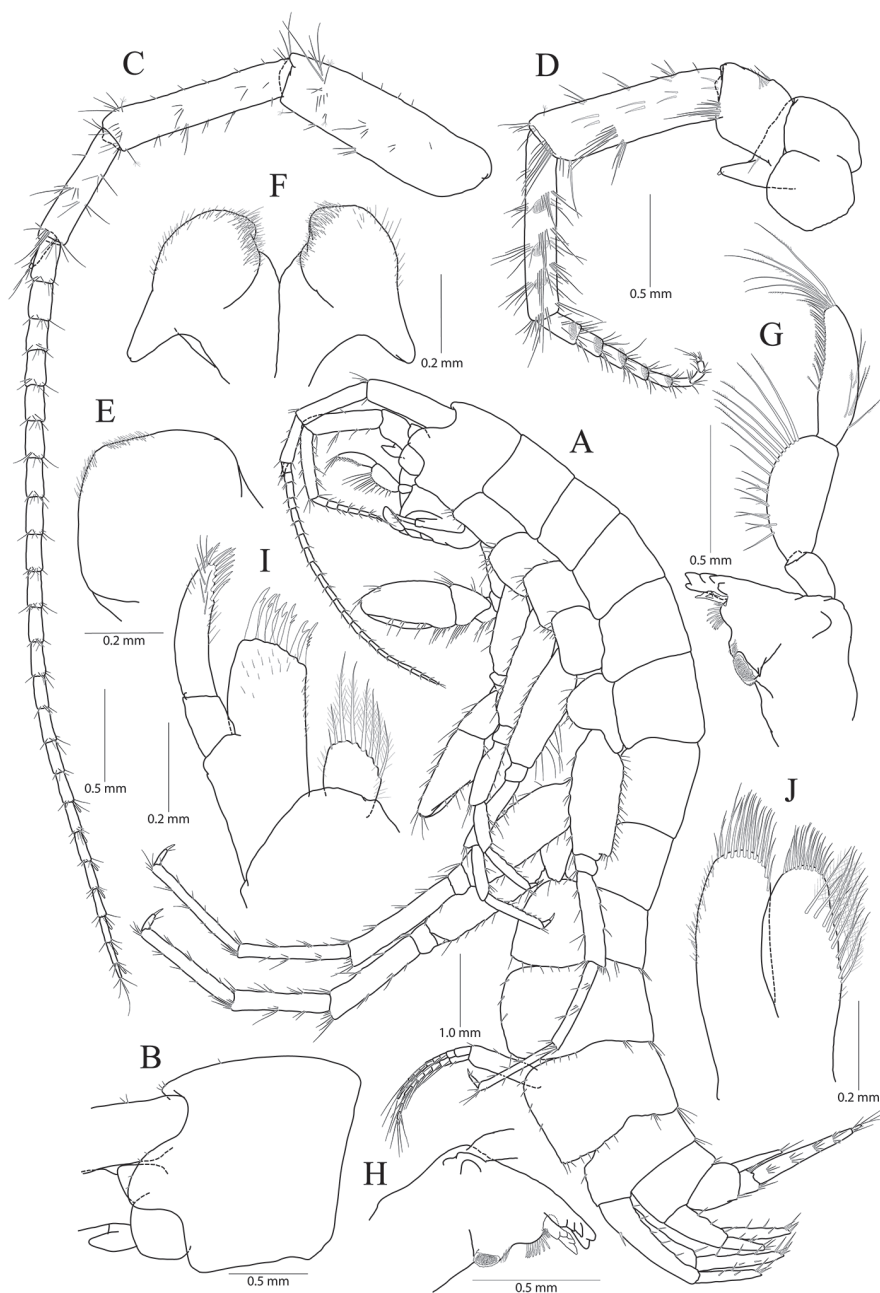
Lower lip (Fig. 17F) inner lobes indistinct; outer lobes covered with minute setae; mandibular processes developed.

Mandible (Fig. 17G, H) incisor 5-dentate on both sides; lacinia mobilis tri-cuspidate (two of them finely dentate and one small, produced upwards) on right and 5-dentate on left side; eight raker setae present on both sides; molar process columnar, triturative, without plumose setae on both sides; palp tri-articulate; 2<sup>nd</sup> article convex and with 18 setae medially; 3<sup>rd</sup> article subfalcate, as long as 2<sup>nd</sup> article, lined with 27 setae from medial margin to apex, with six setae laterally.

Maxilla 1 (Fig. 17I) inner lobe subrhomboid, with seven plumose setae on apical margin; outer lobe with seven dentate robust setae; palp bi-articulate, 2<sup>nd</sup> article apex exceeding apical setae of outer plate, with nine robust setae along distomedial to apical margins, with one oblique row of seven setae subdistally.

Maxilla 2 (Fig. 17J) inner lobe slightly shorter but wider than outer lobe, with one oblique row of ten plumose setae on surface and two rows of simple setae on apical margin; outer lobe apical margin with two rows of simple setae.

Maxilliped (Fig. 18A) inner lobe subrectangular, apex rounded, with six subdentate robust setae mediodistally and with seven plumose setae apically and subapically; outer lobe elongate semicircular, as long as 2<sup>nd</sup> palp article, with six plumose setae on



**Figure 17.** *Pseudocrangonyx villosus* sp. nov. Holotype: female, NIBRV0000862811, 12.4 mm, from Ansan Cave, South Korea. **A** habitus **B** head **C** antenna 1 **D** antenna 2 **E** upper lip **F** lower lip **G** right mandible **H** left mandible **I** maxilla 1 **J** maxilla 2.

apical margin and six dentate robust setae on mediodistal margin; palp composed of four articles; 2<sup>nd</sup> article with many setae on medial margin; 3<sup>rd</sup> article slightly dilated

distally,  $0.63 \times$  as long as 2<sup>nd</sup> article; 4<sup>th</sup> article falcate,  $0.59 \times$  as long as 3<sup>rd</sup> article, apical setae  $0.71 \times$  as long as 4<sup>th</sup> article.

Gnathopod 1 (Fig. 18B) coxa subrectangular,  $1.43 \times$  wider than long, anterodistal corner somewhat produced, with six setae marginally, ventral margin a little convex, posterior margin slightly humped proximally; basis obtuse trapezoidal, posteriorly expanded,  $0.51 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin without setae; ischium  $0.26 \times$  as long as basis, with small anterior lobe; carpus  $0.56 \times$  as long as basis, with two pairs of robust setae on anterior margin, carpal lobe not developed, apex rounded with two rastellate setae and many simple or serrate setae; propodus subovate,  $1.32 \times$  as long and  $1.48 \times$  as wide as basis, posterior margin with four robust setae successively increasing distally, palm irregular, defined by largest lateral seta of posterior margin, finely serrated, lined with ten robust setae medially; dactylus as long as palm, inner margin toothed, outer margin with four setae, unguis developed.

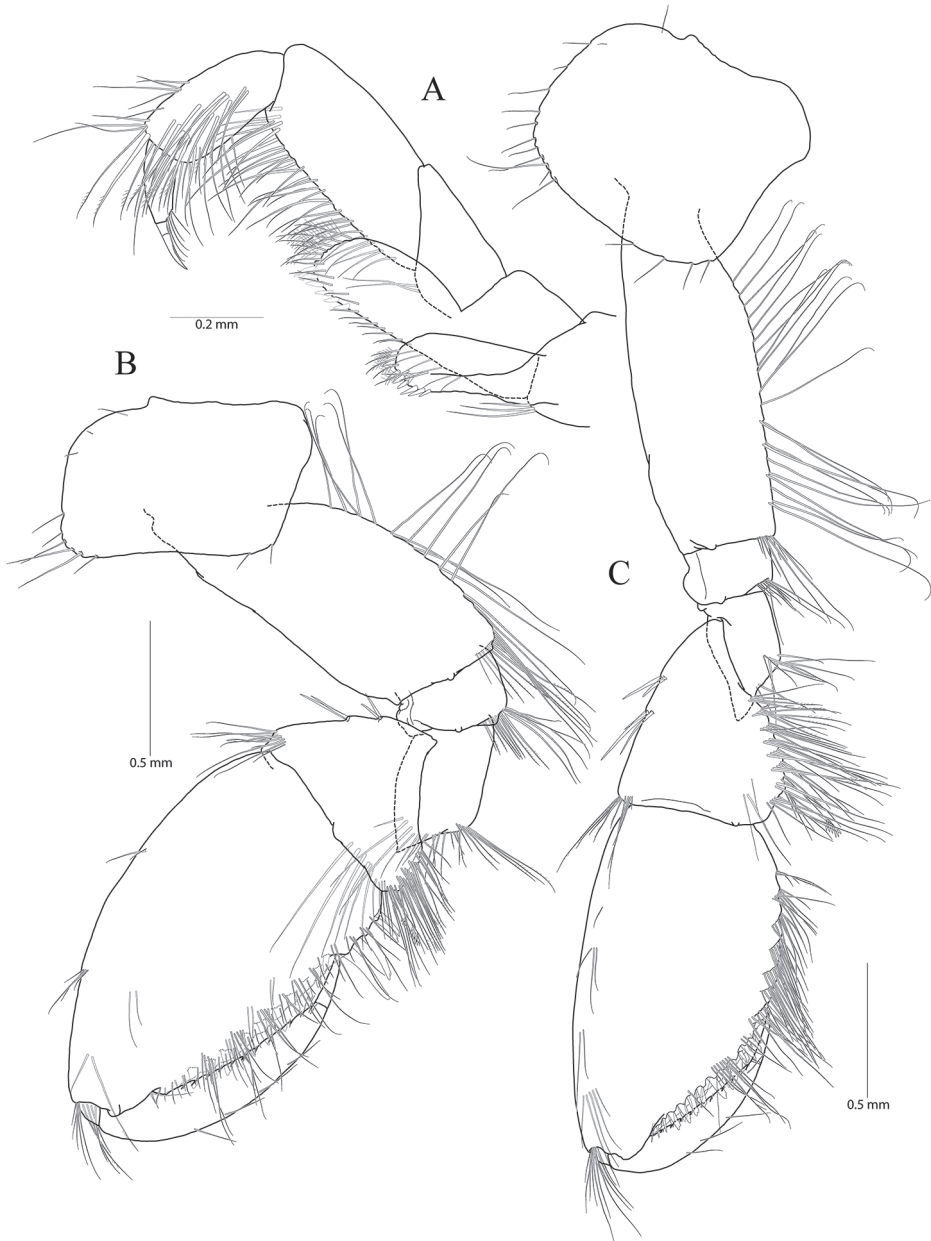
Gnathopod 2 (Fig. 18C)  $1.10 \times$  as long as gnathopod 1; coxa  $1.13 \times$  as long as that of gnathopod 1,  $1.22 \times$  wider than long, anterior and ventral margins not produced, rounded, lined with 15 setae, posterior margin humped proximally; basis somewhat expanded posteroproximally,  $0.34 \times$  wider than long, lined with elongate simple setae posteriorly, anterior margin without setae; ischium  $0.14 \times$  as long as basis, with small anterior lobe; carpus  $0.56 \times$  as long as basis, with two clusters of robust setae on anterior margin, carpal lobe not developed, broader than that of gnathopod 1 margin, weakly crenulate, with two rastellate setae and many simple or serrate setae; propodus trapezoidal,  $1.00 \times$  as long and  $1.54 \times$  as wide as basis, anterior margin slightly convex, posterior margin  $0.57 \times$  as long as anterior margin, lined with seven clusters of elongate setae, with two defining robust setae distally; palm irregular, finely serrated, lined with 12 medial and 14 lateral robust setae; dactylus as long as palm, inner margin toothed, outer margin with three setae, unguis developed.

Pereopod 3 (Fig. 19A) coxa subrectangular,  $1.19 \times$  wider than long, slightly humped posteroproximally, ventral margin a little concave, with eleven setae anteriorly and four setae at posteroventral corner; coxal gill subovate; basis expanded,  $0.69 \times$  as wide and  $3.05 \times$  as long as coxa, width longest at proximal 1/3 and gradually diminished distally, margins lined with setae but posterior ones longer than anterior ones; ischium  $0.16 \times$  as long as basis; merus anterodistally expanded,  $0.30 \times$  wider than long,  $0.49 \times$  as long as basis, anterodistal corner produced, apex blunt; carpus not expanded,  $0.37 \times$  as long as basis; propodus,  $0.42 \times$  as long as basis, linear; dactylus  $0.32 \times$  as long as propodus, unguis developed.

Pereopod 4 (Fig. 19B) similar to pereopod 3; merus, carpus and propodus slightly longer than those of pereopod 3.

Pereopod 5 (Fig. 20A, B) coxa bilobate, anterior lobe larger than posterior lobe, expanded ventrally ( $1.00 \times$  as long as wide), margin rounded, lined with 13 simple setae; posterior lobe with three setae posteriorly; coxal gill subovate; basis expanded, subrectangular, slightly expanded,  $0.43 \times$  wider than long, anterior margin slightly convex, lined with two single robust setae and four clusters of robust and simple setae, posterior margin lined with 28 simple setae, distal corner produced forming an angle;





**Figure 18.** *Pseudocrangonyx villosus* sp. nov. Holotype: female, NIBRV0000862811, 12.4 mm, from Ansan Cave, South Korea. **A** maxilliped **B** gnathopod 1 **C** gnathopod 2.

merus posterodistally expanded,  $0.37 \times$  as wide and  $0.76 \times$  as long as basis, with three clusters of simple setae on anterior margin and one robust seta and two clusters of robust setae on posterior margin; carpus not expanded,  $0.79 \times$  as long as basis, with three setal clusters on medial surface anteriorly and two robust setal clusters on lateral

surface posteriorly; propodus linear, as long as carpus, anterior margin with four setal clusters (longest seta of distal cluster slightly exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with five clusters of simple setae, with one cluster of simple and robust setae at distal corner; dactylus  $0.26 \times$  as long as propodus, unguis developed.

Pereopod 6 (Fig. 20C)  $1.24 \times$  as long as pereopod 5; coxa bilobate, anterior lobe  $0.59 \times$  as long as that of pereopod 5, with three setae ventrally, posterior lobe narrow, expanded backward, with two setae posteriorly; basis expanded, subrectangular, slightly expanded,  $1.16 \times$  as long and  $1.07 \times$  as wide as that of pereopod 5,  $0.40 \times$  wider than long, with three single and four clusters of setae on anterior margin, with 16 setae on posterior margin, posterodistal corner produced forming an angle, but weaker than that of pereopod 5; merus posterodistally expanded,  $0.48 \times$  as wide and  $0.89 \times$  as long as basis, with four anterior and four posterior setal clusters; carpus not expanded,  $0.83 \times$  as long as basis, with four setal clusters on medial surface anteriorly and three setal clusters on lateral surface posteriorly; propodus linear, as long as carpus, anterior margin with four setal clusters (longest seta of distal cluster not exceeding end of propodus) and one pair of locking robust setae distally, posterior margin with one single seta and three clusters of simple setae and one distal cluster of elongate setae; dactylus  $0.27 \times$  as long as propodus, unguis developed.

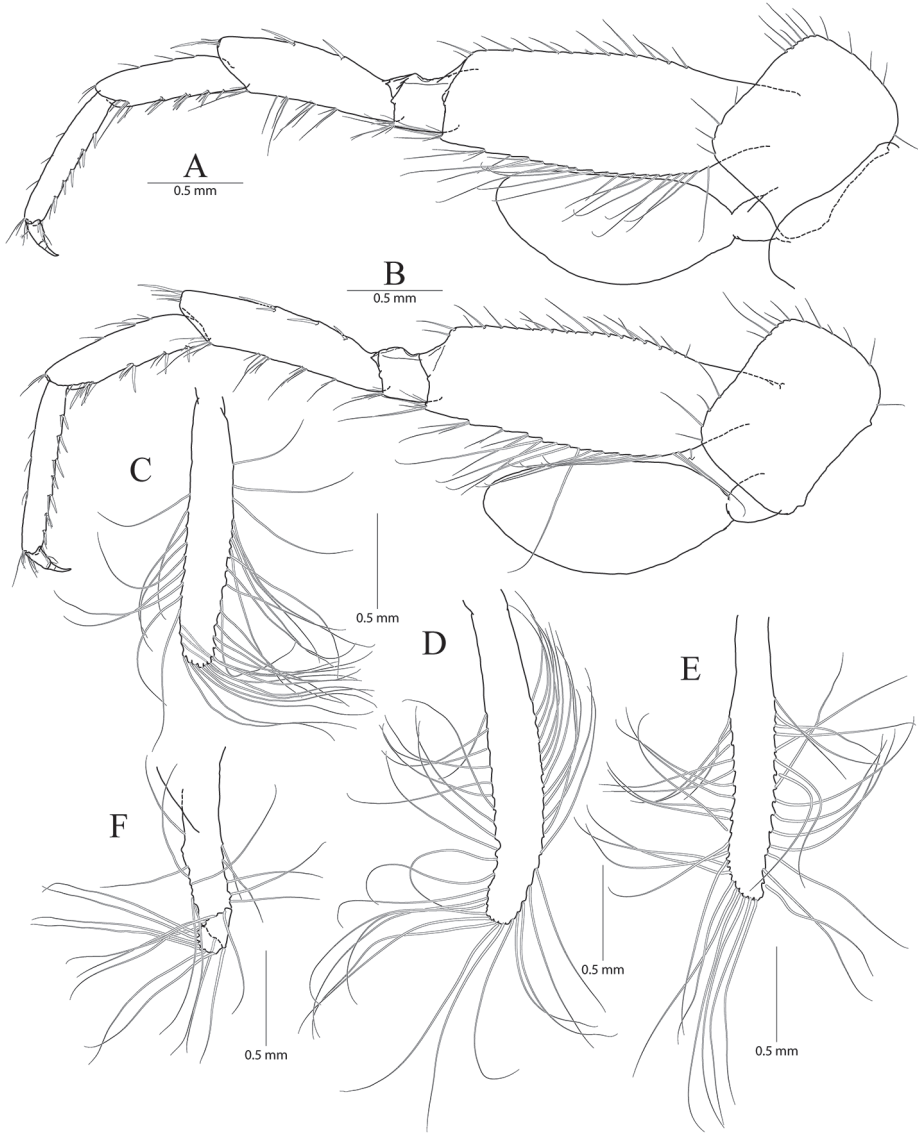
Pereopod 7 (Fig. 20D)  $0.93 \times$  as long as pereopod 6, but width slightly thicker universally; coxa unilobed, subtriangular,  $0.82 \times$  as long as that of pereopod 6, posteriorly expanded with three setae at posterior corner, with one seta on ventral margin; basis expanded, subrectangular, as long and wide as that of pereopod 6, posterodistal expansion weaker than those of pereopods 6 and 7; merus posterodistally expanded,  $0.67 \times$  as wide and  $0.77 \times$  as long as basis, with two setal clusters anteriorly and one single robust seta and two setal clusters posteriorly; carpus as long as merus, rectangular, not narrowed,  $0.24 \times$  as wide as long; propodus linear but thicker than that of pereopod 6,  $1.10 \times$  as long as carpus, anterior margin with four setal clusters (without elongate setae) and one pair of locking robust setae distally, with three clusters of simple setae posteriorly; dactylus  $0.30 \times$  as long as propodus, unguis developed.

Oostegites (Fig. 19C–F) present from gnathopod 2 to pereopod 5, narrow, with marginal seta, shortest in that of pereonite 5.

Sternal gills (Fig. 21A) present from pereonites 2 to 5 ( $1+1+1+1$  in formulae), narrower than oostegites, similar to each other in length.

Epimeral plate 1 subquadrate, a little produced posteroventrally, ventral margin without setae, posterior margin with seven setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 2 subquadrate, slightly larger than epimeron 1, ventral margin with three setae anteriorly, posterior margin with nine setae, posterodistal corner slightly notched bearing one elongate seta. Epimeral plate 3 posterior margin with eight setae, posterodistal corner slightly notched bearing one elongate seta, ventral margin with four submarginal setae anteriorly (Fig. 21B).

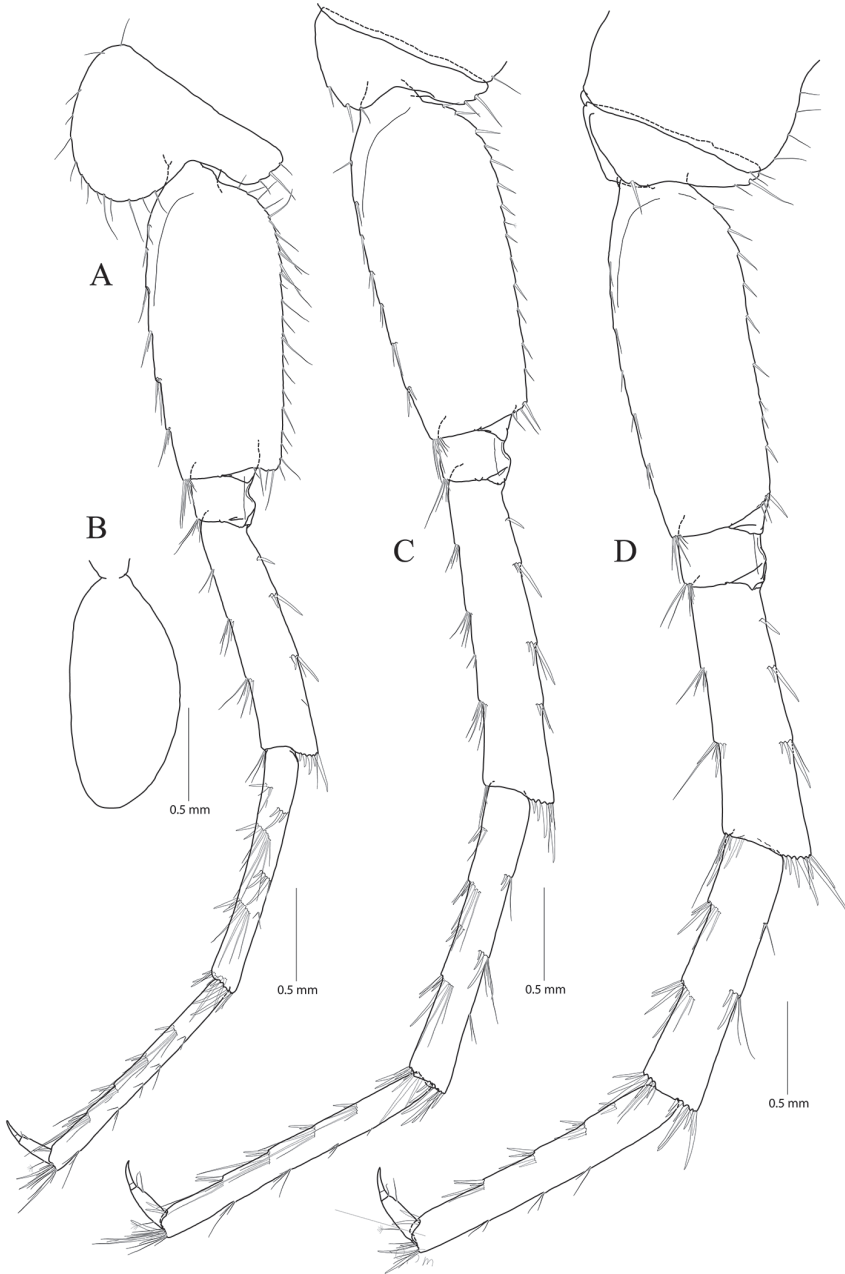
Pleopod 1 (Fig. 21C) peduncle with one pair of retinaculae mediodistally and one pair of simple setae laterodistally, with one seta on lateral margin; outer ramus  $1.55 \times$  as long as peduncle, composed of 15 articles; inner ramus  $1.74 \times$  as long as peduncle, composed of 13 articles (coalesced 1<sup>st</sup> article as long as proximal three articles of outer ramus combined).



**Figure 19.** *Pseudocrangonyx villosus* sp. nov. Holotype: female, NIBRV0000862811, 12.4 mm, from Ansan Cave, South Korea. **A** pereopod 3 **B** pereopod 4 **C–F** oostegites of gnathopod 2–pereopod 5.

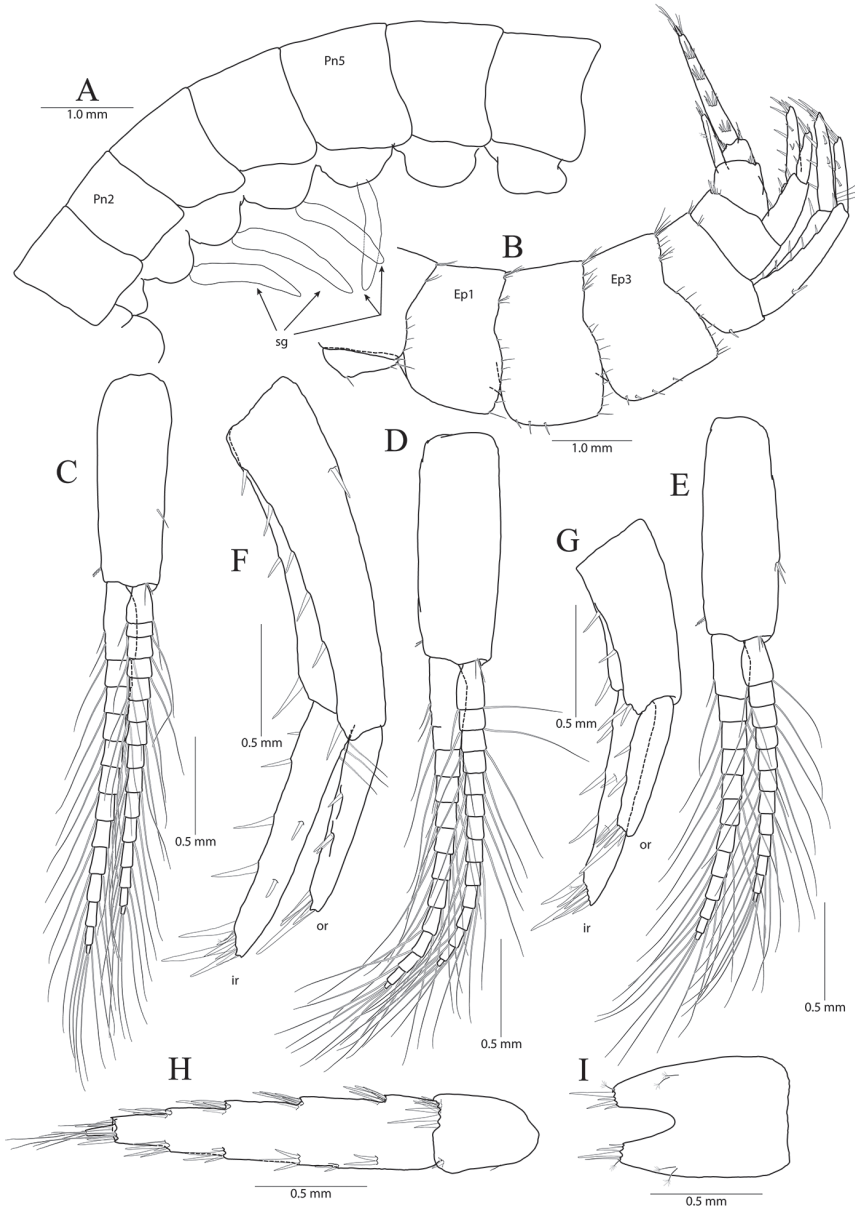
Pleopod 2 (Fig. 21D) peduncle  $1.10 \times$  as long as that of pleopod 1, with one pair of retinaculæ mediodistally and one pair of simple setae laterodistally, margins without setae; outer ramus  $1.33 \times$  as long as peduncle, composed of 14 articles; inner ramus  $1.10 \times$  as long as outer ramus, composed of twelve articles (coalesced 1<sup>st</sup> article with suture, as long as proximal three articles of outer ramus combined).

Pleopod 3 (Fig. 21E)  $0.92 \times$  as long as pleopod 2; peduncle  $0.98 \times$  as long as that of pleopod 2, with one pair of retinaculæ mediodistally and one pair of simple setae latero-



**Figure 20.** *Pseudocrangonyx villosus* sp. nov. Holotype: female, NIBRV0000862811, 12.4 mm, from Ansan Cave, South Korea. **A** pereopod 5 **B** coxal gill of pereopod 5 **C** pereopod 6 **D** pereopod 7.

distally, with one pair of setae on lateral margin; outer ramus  $1.18 \times$  as long as peduncle, composed of twelve articles; inner ramus  $1.15 \times$  as long as outer ramus, composed of twelve articles (1<sup>st</sup> coalesced article reaching middle of 2<sup>nd</sup> article of outer ramus).



**Figure 21.** *Pseudocrangonyx villosus* sp. nov. Holotype: female, NIBRV0000862811, 12.4 mm, from Ansan Cave, South Korea. **A** sternal gills **B** epimeral plates and urosomites **C** pleopod 1 **D** pleopod 2 **E** pleopod 3 **F** uropod 1 **G** uropod 2 **H** uropod 3 **I** telson. Abbreviations: Ep, epimeral plate; Pn, pereonite; sg, sternal gill; ir, inner ramus; and or, outer ramus.

Uropod 1 (Fig. 21F) peduncle with one basofacial seta, with four marginal robust setae and one distal robust seta dorsolaterally, with one marginal robust seta and one distal robust seta dorsomedially; outer ramus  $0.53 \times$  as long as peduncle,

with one robust seta dorsomedially and two robust setae dorsolaterally, apical cluster composed of five robust setae; inner ramus  $1.36 \times$  as long as outer ramus, with four robust setae dorsomedially and two robust setae dorsolaterally, apical cluster composed of seven robust setae and one sensory seta, with three elongate simple setae on ventral margin subproximally.

Uropod 2 (Fig. 21G)  $0.68 \times$  as long as uropod 2; peduncle  $0.50 \times$  as long as that of uropod 1, with two marginal setae and one pair of distal setae dorsolaterally, with one distal seta dorsomedially; outer ramus  $0.78 \times$  as long as peduncle, with two robust setae dorsolaterally, apical cluster composed of five robust setae; inner ramus  $1.48 \times$  as long as outer ramus, with three robust setae dorsomedially and two robust setae dorsolaterally, apical cluster composed of seven robust setae and one sensory seta.

Uropod 3 (Fig. 21H) uniramous,  $0.86 \times$  as long as uropod 1; peduncle short,  $0.57 \times$  as long as uropod 2, with one minute seta on medial margin and one robust seta mediodistally, with one setal cluster on laterodistal margin; ramus  $3.24 \times$  as long as peduncle, bi-articulate, proximal article gradually diminished in width, with six clusters of setae laterally and five clusters of setae medially (longest seta of distal cluster exceeding distal article ramus), distal article  $0.08 \times$  as long as proximal article, with three elongate simple setae apically.

Telson (Fig. 21I)  $0.71 \times$  as wide as long, cleft for 35% of length, each lobe with one pair of penicillate setae dorsally, and one penicillate seta and four robust setae on apex.

**Remarks.** *Pseudocrangonyx villosus* sp. nov. is distinguished from other Korean pseudocrangonyctids such as *P. asiaticus*, *P. coreanus*, *P. concavus* sp. nov., *P. crassus* sp. nov., *P. daejeonensis*, *P. gracilipes* sp. nov., *P. joolaei*, *P. minutus* sp. nov., and *P. villosus* sp. nov. in that antenna 1 is longer than half length of the body and the 2<sup>nd</sup> peduncular article is 0.89 times as long as the 1<sup>st</sup> peduncular article. In addition, maxilla 1 has seven plumose setae on the inner lobe, and a row on the inner lobe of maxilla 2 is composed of ten plumose setae. Both gnathopods have two rastellate setae on the carpus; each basis of pereopods 3 and 4 is more setose along the margins while the bases of pereopods 5–7 are more elongate than those of other Korean pseudocrangonyctids mentioned above. Finally, the sternal gills are present in pereonites 2 to 5 (1+1+1+1 in formulae) and the posterodistal corners of all epimeral plates are notched (Uéno 1934, 1966, Lee et al. 2018, 2020).

### Key to known species of the genus *Pseudocrangonyx* from Korean underground waters [except *P. asiaticus* sensu (Uéno, 1934)]

- |   |   |  |
|---|---|--|
| 1 | Telson apex slightly cleft (less than 15%) .....  | 2  |
| – | Telson apex deeply cleft (more than 15%).....   | 4  |
| 2 | Sternal gill present on pereonites.....   | <i>P. coreanus</i> Uéno, 1966                            |
| – | Sternal gill absent on pereonites .....   | 3  |
| 3 | Maxilla 1 palp with 6 dentate robust setae apically. Uropod 2 outer ramus with robust setae marginally.....     | <i>P. minutus</i> sp. nov.                               |
| – | Maxilla 1 palp with 2 dentate robust setae apically. Uropod 2 outer ramus without robust setae marginally ..... |  |
|   | .....   | <i>P. daejeonensis</i> Lee, Tomikawa, Nakano & Min, 2018 |



- 4 Pereopods 5 carpus elongate and slender. Epimeral plates 2 and 3 posterodistal corner notched..... **5**
- Pereopod 5 carpus not elongate and slender, slightly expanded. Epimeral plates 2 and 3 posterodistal corner not notched ..... **6**
- 5 Maxilla 1 and 2 both inner plates with 4 plumose setae .....  
..... ***P. gracilipes* sp. nov.**
- Maxilla 1 and 2 each inner plate with 7 and 10 plumose setae, respectively..  
..... ***P. villosus* sp. nov.**
- 6 Antenna 2, 4<sup>th</sup> and 5<sup>th</sup> peduncular articles not expanded in male. Epimeral plate 3 ventral margin slightly emarginated..... ***P. concavus* sp. nov.**
- Antenna 2, 4<sup>th</sup> and 5<sup>th</sup> peduncular articles expanded in male. Epimeral plate 3 ventral margin not emarginated ..... **7**
- 7 Pereopod 6, anterior lobe of coxa with 2 robust setae ventrally. Uropods 1–2 outer ramus with robust setae on medial margin.....  
..... ***P. joolaei* Lee, Tomikawa, Nakano & Min, 2020**
- Pereopod 6, anterior lobe of coxa with 5 robust setae ventrally. Uropods 1–2 outer ramus without robust setae on medial margin..... ***P. crassus* sp. nov.**

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# A new species of *Galleria* Fabricius (Lepidoptera, Pyralidae) from Korea based on molecular and morphological characters

Seung Jin Roh<sup>1</sup>, Haechul Park<sup>1</sup>, Seong-Hyun Kim<sup>1</sup>,  
So-Yun Kim<sup>1</sup>, Yong-Su Choi<sup>1</sup>, Jeong-Hun Song<sup>1</sup>

<sup>1</sup> Department of Agricultural Biology, National Institute of Agricultural Sciences, Wanju 55365, South Korea

Corresponding author: Jeong-Hun Song ([jeonghuns@korea.kr](mailto:jeonghuns@korea.kr))

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## Abstract

The greater wax moth, *Galleria mellonella* Linnaeus, is well known as a pest of honey bees and for the biodegradation of wax and polyethylene by their larvae. The genus *Galleria* has long been considered monotypic and found worldwide. A taxonomic study of the genus *Galleria* is presented based on morphological and molecular characters (*COI*, *CAD*, *wg*). A new species (*Galleria similis* Roh & Song, **sp. nov.**) is recognized on the Korean peninsula. The new species is superficially similar to *G. mellonella* but they can be separated by the structures of hindwing venation and male genitalia. Habitus photographs and illustrations of diagnostic characters are provided.

## Keywords

cryptic species, Galleriinae, new species, plastic eating moth, Pyraloidea, wax worms

## Introduction

The family Pyralidae is large group of Lepidoptera, placed in the superfamily Pyraloidea consisting of 1055 genera with 5921 described species (van Nieukerken et al. 2011). A molecular phylogeny and revised classification of the Pyralidae recognized five subfamilies, Chrysauginae, Epipaschiinae, Galleriinae, Phycitinae, and Pyralinae (Regier et al. 2012).

Among the Galleriinae, the monotypic genus *Galleria* Fabricius, 1798 was established with the type species *Phalaena cereana* Blom, 1764. *Galleria mellonella* (Linnaeus) is a ubiquitous pest of honey bees, *Apis mellifera* Linnaeus and *A. cerana* Fabricius (Ellis et al. 2013; Kwadha et al. 2017). They live on honeycomb in beehives, feeding on honey, beeswax, and the skin of bee pupae (Oldroyd 1999, 2007; Martel et al. 2006; Klein et al. 2007; Kong et al. 2019). Recent studies have shown that the larvae have the ability to biodegrade polyethylene in their guts (Yang et al. 2014; Bombelli et al. 2017; Kong et al. 2019).

The genus *Galleria* is superficially similar to the genus *Achroia* Hübner, 1819 (Kwadha et al. 2017), but can be distinguished from the latter by the presence of four stemmata on the head of the larva, concaved in the termen of the forewing, and the Cu vein apparently four-branched from the hindwing (Ellis et al. 2013).

In this paper, we describe *Galleria similis* Roh & Song, sp. nov. based on morphological and molecular characters, and provide habitus photographs and illustrations of diagnostic characters for identification of the two species of the genus *Galleria*.

## Materials and methods

The material examined in this study is deposited in the Systematic Entomology Laboratory, National Institute of Agricultural Sciences (NAS), Wanju, Korea. Specimens were dissected and examined after mounting on glass slides; male genitalia in 60% Euparal and wing venation based on dried specimens. Photographs of adults and male genitalia were taken using a Dhyana 95 scientific CMOS camera (Tucsen, Fuzhou, China) attached to a Leica DM 2000 LED optical microscope (Leica, Wetzlar, Germany). Terminology for morphological characters of the adult follow Smith (1965).

Genomic DNA from four specimens of *Galleria similis* and 19 specimens of *G. mellonella* was extracted from the legs of dried specimens of adults in 100% alcohol using a MagListo 5M Genomic DNA Extraction Kit (Bioneer Corporation, Daejeon, Republic of Korea) according to the manufacturer's protocol. One mitochondrial protein coding gene, the cytochrome oxidase subunit I gene (*COI*) (Folmer et al. 1994) and two nuclear protein coding genes, Carbamoyl-phosphate synthetase 2, Aspartate transcarbamylase, and Dihydroorotase (*CAD*) and Wingless (*wg*) were sequenced (Haines and Rubinoff 2012) (Table 1). Primers and amplification strategies followed Haines and Rubinoff (2012) and are detailed in Table 2. PCR conditions for ampli-

fication followed Haines and Rubinoﬀ (2012), and directly sequenced at Macrogen (Geumcheon-gu, Seoul, Korea). Contigs were assembled in Geneious prime (Kearse et al. 2012). Successful *COI*, *CAD* and *Wingless* sequences were uploaded to GenBank (Table 1).

The barcodes were compared to 93 DNA barcodes of the genera *Galleria* and *Achroia* downloaded from BOLD systems v4 (BIN numbers: BOLD:AAA0965, BOLD:AAL2955, BOLD:ACO9701). A neighbor-joining analysis (NJ) was performed with MEGA X (Kumar et al. 2018) using the Kimura-2-Parameter (K2P)

**Table 1.** *Galleria* species and their *COI* barcodes and nuclear protein coding gene sequences with their associated and GenBank accession numbers as used in this study. Dashes indicate missing data.

Species	Voucher No.	<i>COI</i>	<i>CAD</i>	<i>wg</i>
<i>Galleria mellonella</i>	15310	MT439336	MT447104	MT447124
	15311	MT439337	MT447105	MT447125
	15312	MT439338	MT447109	MT447126
	15313	MT439349	MT447106	MT447127
	15314	MT439350	MT447107	MT447128
	15616	MT439351	MT447110	MT447129
	15617	–	MT447108	MT447130
	21361	MT439339	–	MT447131
	21362	MT439340	MT447111	MT447132
	21363	MT439341	MT447115	MT447133
	21364	MT439342	MT447114	MT447134
	21365	–	MT447119	MT447135
	21412	MT439343	MT447116	MT447136
	21413	MT439352	–	–
	21414	MT439346	MT447112	MT447137
	21415	MT439344	MT447113	MT447138
	21416	MT439347	MT447120	MT447139
	21417	MT439345	MT447118	MT447140
	21418	MT439348	MT447117	MT447141
<i>G. similis</i>	15315	MT447100	MT447121	MT447142
	21366	MT447101	MT447122	MT447143
	21367	MT447102	MT447123	MT447144
	21368	MT447103	–	MT447145

**Table 2.** List of primers and amplification strategies used in this study (abbreviations: s = second, min = minute).

Genes	Primers	Sequences (5' to 3')	Amplification strategies
<i>COI</i>	LCO1490	GGTCAACAAATCATAAAGATATTGG	LCO1490 + HCO2198 (Folmer et al. 1994)
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	
<i>CAD</i>	CAD4_Pyr_F	GAAGAAGCATTTCAAAAAGC	CAD4_Pyr_F + CAD4_Pyr_R (Haines and Rubinoﬀ 2012)
	CAD4_Pyr_R	CKRTCACATGTCRTA	
<i>wg</i>	LepWg1	GARTGYAARTGYCAYGGYATGTCTGG	LepWg1 + LepWg2 (Brower and Desalle 1998)
	LepWg2	ACTICGCARACCARTGGAATGTRCA	

\* PCR amplifications condition

- *COI*: 5-min 95 °C; 35 cycles: 30-s 95 °C, 25-s 48 °C, 45-s at 72 °C; 5-min 72 °C.

- *CAD*: 2-min 94 °C, 1-min 50 °C, 1-min 72 °C; 34 cycles: 1-min 94 °C, 1-min 50 °C, 1-min at 72 °C; 12-min 72 °C.

- *wg*: 2-min 94 °C, 1-min 56 °C, 1-min 72 °C; 34 cycles: 1-min 94 °C, 1-min 56 °C, 1-min at 72 °C; 12-min 72 °C.



model (Kimura 1980) for nucleotide substitutions. Bootstrap support values for each node were also evaluated via MEGA X with 1000 replicates. Parsimony analyses (PA) with bootstrap were conducted in TNT 1.5 (Goloboff and Catalano 2016) using search strategies described by Song and Ahn (2018).

Intra- and inter-specific distances in different taxonomic levels were calculated using the uncorrected pairwise distance method (Srivathsan and Meier 2012). To explore molecular diagnostic characters for the *Galleria* species, we used the “list common synapomorphies” function of TNT and then examined thoroughly listed characters in the alignment file.

Results

Molecular character analysis

A total of 21 new sequences was generated from four specimens of *Galleria similis* and 17 specimens of *G. mellonella* (524–650 bp of partial *COI* barcode region, 613 bp of partial *CAD*, and 432 bp of partial *wg* gene region). All new sequences were uploaded to GenBank (Table 1). The DNA barcodes (*COI*) were compared to those of 72 DNA barcodes in 16 countries (*G. mellonella*), one Australian specimen (*Galleria* sp.) and seven lesser wax moths (*Achroia grisella* Fabricius) downloaded from BOLD systems v4 (Fig. 7).

Genetic divergence of *COI* using uncorrected *p*-distance among the *Galleria* and *Achroia* species ranged from 5.3% to 12.0%, while intraspecific divergence ranged from 0% to 2.2% (Table 3). All four species were strongly supported as a single lineage on both NJ and PA trees (Figs 7, 8). The molecular analyses (*p*-distance, NJ and PA analyses) revealed that *G. mellonella* was closely related to *G. similis* (Table 3; Figs 7, 8). The maximum difference among populations within *G. mellonella* was 2.2%, and within *G. similis* was 0% (Table 3). For these two species, it is difficult to correctly delimit each species, due to their extreme similarities in external morphological characters (see taxonomy section below). In contrast to morphological characters, however, genetic divergence strongly supported the separation of *G. mellonella* and *G. similis*. The minimum inter-specific difference between the two species (5.3%) was much higher than the maximum intraspecific difference of *G. mellonella* (2.2%) (Table 3). Furthermore, molecular diagnostic characters for the *Galleria* species, *G. mellonella* and *G. similis* contained 15 characters for *COI*, one character of *CAD* and four characters of *wg* gene regions (Table 4).

**Table 3.** Inter- and intraspecific genetic differences in the two genera *Galleria* and *Achroia* species for *COI* (658 bp) calculated using *p*-distance.

	<i>G. mellonella</i>	<i>G. similis</i>	<i>Galleria</i> sp.	<i>A. grisella</i>
<i>G. mellonella</i>	0–0.022			
<i>G. similis</i>	0.053–0.066	0		
<i>Galleria</i> sp.	0.112–0.119	0.114	0	
<i>A. grisella</i>	0.107–0.116	0.117–0.119	0.116–0.120	0–0.003

**Table 4.** List of 20 molecular diagnostic characters used to determine the genetic distinctiveness of two cryptic species *Galleria mellonella* and *G. similis* based on mtDNA partial *COI*, nuDNA partial *CAD* and *wg* gene region. Numbers indicate nucleotide sites in the sequenced 658 bp portion of the *COI* gene, 613 bp portion of the *CAD* gene and 432 bp portion of the *wg* gene. Number position follows *G. mellonella*: MT439366 (*COI*), MT447104 (*CAD*) and MT447124 (*wg*).

Species	Genes									
	<i>COI</i>									
	16	34	109	197	232	259	271	274	280	307
<i>G. mellonella</i>	T	A	A	T	T	T	T	T	T	T
<i>G. similis</i>	C	T	G	C	C	C	C	C	C	C
Species	<i>COI</i>					<i>CAD</i>	<i>wg</i>			
	385	391	403	424	470	319	129	241	343	379
<i>G. mellonella</i>	T	T	C	T	T	G	A	T	C	C
<i>G. similis</i>	C	C	T	C	C	A	C	C	T	T

**Table 5.** List of three molecular diagnostic characters used to determine the molecular distinctiveness of two cryptic species *Galleria mellonella* and *G. similis* based on amino acid sequences of partial *COI*, *CAD*, and *wg* protein region. Numbers indicate amino acid site in the sequenced 201 amino acid (aa) portion of the *COI* protein, 204 aa portion of the *CAD* protein and 143 aa portion of the *wg* protein. Number position follows *G. mellonella*: the translated amino acid sequences of MT439366 (*COI*), MT447104 (*CAD*) and MT447124 (*wg*).

Species	Proteins		
	<i>COI</i>	<i>CAD</i>	<i>wg</i>
	152	107	43
<i>G. mellonella</i>	V	A	E
<i>G. similis</i>	I	T	A

We also found three distinct differences in the amino acid sequences of each protein (Table 5). In particular, the transition from G (guanine) to A (adenine) at the 319 site of *CAD* protein led to a change from a hydrophobic amino acid (Alanine, A) to a hydrophilic amino acid (Threonine, T), and the transversion from A to C (cytosine) at the 129 site of the *wg* protein led to a change from a hydrophilic amino acid (Glutamate, E) to a hydrophobic amino acid (A). The molecular characters provided further evidence that new species *G. similis* was distinct and valid.

## Taxonomic accounts

### Genus *Galleria* Fabricius, 1798

*Galleria* Fabricius, 1798: 419, 462. Type species: *Phalaena cereana* Blom, 1764, by subsequent designation by Latreille (1810: 441).

*Cericlepta* Sodoffsky, 1837: 93. Type species: *Galleria mellonella* Linnaeus, 1758, by original designation.

*Vindana* Walker, 1866: 1706. Type species: *Vindana obliquella* Walker, 1866, by monotypy.

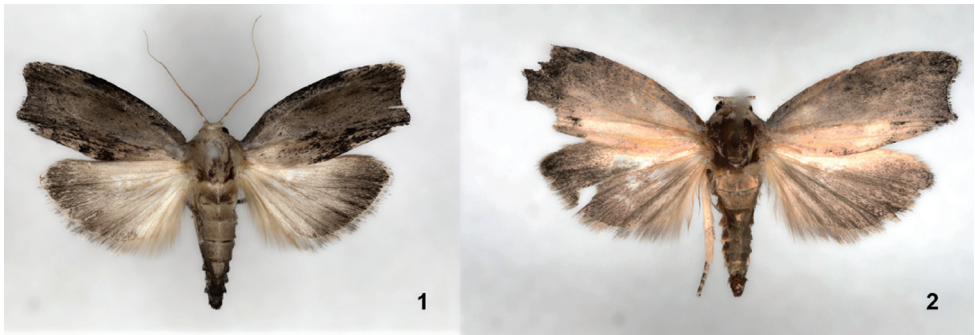
***Galleria similis* Roh & Song, sp. nov.**

<http://zoobank.org/DD9DF8D5-D3D5-4235-80AE-294C9B731EAB>

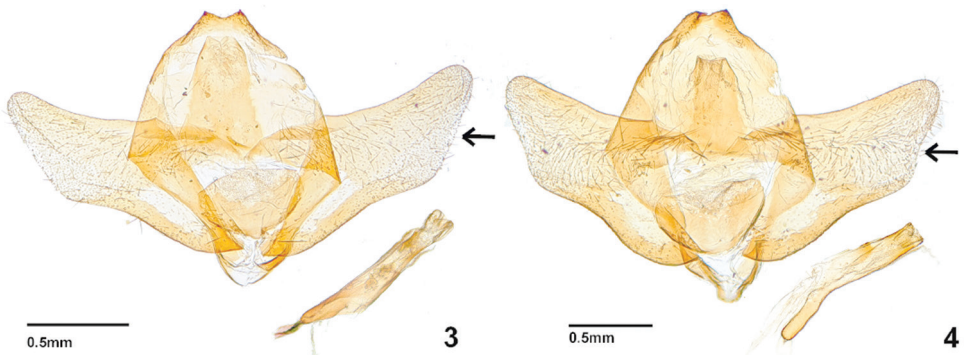
Figures 2, 4, 6

**Type material.** *Holotype*. ♂, **Korea**: Waju-gun, 14.xi.2014, 35°49'45.64"N, 127°02'27.20"E, leg. H.S. Shim, genitalia slide no. 15315, DNA barcode GenBank accession no. MT447100 (NAS). *Paratypes*. 3♂, **Korea**: Tongyeong, 17.i.2020, 34°50'58.58"N, 127°26'51.79"E, leg. J.-H. Song, genitalia slide no. 21366–21368, DNA barcode GenBank accession no. MT447101, MT447102, and MT447103 (NAS).

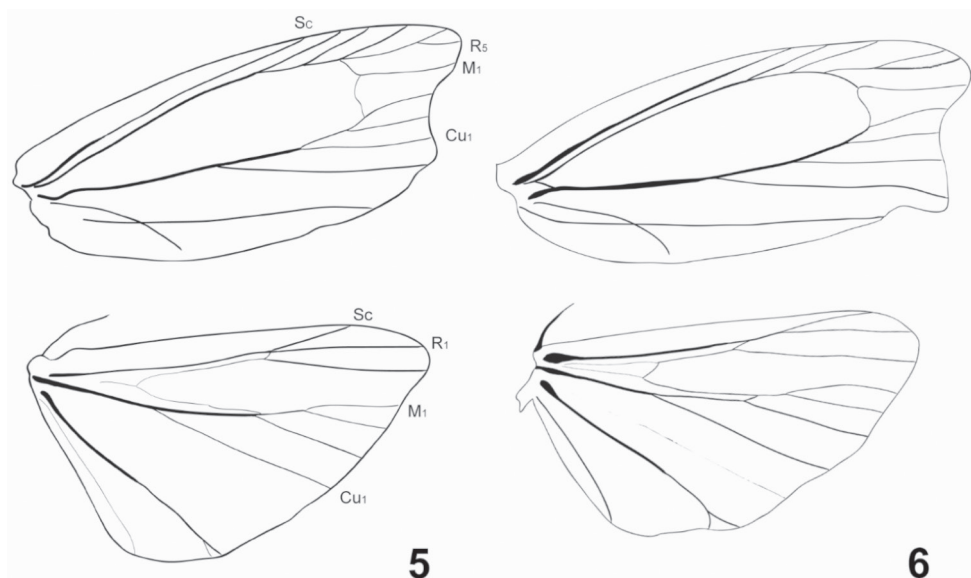
**Diagnosis.** *Galleria similis* sp. nov. (Figs 2, 4, 6) is very similar to *G. mellonella* (Figs 1, 3, 5) but can be distinguished by a square discal cell of its hindwing venation (Fig. 6) and the different shape of male genitalia (Fig. 4, *G. similis*: valva shorter and wider, concave at outer margin). *Galleria similis* sp. nov. had 15, one and four diagnostic characters from 658 bp of partial *COI*, 613 bp of partial *CAD* and 423 bp of partial *wg* gene region, respectively (Table 4). Our study showed that morphological and molecular characters can be used to resolve the status of cryptic species, *G. mellonella*



**Figures 1, 2.** Adults of *Galleria* species. **1** Male of *G. mellonella* **2** male of *G. similis*, holotype.



**Figures 3, 4.** Male genitalia of *Galleria* species. **3** *G. mellonella* (slide no. 21364) **4** *G. similis*, paratype (slide no. 21367).



**Figures 5, 6.** Male wing venation of *Galleria* species. **5** *G. mellonella* **6** *G. similis*, paratype.

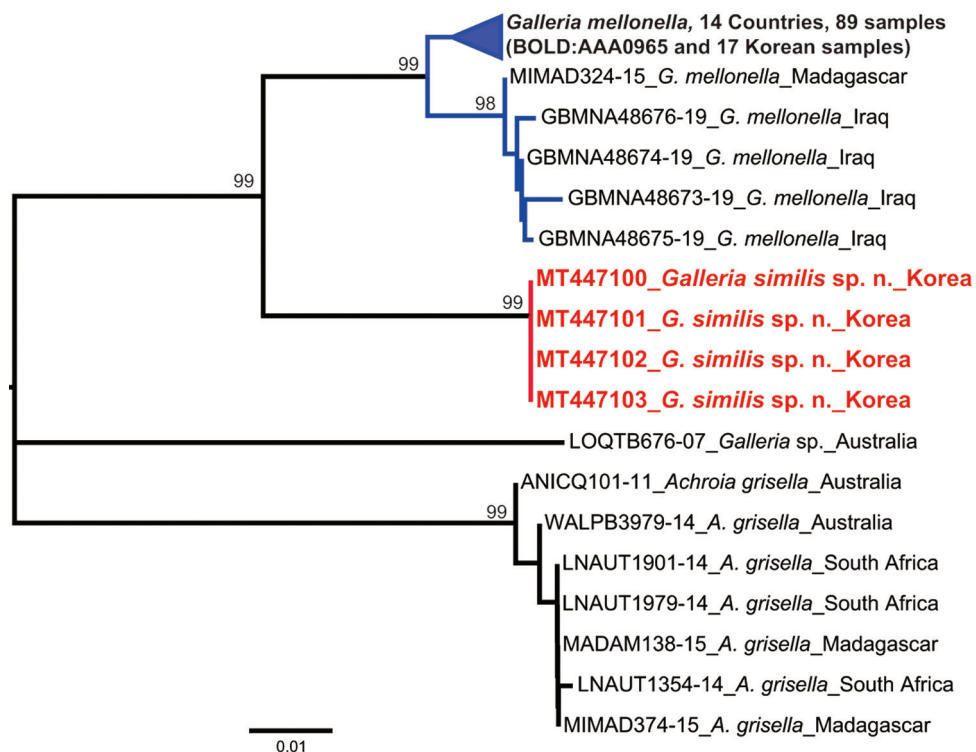
and *G. similis*. A cryptic species was suggested by the unusually high genetic distances within specimens originally identified as *G. mellonella*.

**Description. Adult. Male** (Fig. 2). Head: vertex densely clothed with gray hair-like scales; labial palpus three-segmented. Thorax: Light brown; notum covered with gray scales. Legs with femora, tibiae, and tarsi clothed with light gray piliform scales; tarsi apical and medial spurs covered dark-brown scales. Wingspan 21.5–32.0 mm. Forewing (Fig. 6) narrow, costa straight at base and gently curved beyond 4/5, termen concave; tornus pointed, 9 separate veins originating at the discal cell; Sc terminating at 4/5 costa;  $R_5$  originated at  $R_4$ ,  $M_1$  and  $M_2$  parallel;  $M_2$ ,  $M_3$  originating at distal corner of discal cell;  $Cu_1$  and  $Cu+A_1$  parallel, ground color yellowish white with gray and some dark overscaling. Hindwing (Fig. 6) discal cell square, L/W ratio 1.72; costa straight, apex straightly curved to termen; Sc straight to 3/5 costa;  $R_1$ ,  $R_2$  and  $R_3$  present;  $R_1$  and  $R_2$  terminating at apex;  $M_2$  originating at 1/5  $M_3$ ;  $CuA_1$  and  $CuA_2$  parallel;  $A_1$  originating at 4/5  $Cu_2$ . Hindwing covered with dark-brown scales; postmarginal part present with short light brown hairs. Abdomen: Male genitalia (Fig. 4) with uncus concave and hooked; tegumen wide at base; gnathos long; valva short and wide, costa straight, termen relatively concave, small setae present sparsely on outer and inner surface; vinculum narrower than gnathos; juxta heart shaped; saccus very short and slender; phallus slightly short and thick, vesica with short setae, ductus ejaculatorius present.

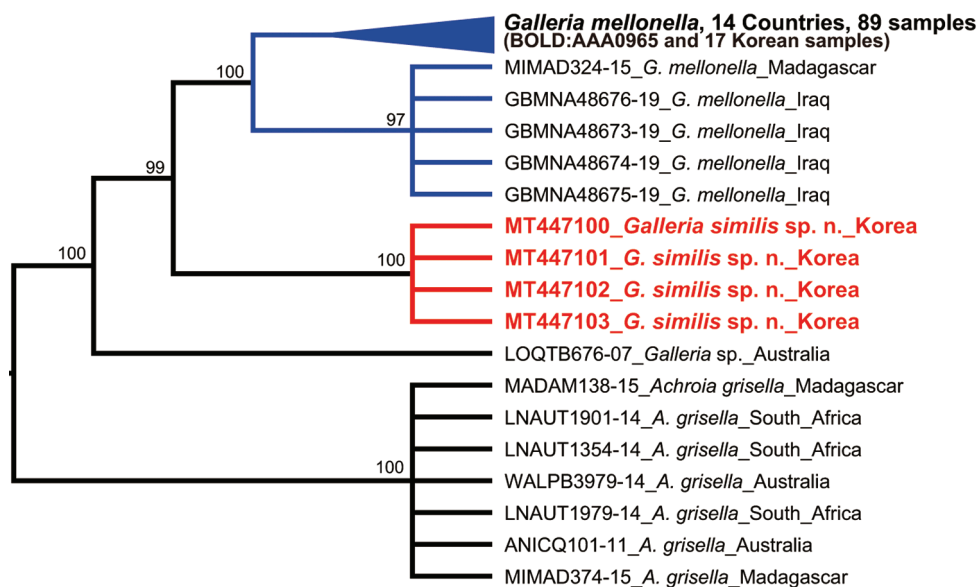
**Female.** Unknown.

**Distribution.** Korea.

**Etymology.** Named from the Latin *similis* meaning “similar”, which refers to the similar morphological characters with *G. mellonella*.



**Figure 7.** Neighbor-Joining tree based on partial *COI* gene sequences with bootstrap values. Scale bar indicates the expected number of substitutions per site.



**Figure 8.** Strict consensus tree of equally parsimonious cladograms based on partial *COI* gene sequences with bootstrap values.

## Acknowledgements

We thank T. Han (Korea National Park Research Institute, Korea) and S.I. Lee (National Institute of Agricultural Sciences, Korea) for assistance with DNA extraction. This work was carried out with the support of “Cooperative Research Program for Agriculture Science and Technology Development (Project No. PJ01504902)” Rural Development Administration, Republic of Korea.

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# A new subterranean species and an updated checklist of *Strumigenys* (Hymenoptera, Formicidae) from Macao SAR, China, with a key to species of the Greater Bay Area

François Brassard<sup>1</sup>, Chi-Man Leong<sup>1,3</sup>, Hoi-Hou Chan<sup>2</sup>, Benoit Guénard<sup>1</sup>

**1** The Insect Biodiversity and Biogeography Laboratory School of Biological Sciences, The University of Hong Kong, Pok Fu Lam Rd, Lung Fu Shan, Hong Kong SAR, China **2** Division of Nature Conservation Studies, Instituto Para Os Assuntos Municipais, Macao SAR, China **3** Macao Science Center, Avenida Dr. Sun Yat-Sen, Macao SAR, China

Corresponding author: François Brassard ([francois.brassard.bio@gmail.com](mailto:francois.brassard.bio@gmail.com))

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## Abstract

In the past few decades, sampling of leaf litter with Winkler extractors revealed how abundant and ubiquitous ants from the genus *Strumigenys* are. It is now known that this genus has the third greatest number of species within the Formicidae family. However, very few subterranean species are known, which may be due to the current under-sampling of the soil stratum. Here, a holistic sampling approach, including the use of subterranean traps, was employed in Macao SAR, China. Subterranean traps allowed the collection of a new cryptic ant species: *Strumigenys subterranea* Brassard, Leong & Guénard, **sp. nov.** Moreover, extensive sampling of the leaf litter in secondary forests provided four new species records for the genus. The list of Macanese *Strumigenys* is here updated, elevating the known diversity in Macao to nine species. Furthermore, to facilitate further research on ants of the Guangdong-Hong Kong-Macao Greater Bay Area, a key to the 29 *Strumigenys* species known from the region is provided. Lastly, recommendations for sampling methods to assess ant biodiversity underground are discussed. In conclusion, this study highlights the importance of using extensive sampling methods, and suggests that relatively small patches of secondary forests within cities can hold a surprisingly high diversity as well as some undescribed species.

## Keywords

ants, hypogaecic, species list, subterranean, taxonomic key, urban

## Introduction

With a total of 851 described extant species (AntCat.org 2020), *Strumigenys* is one of the most diverse ant genera. Primarily distributed within tropical and subtropical regions, several species occur nonetheless within temperate regions (Janicki et al. 2016; Guénard et al. 2017). Yet, the *Strumigenys* diversity currently reported within tropical regions is likely underestimated. For example, in Southeast Asia, several authors have shown that unrecorded and undescribed *Strumigenys* species should be expected within several countries (e.g., Guénard et al. 2010; Eguchi et al. 2011; Liu et al. 2015; Jaitrong et al. 2016; Tang et al. 2019). Accordingly, recent work sampling leaf-litter ant communities in Yunnan and Hong Kong resulted in a substantial increase in their known *Strumigenys* diversity, both because of unrecorded and undescribed species (Liu et al. 2015; Tang et al. 2019).

Morphologically, *Strumigenys* species are easily distinguished by their small body size, the spongiform tissues on their metasoma (when present), their specialized pilosity and their opposable mandibles (Bolton 1999). Phylogenetically, species of *Strumigenys* were recently moved from the Dacetini to the Attini tribe based on molecular analyses, strengthening their position as the sister taxon to the phalacromyrmecine ants (Ward et al. 2015). Ecologically, *Strumigenys* species tend to be associated with primary and secondary forest habitats, with a few species, including several tramp species (e.g., *Strumigenys emmae* Emery, 1890, *Strumigenys membranifera* Emery, 1869), relatively common in open and disturbed habitats such as urban parks (Kitahiro et al. 2014; Tang et al. 2019). At the microhabitat level, *Strumigenys* are typically encountered within the leaf-litter covering forests floors, though a few species nest under bark or epiphytes (Longino 2006), are associated with the accumulated leaf litter in trees (Nadkarni and Longino 1990) or forage on the understory vegetation (Lattke et al. 2018). In general, workers of *Strumigenys* species are collected by leaf litter extractions with Berlese funnels and mini-Winklers. However, these sampling methods may limit the discovery of some *Strumigenys* species, especially those with subterranean habits. The extraction of soil monoliths and the use of subterranean traps are effective methods to sample the poorly known subterranean ant fauna (Andersen and Brault 2010; Wong and Guénard 2017; Martins et al. 2020). An increase in their systematic use is likely to uncover new species, including within the genus *Strumigenys*.

Macao is a special administrative region of China located on the south side of the Pearl River Delta. Despite being an under-sampled and heavily urbanized territory with a land area of ~30 km<sup>2</sup>, it nevertheless harbors a surprisingly high ant diversity (Leong et al. 2017). Until recently, few species of *Strumigenys* were known to inhabit the region. The first *Strumigenys* record was made by Wheeler in 1928, with the mention of the exotic *Strumigenys membranifera*. Seventy-eight years later, a second record, *Strumigenys sylvestrii* Emery, 1906, was published by Hua (2006). This record is, however, most certainly erroneous (Tang et al. 2019). In 2017, opportunistic leaf litter extractions and hand collection expanded the list of *Strumigenys* species for Macao with four additional species records (Leong et al. 2017). Thus prior to this study, two native (i.e., *Strumigenys exilirhina* Bolton, 2000 and

*Strumigenys minutula* Terayama & Kubota, 1989) and three introduced *Strumigenys* species (i.e., *S. emmae*, *S. membranifera*, and *S. nepalensis*) had been recorded in Macao, far less than the 24 species recorded in the neighboring territory of Hong Kong (Tang et al. 2019).

In this study, we used specimens collected through a holistic sampling protocol done to assess the ant fauna of Coloane Island, Macao (Brassard et al. unpublished). In particular, we focus on the *Strumigenys* species found within the region and report four new species records. Moreover, we describe a species collected with a new type of subterranean trap (M.K.L. Wong, unpublished): *Strumigenys subterranea* sp. nov. When available, we also provide new sociometric and ecological information for the species collected. Finally, we provide a taxonomic key for the 29 *Strumigenys* species known from the Guangdong-Hong Kong-Macao Greater Bay Area, a megacity including Macao SAR, Hong Kong SAR, and nine cities in Guangdong province (Hui et al. 2018).

## Materials and methods

The majority of specimens examined were collected in 2019 across multiple sites in Coloane Island, Macao (22.1261°N, 113.5669°E; Suppl. material 1: Fig. S1). Ants were sampled using a variety of methods including hand collection, arboreal traps, subterranean traps (Suppl. material 2: Fig. S2), leaf litter extraction with Winkler extractors, artificial ground nests (Booher et al. 2017) placed in the field between 11 and 18 weeks (Suppl. material 3: Fig. S3), and ground baits (Suppl. material 4: Fig. S4).

Images were taken with a Leica DFC450 camera mounted on a Leica M205 C dissecting microscope. Image montages of the specimens were taken, stacked, enhanced and measured using the Leica Application Suite v. 4.5.

## Results

### Taxonomic accounts

#### *Strumigenys subterranea* Brassard, Leong & Guénard, sp. nov.

<http://zoobank.org/6229098D-6815-4ABB-9753-1D1B625FC215>

**Type locality.** MACAO SAR, CHINA: Coloane Island, Coloane North East hiking trail, 22.1351°N, 113.5700°E, ca. 80 m, subterranean trap placed at a depth of 12.5 cm, 14 May–4 June 2019, F. Brassard leg.

**Repository institution.** Insect Biodiversity and Biogeography Lab (IBBL), School of Biological Sciences, Hong Kong University

**Type specimen. Holotype.** Pinned worker. Original label: “China SAR: Macau, Coloane. Coloane North East Hiking Trail. 78 m, 14v–4vi.2019, 22.13510°N, 113.57000°E, Subterranean Trap 12.5 cm depth. F. Brassard” “MAC\_S12\_12.5\_q4\_Sp.2” [IBBL: ANTWEB1010847].

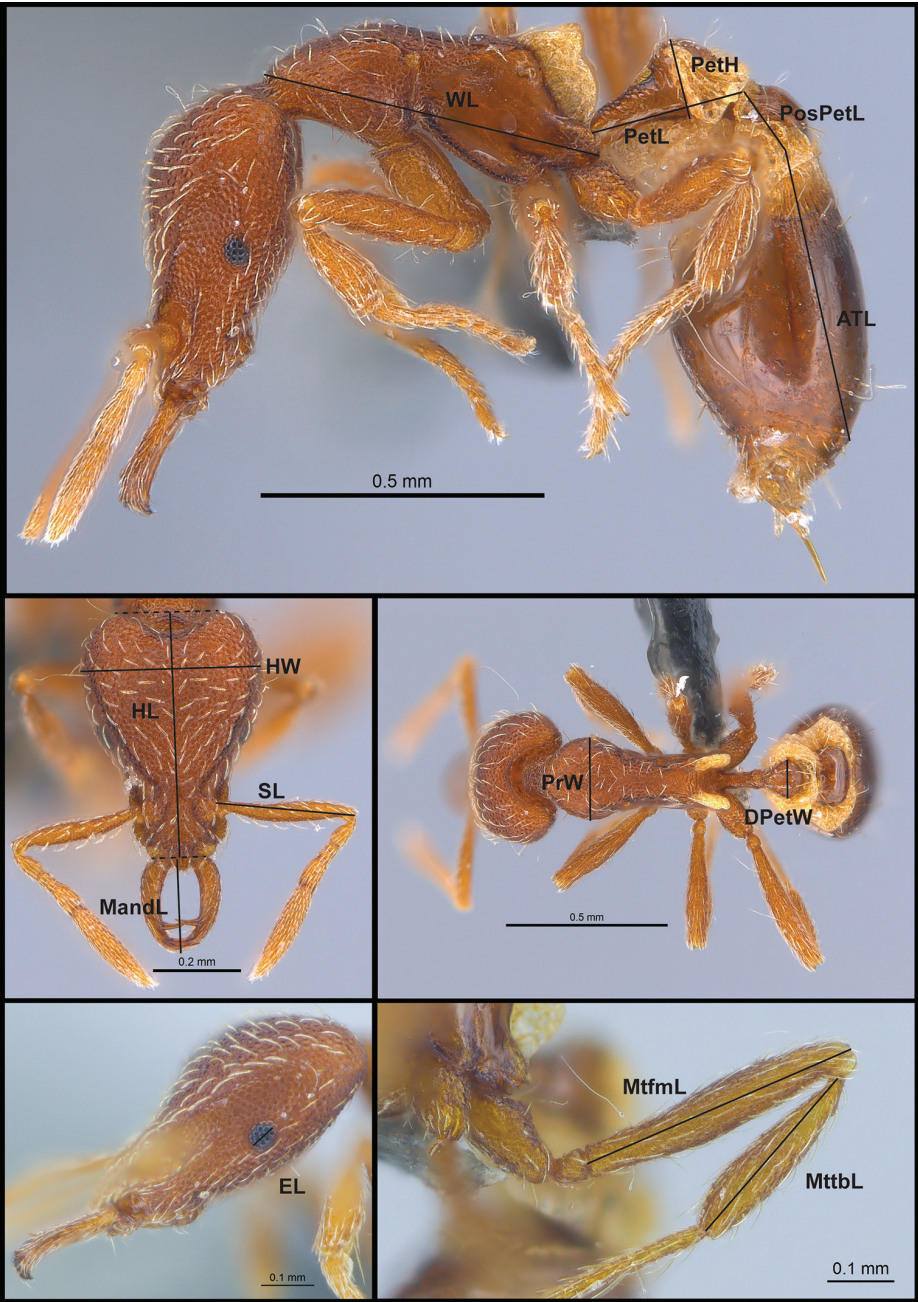
**Table 1.** Morphological measurements used. Morphological terminology follows Tang et al. (2019).

TL	<b>Total Length:</b> measured from the mandibular apex to the posterior margin of abdominal tergite IV. Sum of MandL + HL + ML + PetL + PosPetL + ATL.
HL	<b>Head Length:</b> measured from the midpoint of the occipital margin to the midpoint of the anterior clypeal margin. If one or both margins are concave, measured from the midpoint of a transverse line spanning the apices of the projecting portions.
HW	<b>Head Width:</b> measured at the maximum width of the head in full-face view, excluding the eyes.
MandL	<b>Mandible Length:</b> measured from the mandibular apex to the anterior clypeal margin. If clypeal margin concave medially, measured from the transverse line connecting the anteriormost points.
SL	<b>Scape Length:</b> measured from the basal constriction that occurs distal of the condylar bulb.
EL	<b>Eye Length:</b> maximum diameter of the eye.
PrW	<b>Pronotal Width:</b> maximum width of the pronotum in dorsal view. If present, projecting tubercles or other cuticular prominences at the pronotal humeral angles ignored.
WL	<b>Weber's Length:</b> diagonal length of the mesosoma in profile view. Measured from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.
PetL	<b>Petiolar Length:</b> maximum length of petiole. Measured from posterior petiolar margin to the anteriormost point before posteroventral lobes of the propodeum obscure petiole. If present, spongiform tissues are ignored.
PetH	<b>Petiolar Height:</b> maximum distance measured between two parallel lines, one tangent with the node apex and the other tangent with the ventral-most point of the petiole in profile. If ventral margin concave upward, measure from the lower line tangent to the uppermost portion of the curve. If present, spongiform tissues ignored.
DPetW	<b>Dorsal Petiolar Width:</b> maximum width of petiolar node in dorsal view.
PosPetL	<b>Postpetiole Length:</b> maximum length of postpetiole, measured from the anterior margin to the posterior margin. If present, spongiform tissues are ignored.
ATL	<b>Abdominal tergum IV Length:</b> maximum length of the fourth abdominal tergite, measured from the anterior margin to the posterior margin.
MtfmL	<b>Metafemur length:</b> maximum length of the metafemur, not including the trochanter.
MttbL	<b>Metatibia length:</b> maximum length of the metatibia.
CI	<b>Cephalic Index:</b> HW / HL × 100
MI	<b>Mandibular Index:</b> MandL / HL × 100
SI	<b>Scape Index:</b> SL / HW × 100
PI	<b>Pronotum Index:</b> PrW / HW × 100
OI	<b>Ocular Index:</b> EL / HW × 100
LPI	<b>Lateral Petiolar Index:</b> PetH / PetL × 100
DPI	<b>Dorsal Petiolar Index:</b> DPetW / PetL × 100

**Worker measurements.** ( $n = 1$ ): TL 1.809 mm, HL 0.454 mm, HW 0.348 mm, CI 77, MandL 0.098 mm, MI 22, SL 0.226 mm, SI 65, PrW 0.189 mm, PI 54, EL 0.006 mm, OI 2, WL 0.458 mm, PetH 0.124 mm, PetL 0.183 mm, MtfmL 0.295 mm, MttbL 0.230 mm, LPI 68, DPetW 0.117 mm, DPI 64, PosPetL 0.184 mm, ATL 0.356 mm.

**Diagnosis.** Mandibles in full-face view triangular, eyes with a single ommatidium, anterior margin of clypeus shallowly convex, clypeal margin fringed with a continuous row of appressed spatulate hairs incurved towards midline of head, conspicuous preocular carina, dorsoventrally flattened scape, spatulate to spoon-shaped hairs on leading edge of scape, pair humeral hairs present, dorsum of head behind clypeus reticulate-punctate, side of mesosoma and disc of postpetiole smooth, postpetiole with





**Figure 1.** Morphological measurements used. For definition of each abbreviation see Table 1.

concave anterior margin and a projecting lobe on convex posterior margin, total dental count of eight, lack of propodeal spines, and propodeal declivity angular.

**Worker description.** (Figs 2–4). **Head.** In full-face view, head noticeably longer than wide (CI: 77) (Fig. 3A), with its widest portion nearby the anterior end of the



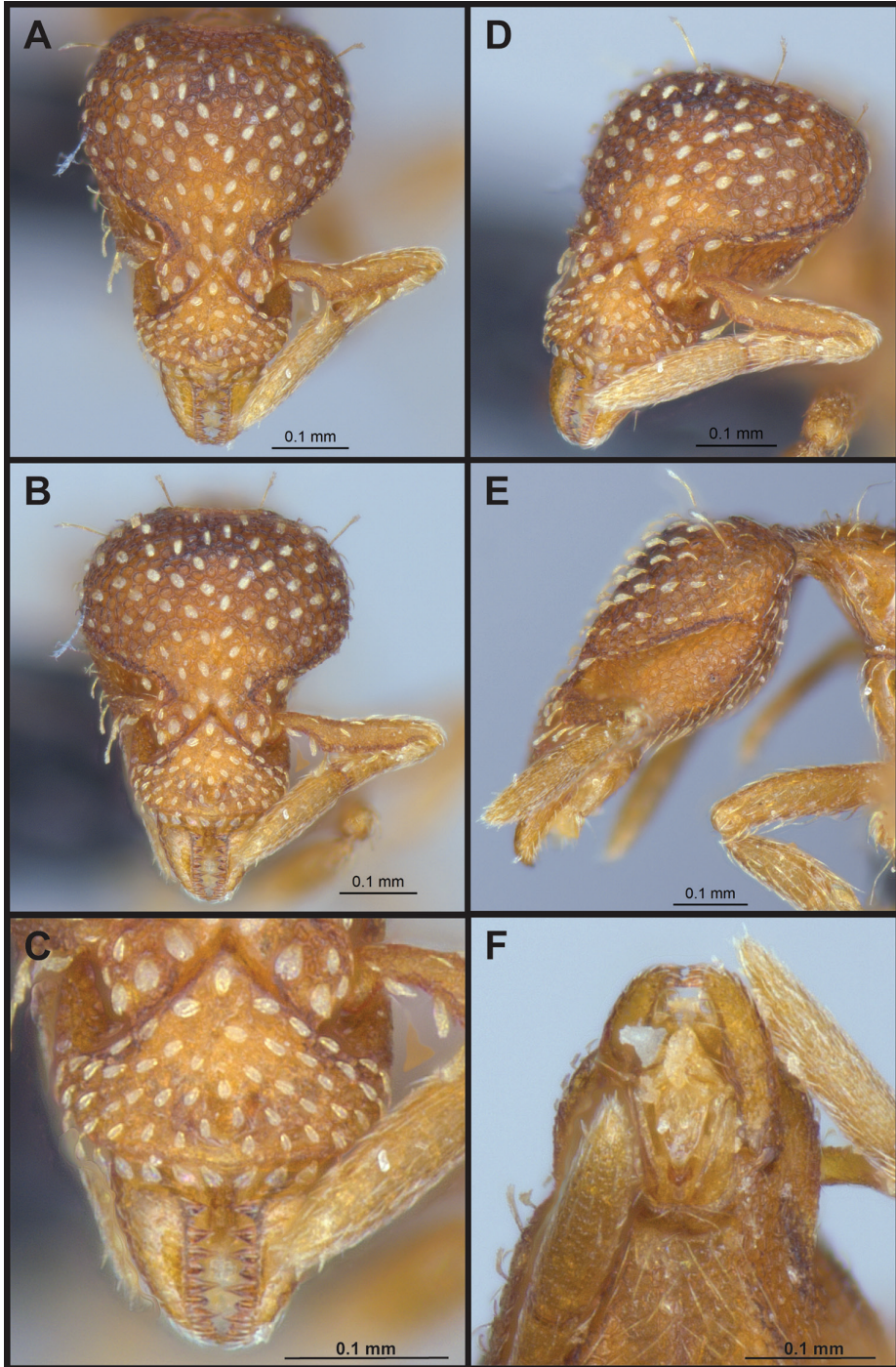


**Figure 2.** *Strumigenys subterranea* sp. nov. (ANTWEB1010847), worker in profile view.

posterior third of its length. In lateral view, eye with a single facet, inconspicuous, and located at the widest level of the head (Fig. 3E). Posterior cephalic margin shallowly concave; corners of posterior margin of head weakly developed and evenly rounded through the lateral margins. Posterolateral margins evenly rounded on half of their length, then converging at a slightly steeper angle towards the center of the head. Anteromedian clypeal margin slightly convex. Scapes with a moderately developed subbasal lobe on their anterior portion. Apex of scape not reaching posterior margin of head, antenna including scape with six articles, with the last two articles distinctly enlarged and forming a club; ratio of antennal segments from 2<sup>nd</sup> to 6<sup>th</sup> segment = 3.83 : 1.33 : 1 : 3.05 : 11.56 (Fig. 3D). Mandibles triangular with eight teeth (T) and four denticles (D), arranged from basal to apical as such: T-D-T-T-T-T-T-D-D-D-T (Fig. 3C). Basal angle between the basal margin and masticatory margin rounded triangular. Basal lamella a thin strip, widest at the basal tooth and almost fully disappearing at the midpoint of the masticatory margin. Labrum terminates in a pair of short triangular lobes (Fig. 3F).

**Mesosoma.** In lateral view, dorsum of mesosoma broadly convex but slightly concave at the metanotal groove (Fig. 4A). Anterior portion of promesonotum in dorsal view convex (Fig. 4B), with its widest point slightly posterior to the humeral hairs. Median anterior margin of promesonotum slightly convex. Lateral margin of promesonotum subparallel and slightly convex. Metanotal groove distinct but weakly incised. In dorsal view, propodeum approximately half of the maximal width of the promesonotum. In lateral view, propodeum with an angular declivity. Propodeal declivity with a spongiform lamella.

**Metasoma.** Petiole in lateral view elongate (LPI: 68) and subclavate, with long and thin peduncle. Petiolar node well developed; dorsum of node convex, with its widest



**Figure 3.** *Strumigenys subterranea* sp. nov. (ANTWEB1010847) **A–F** worker **A** full-face view **B** face view tilted posteriorly to showcase hairs on vertex **C** mandibles **D** left antenna **E** side view to showcase the eye **F** ventral view to showcase labrum.

point at the posterodorsal corner. Petiolar node in dorsal view subcircular (DPI: 64), widest towards the posterior part. Postpetiolar disc in dorsal view suboval and distinctly wider than long; the median portion of the anterior margin distinctly concave whereas the posterior margin convex with a lobe projecting from the median portion (Fig. 4C). Limbus in dorsal view strongly concave, with a thin spongiform pad along its length. Spongiform tissues present on both petiole and postpetiole. Spongiform tissue on the lateral side of petiole restricted to the posterior portion of the node in profile. Excluding the anteriormost part of the ventral portion of petiole, spongiform tissue covers the ventral portion of both the petiole and postpetiole entirely. Depth of spongiform tissue under petiole nearly as much as petiole height. Spongiform tissue particularly extensive on the ventral lobes of the postpetiole. In dorsal view spongiform tissue present along the posterior margin of the petiolar node, and surrounding disc of postpetiole.

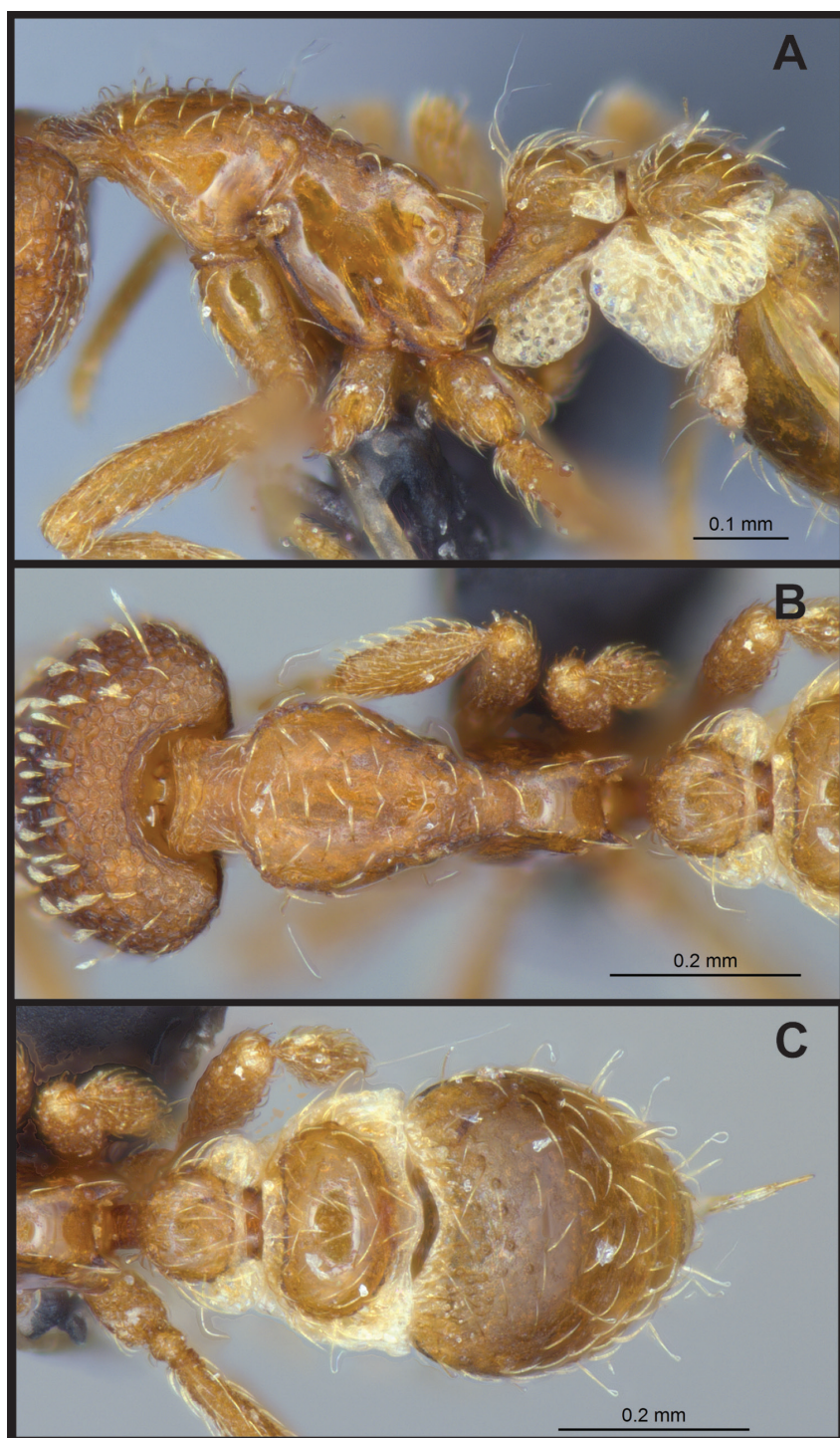
**Pilosity.** On head, spatulate hairs arising from their base and then abruptly curving towards the mandibles, forming a space between the scale of the hair and the head surface. In full-face view of head, numerous evenly spaced spatulate hairs (ca. 95) along the frons, with around two-thirds as much spatulate hairs (ca. 60) evenly spaced but more densely arranged on the clypeus. A total of 16 smaller spatulate hairs present on anterior margin of clypeus. On each side of the anterior margin of the clypeus, three hairs on lateral portion and five on the anterior portion, all incurved towards the midline of the head. Largest spatulate hairs ( $n = 6$ ) fully extending and found on subbasal lobe of antennal scape; with the first two basal hairs curved towards the apex of the scape, whereas the four most posterior hairs are curved towards the base of the scape. Two pairs of thin remiform hairs on the vertex; with one pair on the lateral portions of vertex and the other in posteromedial position (Fig. 3B). In profile view, appressed simple hairs present below antennal scrobe towards ventral portion of head. On the mesosoma and metasoma, decumbent hairs evenly spaced with a pair of long flagellate humeral hair present on petiolar node; several erected simple, appressed and filiform hairs present on first gastral tergite, whereas other tergites and sternites are mostly covered by appressed simple hairs. Appressed simple hairs present on tibia, femur and tarsus. Meso- and meta-basitarsal hairs flagellate. Flagellate hairs absent from femurs and tibiae.

**Sculpture.** In full-face and lateral view, head covered by areolate sculpturing (0.10 – 0.23 mm). In dorsal view, superficial sculpturing on the surrounding of the pronotum and on its posterior section. Center of the dorsal portion of the pronotum and propodeum smooth; lateral portions of mesosoma smooth (Fig. 4A). In dorsal view, discs of petiole and postpetiole smooth. In lateral view, petiole with weak sculpturing. Basigastral costulae present as weakly developed and irregular imprints on the central part of the limbus, extending around half the length of the postpetiole disc. Sculpturing on tibiae and femurs areolate. Leg bullae absent.

**Color.** Body coloration concolor yellowish brown, with slightly lighter coloration on the legs, antennae, mandibles and at the apex of the gaster. First gastral tergite and sternite with darker coloration.

**Comments.** *Strumigenys subterranea* sp. nov. belongs to the *Strumigenys rostrata* group of the Malesian-Oriental-East Palearctic region (Bolton 2000), due to a com-





**Figure 4.** *Strumigenys subterranea* sp. nov. (ANTWEB1010847) **A–C** worker **A** lateral view of mesosoma **B** dorsal view of mesosoma **C** dorsal view of metasoma.

bination of morphological characters: mandibles in full-face view triangular, basal lamella of mandible low and rounded-triangular, anterior margin of clypeus broad and shallowly convex, clypeal margin fringed with a continuous row of curved spatulate to spoon-shaped hairs, conspicuous preocular carina, dorsoventrally flattened scape, spatulate to spoon-shaped hairs on leading edge of scape, cuticle within scrobe reticulate or reticulate-punctate, pronotum dorsum without a median longitudinal carina, spongiform appendages present on petiole and postpetiole, pronotal humeral hair present, dorsum of head behind clypeus reticulate-punctate, side of propodeum and disc of postpetiole smooth.

However, *S. subterranea* sp. nov. can be distinguished from the other 17 species within this group (Table 2) by a combination of the following characters: eyes with a single ommatidia, clypeal margin shallowly convex, evenly spaced appressed spatulate hairs along frons (with appressed spatulate hairs evenly spaced but more densely arranged on clypeus), postpetiole with concave anterior margin and a projecting lobe on convex posterior margin, total dental count of nine, lack of propodeal spines, and propodeal declivity angular, not rounded.

We found that the most peculiar characteristic of *S. subterranea* (i.e., having very small eyes) is shared with *Strumigenys atropos* Bolton, 2000. However, the shape of the postpetiolar node (straight anterior margin in *S. atropos* but concave in *S. subterranea* sp. nov.) and the shape of the anterior margin of the clypeus differ (slightly convex in *S. subterranea* sp. nov., but noticeably concave in *S. atropos*). Moreover, large spatulate hairs are present up to two-third of the length of the lateral margins of the head of

**Table 2.** Comparison of five diagnostic characters for *S. rostrata* group. Characters are (A) appressed spatulate hairs on cephalic region, (B) margin of clypeus convex, (C) anterior margin of postpetiole concave, (D) propodeal spines small or absent and (E) eye composed of a single ommatidium. Values represent the presence (1) or absence (0) of a character.

Species	Characters				
	A	B	C	D	E
<i>subterranea</i>	1	1	1	1	1
<i>ambatrix</i>	1	1	1	0	0
<i>arizonica</i>	0	0	0	0	0
<i>atropos</i>	0	0	0	1	1
<i>Bunki</i>	1	0	0	1	0
<i>californica</i>	1	0	0	0	0
<i>carolinensis</i>	1	0	0	0	0
<i>chiricahua</i>	0	0	0	0	0
<i>emeswangi</i>	0	0	1	1	0
<i>Fautrix</i>	1	1	1	0	0
<i>hyalina</i>	1	0	0	0	0
<i>incerta</i>	0	0	1	1	0
<i>inopina</i>	0	0	1	0	0
<i>nepalensis</i>	1	0	1	0	0
<i>rostrata</i>	1	0	0	0	0
<i>rostrataeformis</i>	1	1	0	0	0
<i>symmetrix</i>	1	1	1	0	0
<i>Victrix</i>	1	0	1	1	0

*S. atropos*, but not in *S. subterranea*. Lastly, large spatulate hairs are present on the dorsal portion of the pronotum of *S. atropos*, whereas hairs on the dorsal portion of *S. subterranea* are fine.

**Etymology.** The name of this new species refers to the stratum it was collected in and to its suggested subterranean ecology.

**Ecology.** A single worker from this species has been collected so far, found within a subterranean trap; a 15 mL falcon tube placed at a depth of 12.5 cm below the ground surface. It contained ethanol 70% and was baited with tuna mixed with honey (see Suppl. material 1: Fig. S1 for sampling design). The trap was placed in young secondary forest and was operating continuously for a period of 21 days. Little is known about the ecology of this species. However, due to the extremely reduced eyes present on the specimen and its collection through a subterranean trap, it is here suggested that the species has subterranean habits. Further reinforcing this hypothesis is the fact that extensive sampling in Hong Kong and Macao over the past 6 years focusing on ground-dwelling and leaf-litter ants using Winklers and pitfall traps never yielded this species. Nevertheless, only a single worker was found within one out of 256 subterranean traps retrieved during our sampling on Coloane Island, which indicates this species is uncommon. Our data also suggests it cohabits within the same soil layer with other ant species, including other subterranean species. Indeed, we found within the same trap one worker of *Pheidole ochracea* Eguchi, 2008 and hundreds of workers of *Carebara zengchengensis* Zhou, Zhao & Jia, 2006. Additionally, within the same quadrat (1 × 1 m) we also found *C. zengchengensis* at depths of 25, 37.5 and 50 cm, as well as *Solenopsis jacoti* Wheeler, 1923 and *Buniapone amblyops* Emery, 1887 at a depth of 50 cm.

### ***Strumigenys elegantula* Terayama & Kubota, 1989**

Figure 5

*Smithistruma elegantula* Terayama & Kubota, 1989: 788, figs 23–27 (w.q.) TAIWAN.  
Indomalaya

*Pyramica elegantula* (Terayama & Kubota, 1989). Combination in *Pyramica*: Bolton 1999: 1673.

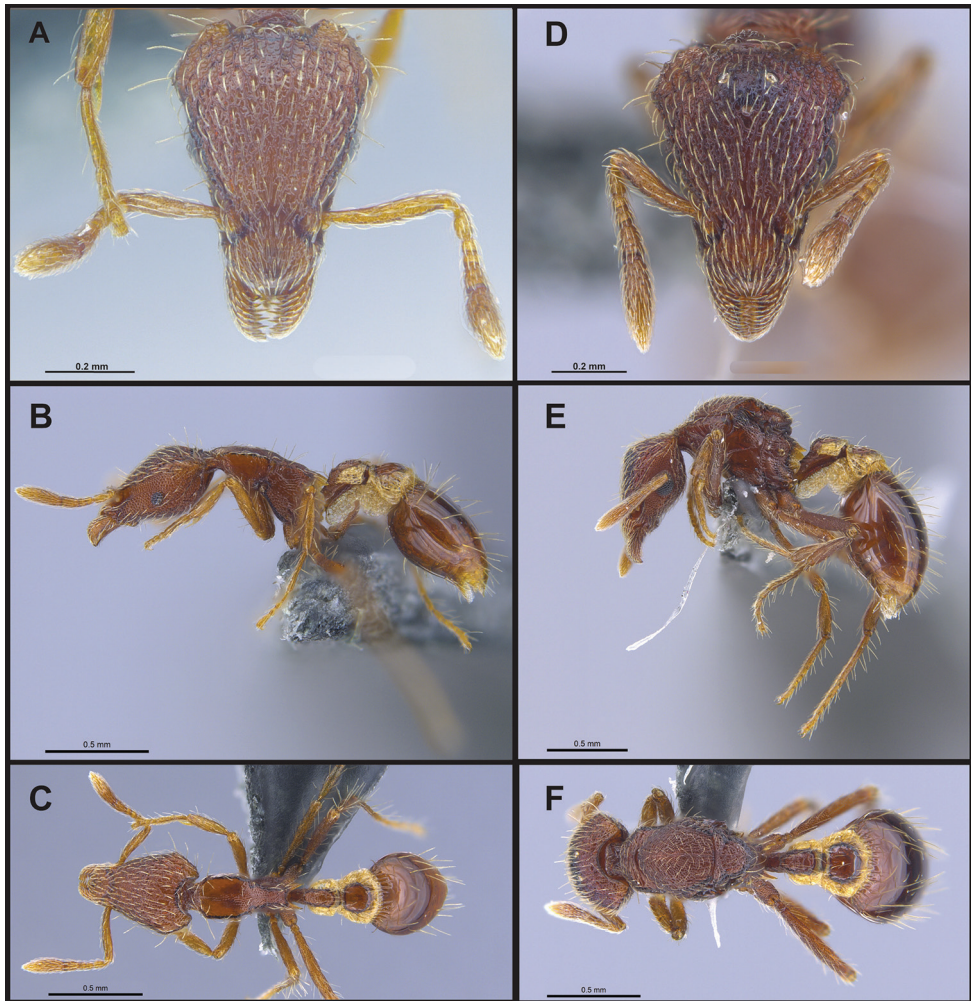
*Strumigenys elegantula* (Terayama & Kubota, 1989). Combination in *Strumigenys*: Baroni Urbani and De Andrade 2007: 119.

**Geographic distribution.** China (Guangdong, Guangxi, Hong Kong, Macao, Taiwan), Thailand.

**Comments.** This is a new species record for Macao. Originally described from Taiwan, this species is more widespread within continental Asia since it has also been recorded in Hong Kong, Macao, Guangdong, Guangxi (China) as well as in Thailand. In both Macao and Hong Kong (Tang et al. 2019), this species is relatively common and is known from two and ten sites within these regions, respectively.

**Material examined.** MACAO SAR, CHINA • 28 Workers; Macao, Coloane Island, Ka Ho; 22.1294°N, 113.5914°E, ca. 30 m; 20 Mar. 2019; F. Brassard leg.; Win-





**Figure 5.** *Strumigenys elegantula* in full-face, profile and dorsal view **A–C** worker (MAC\_S04\_LLSP\_sp.9) **D–F** queen (MAC\_S04\_LLSP\_sp.9).

kler; MAC\_S04\_LLSP\_Sp.9; IBBL. • 1 Worker; Macao, Coloane Island, Ka Ho; 22.1294°N, 113.5914°E, ca. 30 m; 20 Mar. 2019; F. Brassard leg.; Winkler; MAC\_S04\_LLSP\_Sp.1; IBBL. • 1 Worker; Macao, Coloane Island, Ka Ho Family Trail Peak; 22.1284°N, 113.5702°E, ca. 180 m; 16 May 2019; F. Brassard leg.; Winkler; MAC\_S14\_LLSP\_Sp.1; IBBL. • 1 Worker; Macao, Coloane Island, Ka Ho Family Trail Peak; 22.1284°N, 113.5702°E, ca. 180 m; 16 May 2019; F. Brassard leg.; Winkler; MAC\_S14\_LLSP\_Sp.3; IBBL. • 1 Worker; Macao, Coloane Island, Ka Ho Height Family trail peak near 1-09-03; 22.1284°N, 113.5702°E, ca. 140 m; 16 May 2019; F. Brassard leg.; Ground Bait; MAC\_S14\_B06\_Sp.1; IBBL. • 1 Queen; Macao, Coloane Island, Ka Ho; 22.1294°N, 113.5914°E, ca. 30 m; 20 Mar. 2019; F. Brassard leg.; Winkler; MAC\_S04\_LLSP\_Sp.9; IBBL.



***Strumigenys emmae* Emery, 1890**

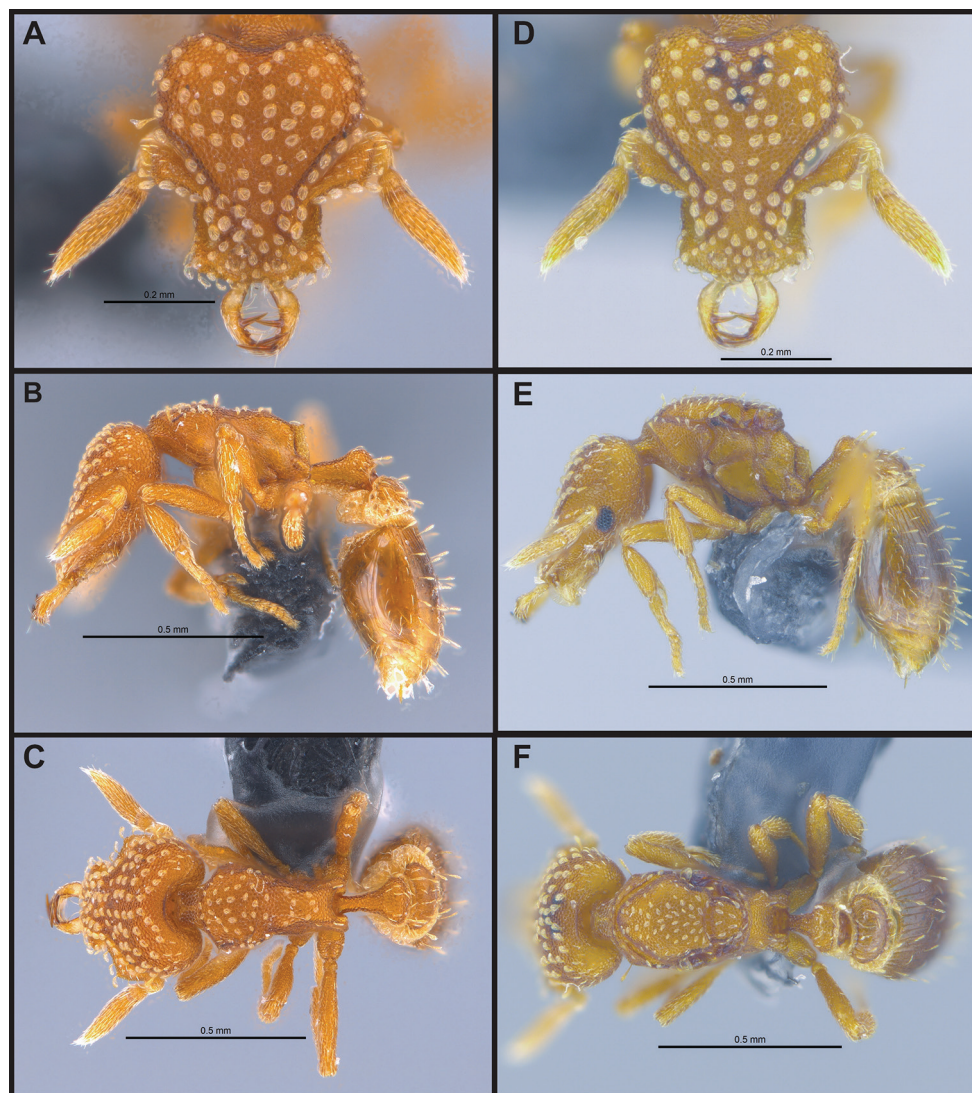
Figure 6

*Epitritus emmae* Emery, 1890: 70, pl. 8, fig. 6 (w.) Antilles. Neotropics.

*Quadristruma emmae* (Emery, 1890). Combination in *Quadristruma*: Brown 1949: 48.

*Strumigenys emmae* (Emery, 1890). Combination in *Strumigenys*: Bolton 1999: 1674.

**Geographic distribution.** *Native*: Australia. *Introduced*: Widespread, Afrotropical, Malagasy, Nearctic, Neotropical, Oceanian, Oriental, Panamanian, Saharo-Arabian



**Figure 6.** *Strumigenys emmae* in full-face, profile and dorsal view **A–C** worker (MAC\_S20\_LLSP\_Sp.7) **D–F** queen (MAC\_S19\_LLSP\_Sp.1).

realms, see antmaps.org for a global account (Janicki et al. 2016; Guénard et al. 2017). Within China, found in Hong Kong and Macao.

**Comments.** Originally from Australia, *S. emmae* is now a widespread exotic species. Although the exact date at which this species was introduced in the region is unknown, it is known from Hong Kong since the 1990s (Fellowes 1999), and was more recently recorded from Macao (Leong et al. 2017).

**Material examined.** Macao SAR, China • 3 Workers; Macao, Coloane Island, Caesars Golf Macau, 22.1351°N, 113.5611°E, ca. 10 m; 25 June 2019; MAC\_S19\_LLSA\_Sp.1, F. Brassard leg., Winkler; IBBL. • 2 Workers; Macao, Coloane Island, Cotai Ecological Zone II; 22.1418°N, 113.5519°E, ca. 0 m; 26 June 2019; F. Brassard leg.; Winkler; MAC\_S20\_LLSA\_Sp.6; IBBL. • 3 Workers; Macao, Coloane Island, Cotai Ecological Zone II; 22.1418°N, 113.5519°E, ca. 0 m; 26 June 2019; F. Brassard leg.; Winkler; MAC\_S20\_LLSP\_Sp.7; IBBL. • 1 Worker; Macao, Taipa Island, Siu Tam Hill; 22.1608°N, 113.5466°E, ca. 80 m; 15 Aug. 2018; C.M. Leong leg.; CML-FW-15viii2018; IBBL. • 1 Worker; Macao, Macao Peninsula, Guia Hill; 22.1983°N, 113.5511°E, ca. 60 m; 18 Aug. 2018; C.M. Leong leg.; IBBL. • 1 Queen; Macao, Coloane Island, Caesars Golf Macau; 22.1351°N, 113.5611°E, ca. 10 m; 25 June 2019; F. Brassard leg.; Winkler; MAC\_S19\_LLSA\_Sp.1; IBBL]. • 1 Queen; Macao, Taipa Island, Siu Tam Hill; 22.1608°N, 113.5466°E, ca. 80 m; 26 Aug. 2016; C.M. Leong leg.; IBBL.

### *Strumigenys exilirhina* Bolton, 2000

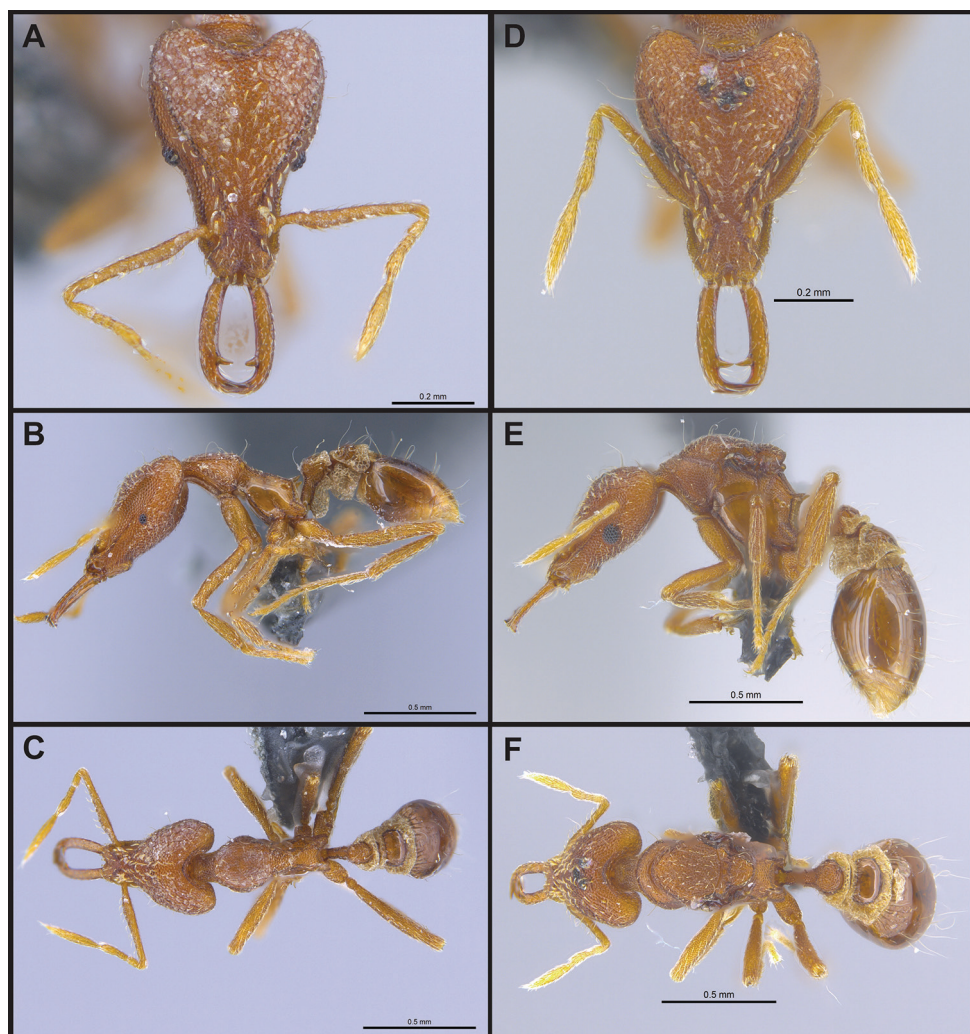
Figure 7

*Strumigenys exilirhina* Bolton, 2000: 881 (w.q.) Nepal. Indomalaya.

**Geographic distribution.** Bhutan, China (Guangdong, Hong Kong, Jiangxi, Macao, Xizang, Yunnan), India, Japan, Nepal, Thailand.

**Comments.** This species, first recorded in Macao in 2017 (Leong et al. 2017), is one of the most commonly collected *Strumigenys*. During the 2019 survey, it was found at 12 different sites within nature parks. In Hong Kong, it is recorded from various habitats including disturbed urban forests, tree plantations, shrubland, secondary forests and Feng Shui woods (Tang et al. 2019).

**Material examined.** MACAO SAR, CHINA • 3 Workers; Macao, Coloane Island, Coloane Park; 22.1214°N 113.5649°E, ca. 110 m; 18 Mar. 2019; F. Brassard leg.; Winkler; MAC\_S01\_LLSA\_Sp.3; IBBL. • 2 Workers; Macao, Coloane Island, Hillside of Department of Green Areas and Gardens; 22.1275°N, 113.5612°E, ca. 70 m; 20 May 2019; F. Brassard leg.; Winkler; MAC\_S16\_LLSA\_Sp.9; IBBL. • 1 Worker; Macao, Coloane Island, Wetland Alto de Coloane; 22.1230°N, 113.5597°E, ca. 90 m; 19 Apr. 2019; F. Brassard leg.; Winkler; MAC\_S02\_LLSA\_Sp.7; IBBL. • 1 Worker; Macao, Coloane Island, Seoc Pai Van Park; 22.1249°N, 113.5566°E, ca. 40 m; 20 Mar. 2019; F. Brassard leg.; Winkler; MAC\_S05\_LLSP\_Sp.7; IBBL. • 4 Workers; Macao, Coloane Island, Hac



**Figure 7.** *Strumigenys exilirhina* in full-face, profile and dorsal view **A–C** worker (MAC\_S01\_LLSA\_Sp.3) **D–F** queen (MAC\_S16\_LLSA\_Sp.9).

Sa Reservoir Family trail near 1-05-12; 22.1237°N, 113.5684°E, ca. 90 m; 8 Apr. 2019; F. Brassard leg.; Winkler; MAC\_S06\_LLSA\_Sp.3; IBBL. • 7 Workers; Macao, Coloane Island, Hac Sa Reservoir Family trail near 1-05-12; 22.1237°N, 113.5684°E, ca. 90 m; 8 Apr. 2019; F. Brassard leg.; Winkler; MAC\_S06\_LLSP\_Sp.4; IBBL. • 11 Workers; Macao, Coloane Island, Coloane trail near 1-01-10; 22.1165°N, 113.5589°E, ca. 100 m; 10 Apr. 2019; F. Brassard leg.; Winkler; MAC\_S10\_LLSA\_Sp.4; IBBL. • 1 Worker; Macao, Coloane Island, Coloane trail near 1-01-15; 22.1151°N, 113.5645°E, ca. 80 m; 11 Apr. 2019; F. Brassard leg.; Winkler; MAC\_S11\_LLSA\_Sp.4; IBBL. • 2 Workers; Macao, Coloane Island, Ka Ho height family trail peak near 1-09-03; 22.1284°N, 113.5702°E, ca. 140 m; 16 May 2019; F. Brassard leg.; Winkler; MAC\_S14\_LLSP\_Sp.3; IBBL. • 2



Workers; Macao, Coloane Island, Oscar farm hillside; 22.1131°N, 113.5557°E, ca. 80 m; 24 June 2019; F. Brassard leg.; Winkler; MAC\_S18\_LLSA\_Sp.11; IBBL. • 1 Worker; Macao, Macao Peninsula, Mongha Hill; 22.2085°N, 113.5476°E; 18 Feb. 2018; C.M. Leong leg.; CML-FW-18ii2018. • 1 Worker; Macao, Coloane Island, Ka Ho Reservoir; 22.1341°N, 113.5786°E; 27 Feb. 2018; C.M. Leong leg.; Winkler; CML-FW-27ii2018; IBBL. • 2 Workers; Macao, Coloane Island, Ka Ho Reservoir; 14 Aug. 2018; C.M. Leong leg.; IBBL]. • 1 Worker; Macao, Coloane Island, Hac Sa Reservoir; 22.1264°N, 113.5733°E; C.M. Leong leg.; IBBL. • 1 Queen; Macao, Coloane Island, Ka Ho Reservoir; 22.1608°N, 113.5466°E; 15 Jul. 2018; C.M. Leong leg.; Winkler; CML-FW-15vii2018; IBBL. • 1 Queen; Macao, Coloane Island, Hillside of Department of Green Areas and Gardens; 22.1275°N, 113.5612°E, ca. 70 m; 20 May 2019; F. Brassard leg.; Winkler; MAC\_S06\_LLSA\_Sp.3; IBBL. • 2 Queens; Macao, Coloane Island, Coloane trail near 1-01-10; 22.1165°N, 113.5589°E, ca. 100 m; 10 Apr. 2019; F. Brassard leg.; Winkler; MAC\_S10\_LLSP\_Sp.2; IBBL. • 1 Queen; Macao, Coloane Island, Hillside of Department of Green Areas and Gardens; 22.1275°N, 113.5612°E, ca. 70 m; 20 May 2019; F. Brassard leg.; Winkler; MAC\_S16\_LLSA\_Sp.9; IBBL.

### ***Strumigenys feae* Emery, 1895**

Figure 8

*Strumigenys feae* Emery, 1895: 473 (w.q.) Myanmar. Indomalaya.

**Geographic range.** Cambodia, China (Hong Kong, Macao, Yunnan), Myanmar, Thailand, and Vietnam.

**Comments.** A single worker of *S. feae* has been collected in Macao in 2019 (within a nature park consisting of young secondary forest), and as such the species is considered relatively rare in the region. In Hong Kong, *S. feae* has been collected in tree plantations of *Lophostemon confertus* Wilson & Waterh, 1982 and in secondary forests (Tang et al. 2019).

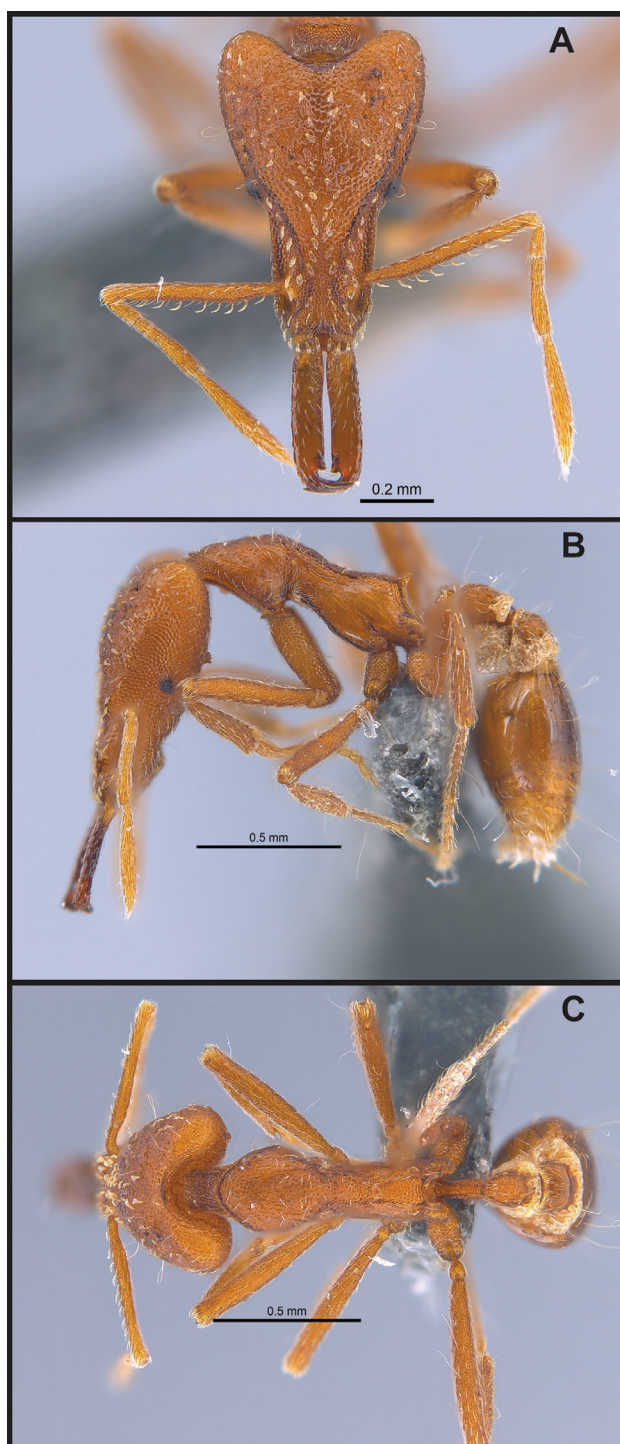
**Material examined.** MACAO SAR, CHINA • 1 Worker; Macao, Coloane Island, Coastal Trail; 22.1144°N, 113.5699°E, ca. 110 m; 17 May 2019; F. Brassard leg.; Winkler; MAC\_S15\_LLSP\_Sp.8; IBBL.

### ***Strumigenys membranifera* Emery, 1869**

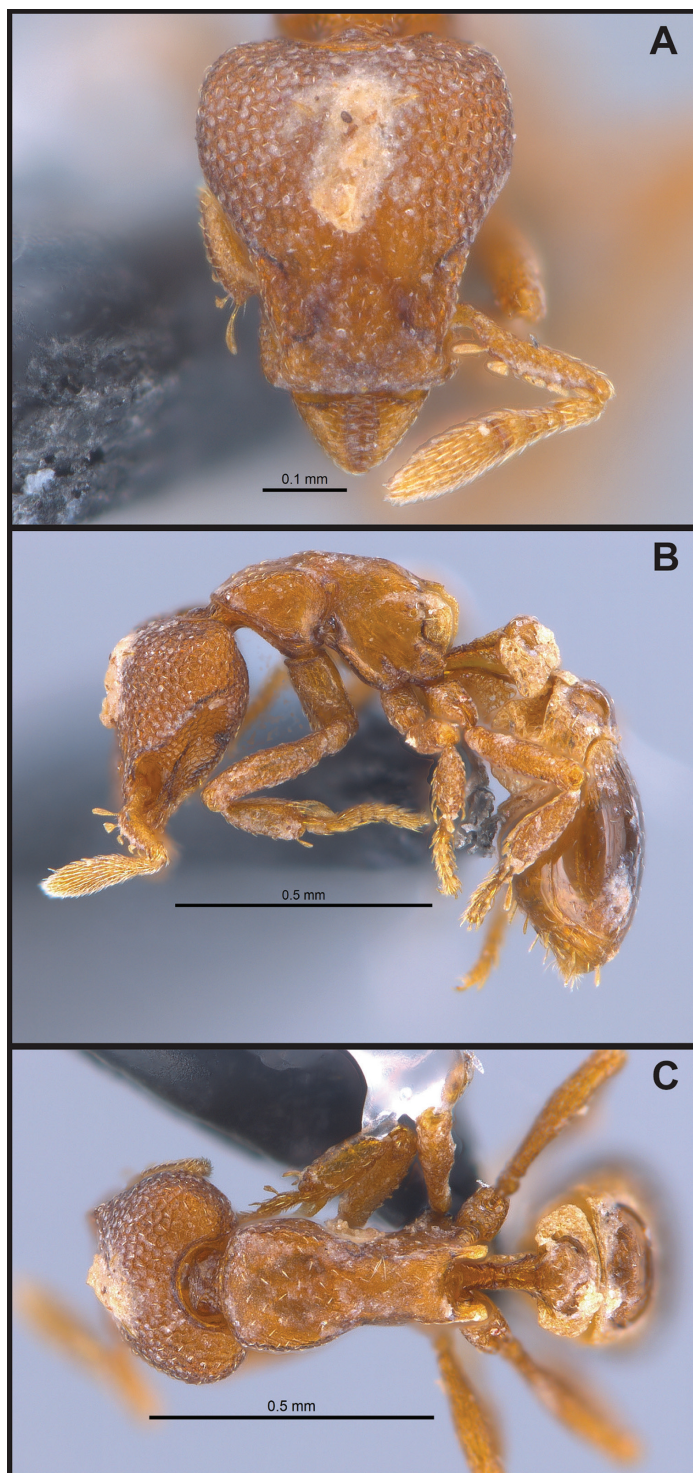
Figure 9

*Strumigenys* (*Trichoscapa*) *membranifera* Emery, 1869: 24, fig. 11 (w.) Italy. Palearctic. *Strumigenys* (*Cephaloxys*) *membranifera* (Emery, 1869). Combination in *Strumigenys* (*Cephaloxys*): Emery 1916: 205.

*Trichoscapa membranifera* (Emery, 1869). Combination in *Trichoscapa*: Brown 1948: 113. *Pyramica membranifera* (Emery, 1869). Combination in *Pyramica*: Bolton 1999: 1673.



**Figure 8.** *Strumigenys feae* **A–C** worker (MAC\_S15\_LLSP\_Sp.8) **A** full-face view **B** profile view **C** dorsal view.



**Figure 9.** *Strumigenys membranifera* **A–C** worker **A** full-face view **B** profile view **C** dorsal view.



*Strumigenys membranifera* (Emery, 1869). Combination in *Strumigenys* : Baroni Urbani and De Andrade 2007: 123.

Senior synonym of *S. fochowensis*, *S. membranifera marioni*, *S. membranifera santschii*, *S. silvestriana*, *S. membranifera simillima*, *S. vitiensis*, *S. membranifera williamsi*: Brown, 1948: 114.

**Geographic distribution.** *Native*: Ghana, Sierra Leone, South Africa. *Introduced*: Widespread, Australasia, European, Indo-Malayan, Malagasy, Nearctic, Neotropical, Oceanian, Saharo-Arabian realms, see antmaps.org for a global account (Janicki et al. 2016). Within China, found in Guangdong, Hong Kong, Fujian, Macao, Sichuan, and Yunnan.

**Comments.** This species, originally from Africa, is associated with disturbed habitats. For instance, in Hong Kong it was collected near Disneyland and the Hong Kong Airport; two heavily disturbed localities (Tang et al. 2019). The exact date of its introduction in the region is unknown. It was first recorded in Hong Kong in 2019 (Tang et al. 2019), but has been known in Macao since 1928 where it was described from six specimens as *S. silvestriana* (Wheeler, 1928). As such, its initial introduction to the Greater Bay Area may date beyond a hundred years. Nevertheless, during the 2019 survey in Coloane the species was not frequently collected and was found only in two nature parks, which consisted of relatively small patches of young secondary forests within an urban matrix.

**Material examined.** MACAO SAR, CHINA • 1 Worker; Macao, Coloane Island, Coloane Trail (Near C3 information point); 22.1217°N, 113.5560°E, ca. 110 m; 27 June 2019; F. Brassard leg.; Winkler; MAC\_S21\_LLSP\_Sp.2; IBBL. • 2 Workers; Macao, Coloane Island, Morro de Hac Sa family trail near 1-07-08; 22.1144°N, 113.5699°E, ca. 50 m; 5 June-11 Sep 2019; F. Brassard leg.; Ground Nest; MAC\_S15\_GN3\_H3\_n1; IBBL.

### *Strumigenys minutula* Terayama & Kubota, 1989

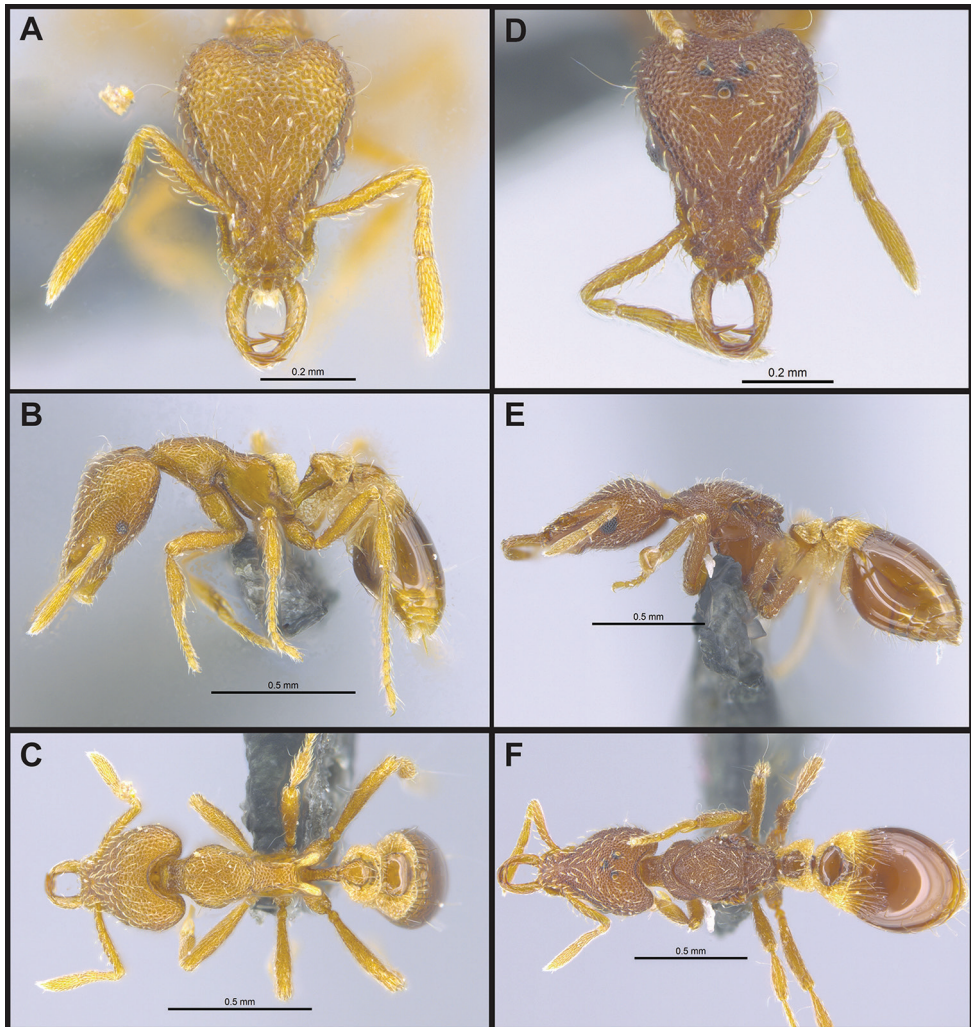
Figures 10, 11

*Strumigenys minutula* Terayama & Kubota, 1989: 782, figs 13–17 (w.q.) Taiwan. Indomalaya.

**Geographic distribution.** China (Hong Kong, Macao, Taiwan), Japan (Ryukyu Islands).

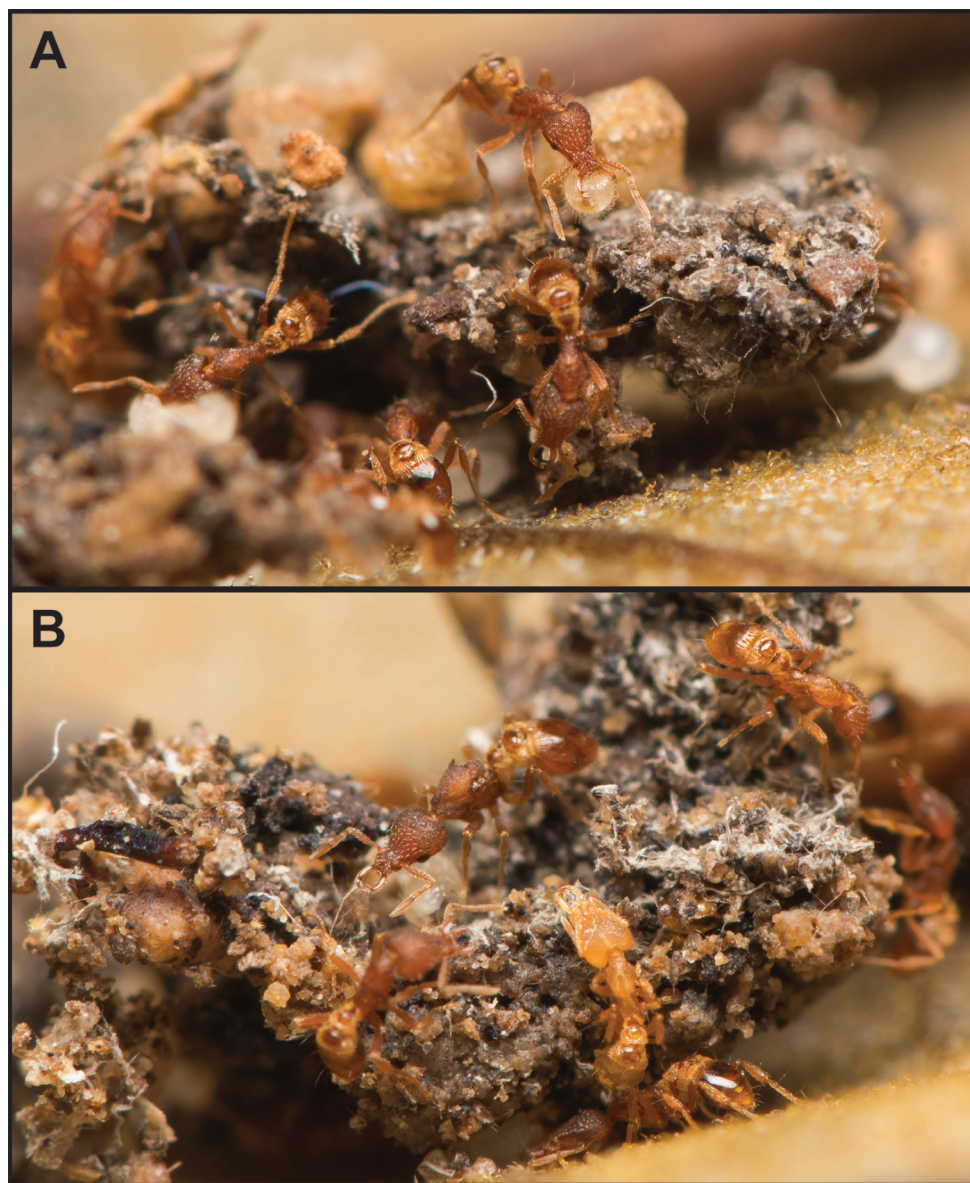
**Comments.** In contrast to Hong Kong, where this species has been rarely collected (Tang et al. 2019), *S. minutula* was frequently found in Macao since its first collection in 2017 (Leong et al. 2017). Individuals were commonly found within leaf litter samples, and a full colony was also retrieved within one of the ground nests deployed (see Fig. 11). At the time of collection on (29 August 2019), the colony consisted of 135 workers, two dealate queens, eight larvae, and 12 pupae (eggs were not counted). This represents a similar colony size as described previously from Japan, where a polygynous colony of 300 individuals was recorded (Terayama et al. 2014). Note that, on the left foreleg of the queen imaged (Fig. 10E), a mite is attached. It remains to be investigated which mite species it is, and if this represent a case of parasitism, phoresis or myrmecophily in *S. minutula*.





**Figure 10.** *Strumigenys minutula* in full-face, profile and dorsal view **A–C** worker (MAC\_S11\_GN3\_H4\_n1) **D–F** queen (MAC\_S11\_GN3\_H4\_n1).

**Material examined.** MACAO SAR, CHINA • 22 Workers; Macao, Coloane Island, Hac Sa Reservoir family trail near 1-05-12; 22.1237°N, 113.5684°E, ca. 90 m; 8 April 2019; F. Brassard leg.; Winkler; MAC\_S06\_LLSA\_Sp.6; IBBL. • 1 Worker; Macao, Coloane Island, Coloane trail near 1-01-10; 22.1165°N, 113.5589°E, ca. 100 m; 10 April 2019; F. Brassard leg.; Winkler MAC\_S10\_LLSA\_Sp.2; IBBL. • 2 Workers; Macao, Coloane Island, Ka Ho Family Trail Peak; 22.1284°N, 113.5702°E, ca. 180 m; 16 May 2019; F. Brassard leg.; Winkler; MAC\_S14\_LLSP\_Sp.4; IBBL. • 135 Workers; Macao, Coloane Island, Coloane Trail (Near 1-01-10 distance post); 22.1351°N, 113.5700°E, ca. 80 m; 16 May 2019; F. Brassard leg.; Ground nest; MAC\_S11\_GN3\_H4\_n1; IBBL. • 1 Worker; Macao, Coloane Island, Ka Ho Fam-



**Figure 11.** Photos of *S. minutula* (MAC\_S11\_GN3\_H4\_n1) showing some of the workers, including one carrying a larva (**A**), a queen (see center of **B**), and debris (**A–B**) found inside a ground nest.

ily Trail Peak; 22.1284°N, 113.5702°E, ca. 180 m; 16 May 2019; F. Brassard leg.; Winkler; MAC\_S14\_LLSA\_Sp.11; IBBL]. • 1 Worker; Macao, Coloane Island, Ka Ho Lighthouse 2; 22.1292°N, 113.5909°E, ca. 30 m; 21 May 2019; F. Brassard leg.; Winkler; MAC\_S17\_LLSA\_Sp.10; IBBL]. • 13 Workers; Macao, Coloane Island, Ka Ho Lighthouse 2; 22.1292°N, 113.5909°E, ca. 30 m; 21 May 2019; F. Brassard leg.;

Winkler; MAC\_S17\_LLSP\_Sp.4; IBBL. • 1 Worker; Macao, Coloane Island, Caesars Golf Macau; 22.1351°N, 113.5612°E, ca. 10 m; 25 June 2019; F. Brassard leg.; Winkler; MAC\_S19\_LLSP\_Sp.4; IBBL. • 1 Worker; Macao, Taipa Island, Siu Tam Hill; 22.1603°N, 113.5471°E; 22 July 2018; C.M. Leong leg.; IBBL. • 1 Worker; Macao, Coloane Island, Ka Ho Reservoir; 22.1251°N, 113.5692°E; 20 July 2016; C.M. Leong leg.; IBBL. • 1 Worker; Macao, Coloane Island, Ka Ho Reservoir; 22.1251°N, 113.5691°E; 20 August 2016; C.M. Leong leg.; IBBL. • 1 Worker; Macao, Coloane Island, Hac Sa Reservoir; 20 August 2016; C.M. Leong leg.; IBBL. • 2 Queens; Macao, Coloane Island, Coloane Trail (Near 1-01-10 distance post); 22.1351°N, 113.5700°E, ca. 80 m; 16 May 2019; F. Brassard leg.; MAC\_S11\_GN3\_H4\_n1; Ground nest; IBBL.

### ***Strumigenys nepalensis* Baroni Urbani & De Andrade, 1994**

Figure 12

*Strumigenys nepalensis* Baroni Urbani & De Andrade, 1994: 57, figs 33, 34 (w.q.) Nepal. Indomalaya.

*Smithistruma nepalensis* (Baroni Urbani & De Andrade, 1994). Combination in *Smithistruma*: Bolton 1995: 385.

*Pyramica nepalensis* (Baroni Urbani & De Andrade, 1994). Combination in *Pyramica*: Bolton 1999: 1673.

*Strumigenys nepalensis* (Baroni Urbani & De Andrade, 1994). Combination in *Strumigenys*: Baroni Urbani and De Andrade 2007: 124.

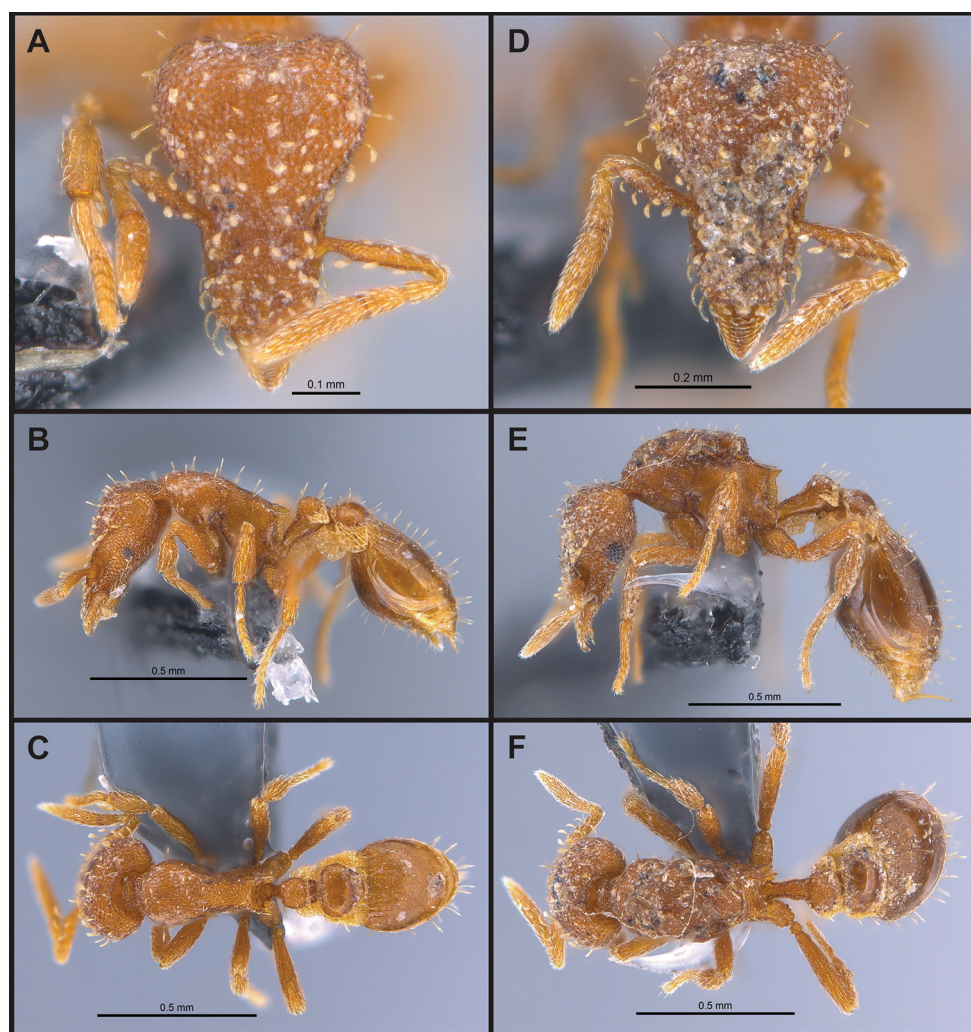
**Geographic distribution.** *Native*: China (Yunnan), India (north), Malaysia, Nepal, Singapore, Thailand, Vietnam. *Introduced*: China (Hong Kong, Macao), Mascarene Islands, India (Kerala).

**Comments.** This species was first recorded in Macao in 2017 (Leong et al. 2017). In 2019, of the three sites at which *S. nepalensis* was collected from, two were heavily disturbed; they consisted of a golf course, and a thin strip of forest bordered by the ocean and a highway. The last one was a patch of young secondary forest nearby another golf course. Our records in Macao support the hypothesis of Tang and collaborators (2019) that this species is a potential tramp species adapted to human-disturbed habitats.

**Material examined.** MACAO SAR, CHINA • 3 Workers; Macao, Coloane Island, Caesars Golf Macau; 22.1351°N, 113.5611°E, ca. 10 m; 25 June 2019; F. Brassard leg.; Winkler; MAC\_S19\_LLSP\_Sp.3; IBBL. • 3 Worker; Macao, Coloane Island, Ka Ho Reservoir hillside; 22.1333°N, 113.5744°E, ca. 90 m; 9 April 2019; F. Brassard leg.; Winkler; MAC\_S09\_LLSA\_Sp.5; IBBL. • 21 Workers; Macao, Coloane Island, Caesars Golf Macau; 22.1351°N, 113.5612°E, ca. 10 m; 25 June 2019; F. Brassard leg.; Winkler; MAC\_S19\_LLSA\_Sp.2; IBBL. • 19 Workers; Macao, Coloane Island, Cotai Ecological Zone II; 22.1418°N, 113.5519°E, ca. 0 m; 26 June 2019; F. Brassard leg.; MAC\_S20\_LLSA\_Sp.7; Winkler; IBBL. • 1 Worker; Macao, Coloane Island, Cotai



Ecological Zone II; 22.1418°N, 113.5519°E; ca. 0 m; 26 June 2019; F. Brassard leg.; Winkler; MAC\_S20\_LLSP\_Sp.8; IBBL. Worker, Macao, Hac Sa Reservoir, 20 August 2016, C.M. Leong leg., [IBBL], ( $n = 1$ ). • 4 Queens; Macao, Coloane Island, Caesars Golf Macau; 22.1351°N, 113.5612°E, ca. 10 m; 25 June 2019; F. Brassard leg.; Winkler; MAC\_S19\_LLSP\_Sp.2; IBBL. • 3 Queens; Macao, Coloane Island, Caesars Golf Macau; 22.1351°N, 113.5611°E, ca. 10 m; 25 June 2019; F. Brassard leg.; Winkler; MAC\_S19\_LLSP\_Sp.3; IBBL. • 3 Queens; Macao, Coloane Island, Cotai Ecological Zone II; 22.1418°N, 113.5519°E, ca. 0 m; 26 June 2019; F. Brassard leg.; Winkler; MAC\_S20\_LLSP\_Sp.7; IBBL. • 3 Queens; Macao, Coloane Island, Cotai Ecological

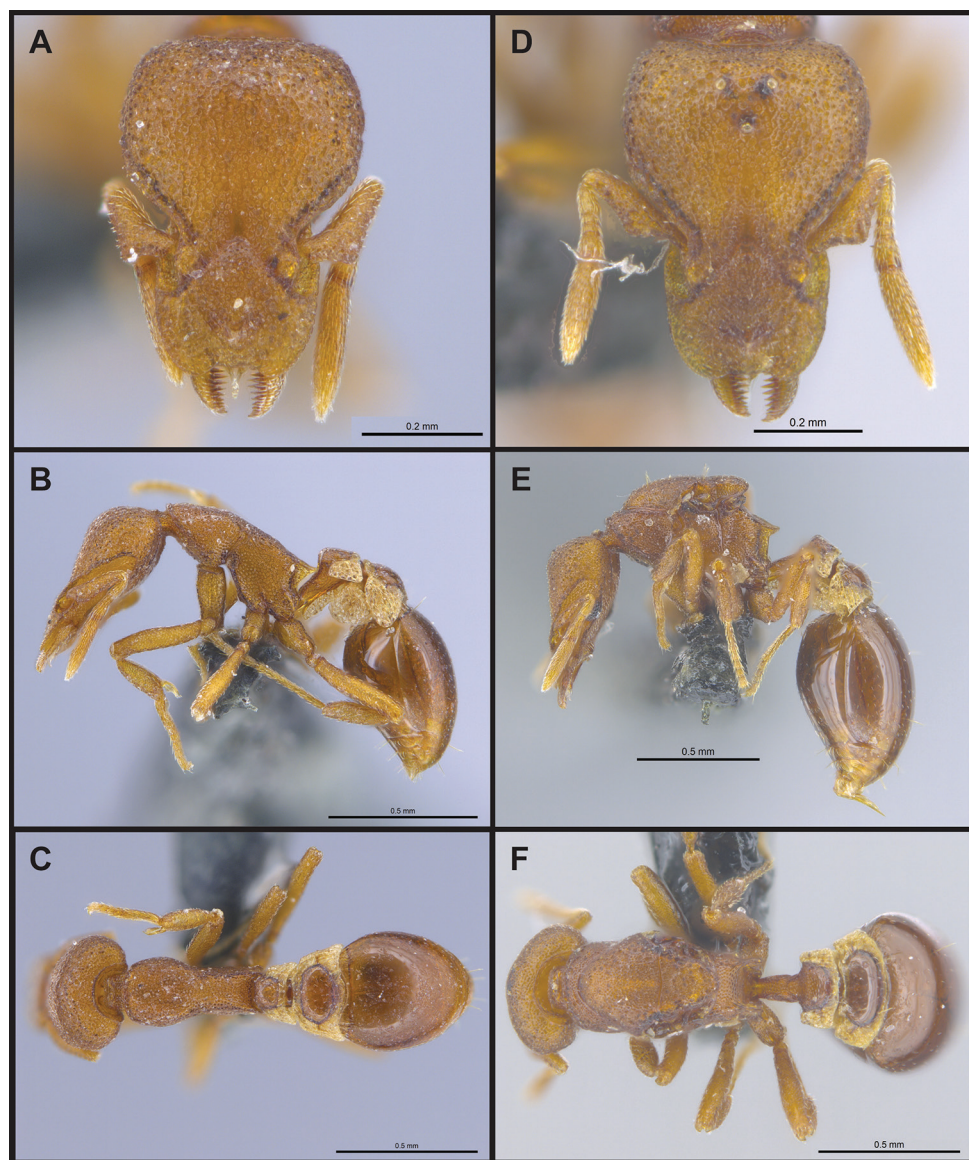


**Figure 12.** *Strumigenys nepalensis* in full-face, profile and dorsal view **A–C** worker (MAC\_S19\_LLSP\_Sp.3) **D–F** queen (MAC\_S19\_LLSP\_Sp.3).

Zone II; 22.1418°N, 113.5519°E, ca. 0 m; 26 June 2019; F. Brassard leg.; Winkler;  
MAC\_S20\_LLSP\_Sp.8; IBBL.

***Strumigenys sauteri* Forel, 1912**

Figure 13



**Figure 13.** *Strumigenys sauteri* in full-face, profile and dorsal view **A–C** worker (MAC\_S04\_LLSP\_sp.2)  
**D–F** queen (MAC\_S11\_LLSP\_Sp.4).

*Pentastruma sauteri* Forel, 1912: 51 (w.) Taiwan. Indomalaya.

*Pyramica sauteri* (Forel, 1912). Combination in *Pyramica*: Bolton 1999: 1673.

*Strumigenys sauteri* (Forel, 1912). Combination in *Strumigenys*: Baroni Urbani and De Andrade 2007: 127.

**Geographic distribution.** China (Fujian, Guangxi, Hong Kong, Hunan, Macao, Taiwan, Yunnan), Japan (Ryukyu Islands), Thailand.

**Comments.** Although widely distributed in Hong Kong across multiple habitats, including shrublands, plantations, urban forest remnants, secondary forest and Feng Shui woods (Tang et al. 2019), this species appears less common in Macao where it has been collected at four different sites, all of which were relatively small patches of young secondary forests. This is a new species record for Macao.

**Material examined.** MACAO SAR, CHINA • 1 Worker; Macao, Coloane Island, Ka Ho; 22.1936°N, 113.5914°E, ca. 30 m; 20 March 2019; F. Brassard leg.; Winkler; MAC\_S04\_LLSA\_Sp.2; IBBL. • 5 Workers; Macao, Coloane Island, Coloane trail near 1-01-15; 22.1151°N, 113.5645°E, ca. 80 m; 11 April 2019; F. Brassard leg.; Winkler; MAC\_S11\_LLSP\_Sp.4; IBBL. • 3 Workers; Macao, Coloane Island, Oscar Farm hillside; 22.1131°N, 113.5557°E, ca. 80 m; 24 June 2019; F. Brassard leg.; Winkler; MAC\_S18\_LLSA\_Sp.10; IBBL. • 1 Worker; Macao, Taipa Island, Tai Tam Hill; 22.1578°N, 113.5679°E; 26 July 2018; C.M. Leong leg.; IBBL. • 1 Queen; Macao, Coloane Island, Coloane Trail (Near 1-01-15 distance post); 22.1151°N, 113.5644°E, ca. 80 m; 11 April 2019; F. Brassard leg.; Winkler; MAC\_S11\_LLSP\_Sp.4; IBBL.

### Key of the twenty-nine *Strumigenys* species recorded from the Guangdong-Hong Kong-Macao Greater Bay Area

The following key relies heavily on couplets elaborated by Bolton (2000), which were subsequently used for a key to the *Strumigenys* (as *Pyramica*) of China (Xu and Zhou 2004). For species present in the Greater Bay Area that are within Bolton's key, we used his couplets. New couplets were added for species absent from Bolton's key.

- 1 Mandibles relatively short, not kinetic, not forming a snapping mechanism (Fig. 14A). Maximum opening of mandibles 90° or less (17 spp.) ..... **2**
- Mandibles relatively elongate, edentate along inner margin and forming a snapping mechanism (i.e., trap-jaw) (Fig. 14B). If not elongate, mandibles forming a snapping mechanism, either curvilinear (Fig. 14C) or with outer margin flared outwards near base and with strongly projecting basal angle (Fig. 14D). Maximum opening of mandibles 170° or more (12 spp.) ..... **18**
- 2 Antenna with 4 segments (Fig. 15A); first funicular segment not separated from the 2-segmented apical club (2 spp.) ..... **3**
- Antenna with 6 segments (Fig. 15B); first funicular segment separated from the 2-segmented apical club by one or two small segments (15 spp.) ..... **4**



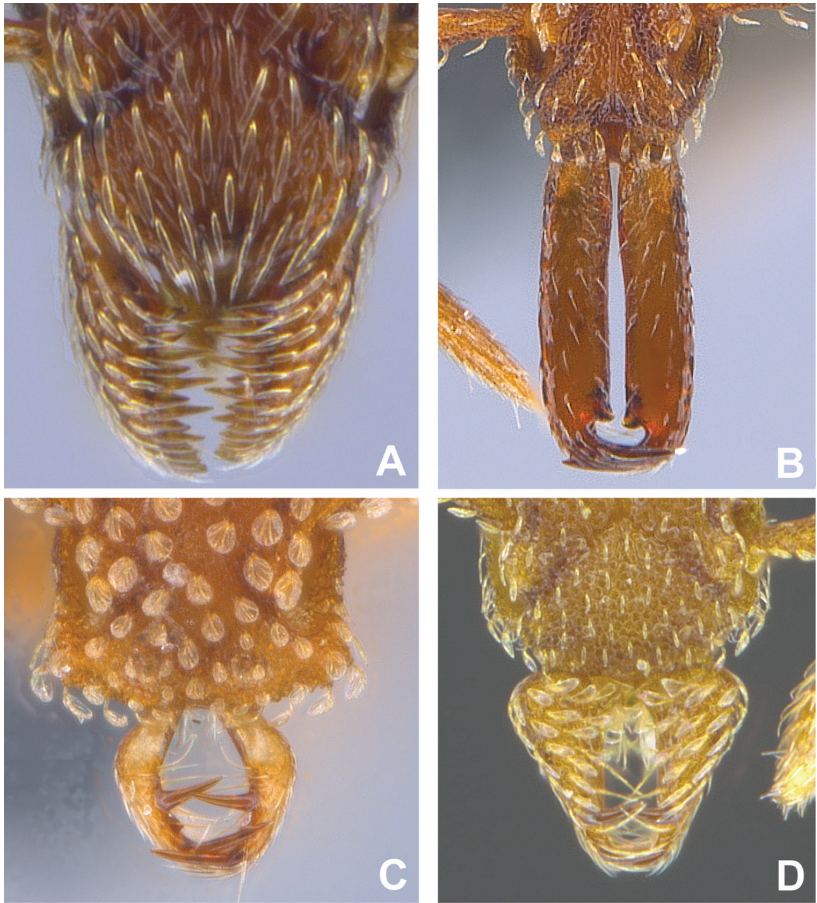
- 3 Vertexal corners prominent (Figs 16, 18A). Pilosity on head, mesosoma, petiole, potspetiole and legs consisting of large appressed spatulate hairs (*Native*. China: Hong Kong) ..... ***S. lantau***
- Vertexal corners less prominent (Figs 17, 18B). Pilosity on head, mesosoma, petiole and postpetiole consisting of finer erect spatulate hairs. Pilosity on legs consisting of appressed simple hairs (*Native*. China: Yunnan; Northern India, Malaysia, Nepal, Singapore, Thailand, Vietnam. *Introduced*. China: Hong Kong, Macao; Mascarene Islands, India: Kerala) ..... ***S. nepalensis***
- 4 With head in full-face view, the leading edge of the scape with a row of conspicuous projecting curved hairs, of which one or more, distal to the subbasal bend, distinctly curved toward the base of the scape (Fig. 19A). These hairs may be spatulate, remiform, spoon-shaped or broadly clavate apically; basal stem of each hair (which may be short) erect or sub-erect with respect to the long axis of the scape (4 spp.) ..... **5**
- With head in full-face view the leading edge of the scape lacking projecting hairs that curve toward the base of the scape (Fig. 19B). Scape edge may have elongate simple straight projecting hairs present, or entirely apically directed short hairs that may be simple, narrowly to broadly spatulate, or spoon-shaped; in some species the leading edge may be hairless (11 spp.) ..... **8**
- 5 Vertexal margin strongly concave (Figs 20, 21A). Vertexal corners forming two conspicuous protrusions. In full-face view, appressed spatulate hairs solely bordering the upper half of clypeus ..... ***S. formosa***
- Vertexal margin weakly concave (Fig. 21B). Vertexal corners not forming two conspicuous protrusions. In full-face view appressed spatulate hairs or simple hairs found across the whole head, not just on the clypeal margin (3 spp.) .... **6**
- 6 Pilosity on head consisting of spatulate hairs. Eye composed of a single ommatidium (Fig. 22A) (2 spp.) ..... **7**
- Pilosity on head consisting of small appressed simple hairs. Eye composed of more than one ommatidium (Figs. 22B, 23) (*Native*. Ghana, Sierra Leone, South Africa. *Introduced*. widespread, including China: Guangdong, Hong Kong, Fujian, Macao, Sichuan, Yunnan) ..... ***S. membranifera***
- 7 Two pairs of thin remiform hairs on the vertex, with one pair on the lateral portions of vertex and the other in posteromedial position (Fig. 24B). Dorsum of promesonotum with erect simple hairs (Fig. 24C) (*Native*: Macao) ....  
..... ***S. subterranea* sp. nov.**
- Pilosity on head consisting solely of appressed spatulate hairs (Fig. 25A), without erect simple hairs. Dorsum of pronotum with appressed spatulate hairs (Fig. 25B). (*Native*: Guangdong) ..... ***S. lachesis***
- 8 Petiole node in profile long and relatively flat (Fig. 26A). Petiole node in dorsal view long and narrow (3 spp.) ..... **9**
- Petiole node in profile short and with a dorsal protrusion (Fig. 26B). Petiole node in dorsal view short and broad (8 spp.) ..... **11**

- 9 Mesopleuron and metapleuron smooth and shiny (Figs 27, 28A). Pilosity on dorsum of mesosoma and posterior margin of head consisting of reduced and appressed simple hairs. Pilosity on first gastral segment short. Propodeal lamella with a thin layer of spongiform tissue (*Native*. China: Hong Kong).....  
.....***S. nathistorisoc***
- Mesopleuron and metapleuron sculptured (Fig. 28B). Pilosity on dorsum of mesosoma and posterior margin of head consisting of long and erect simple hairs. Pilosity of first gastral segment consisting of long and erect simple hairs. Spongiform tissue on propodeal lamina prominent..... **10**
- 10 Dorsum of pronotum with distinct transverse striations and without a median long stria (see Zhou 2011) (*Native*. China: Guangdong).....  
.....***S. nankunshana***
- Dorsum of pronotum without transverse striations and with a median long stria (Fig. 29C) (China: Guangdong, Guangxi, Hong Kong, Macao, Taiwan; Thailand) .....***S. elegantula***
- 11 Dorsal (outer) surfaces of middle and hind tibiae with one or more conspicuous freely laterally projecting long hairs that are at a right-angle or near right-angle to the long axis of the segment (Fig. 30A); these hairs may be straight, curved or flagellate; one or more similar hairs present on basitarsi (2 spp.)..... **12**
- Dorsal (outer) surfaces of middle and hind tibiae and basitarsi with small simple to spatulate decumbent or appressed hairs (Fig. 30B), or with minute appressed pubescence only; lacking freely laterally projecting long hairs that are at a right-angle or near right-angle to the long axis of the segment (6 spp.)..... **13**
- 12 Cuticle on side of head within the scrobe smooth and shining. Dorsal part of mesosoma smooth and shining. Eye with a single ommatidium (Fig. 31) (China: Guangxi, Hong Kong, Taiwan; Japan)..... ***S. mazu***
- Cuticle on side of head within the scrobe reticulate-punctate. Dorsum of mesosoma sculptured. Eye with more than one ommatidium (Fig. 32) (Bhutan, China: Fujian, Hunan, Yunnan, Hong Kong) ..... ***S. kichijo***
- 13 With head in full-face view the entire dorsum clothed with ground pilosity of very conspicuous pale orbicular hairs (Fig. 33A) (2 spp.)..... **14**
- With head in full-face view the dorsum either without hairs or with ground pilosity of short hairs that are simple to narrowly spatulate and usually inconspicuous (Fig. 33B) (4 spp.) ..... **15**
- 14 Apical half of mandible with two preapical teeth, the proximal slightly longer than the distal. With alitrunk in profile posterior surface of mesonotum narrowly convex and weakly bulging, overhanging the metanotal groove. Posterodorsal corner of propodeum dentate. Head broader than long (Fig. 34) (*Native*. China: Taiwan; Japan: mainland and Ryukyu Islands ; South Korea. *Introduced*. China: Hong Kong; Japan: Ogasawara Islands; United States of America) .....***S. hexamera***

- Apical half of mandible with a single small inconspicuous preapical tooth, located very close to the spiniform apicodorsal tooth. With alitrunk in profile mesonotum meets propodeum at the metanotal groove, the former not narrowly convex nor bulging posteriorly, not overhanging the metanotal groove. Posterodorsal corner of propodeum rounded. Head slightly longer than broad (Fig. 35) (China: Hong Kong, Guangdong, Hubei, Hunan) ..... ***S. tisiphone***
- 15 With head in full-face view, the outer margins of the fully closed mandibles intersect the anterior clypeal margin mesad of the anterolateral clypeal angles, so that there is a section of the anterior clypeal margin that projects laterally beyond the outer line or the mandible (Fig. 36A). Small to minute species (TL: > 2 to 3 mm) (2 spp.) ..... **16**
- With head in full-face view, the outer margins of the fully closed mandibles intersect the anterior clypeal margin at the anterolateral clypeal angles, so that there is no section of the anterior clypeal margin that projects laterally beyond the outer line of the mandible (Fig. 36B). Minute species (TL < 2 mm) (2 spp.) ..... **17**
- 16 Anterior clypeal margin shallowly transversely concave across its entire width (Fig. 37A). Mandible with 14 teeth distal of a long low basal lamella (China: Hong Kong, Macao; Japan, South Korea, Vietnam) ..... ***S. canina***
- Anterior clypeal margin with a deep semicircular median impression, the anterolateral angles broadly convex on each side of the impression (Fig. 38A). Mandible with 12 teeth distal of a triangular rounded basal lamella (China: Fujian, Guangxi, Hong Kong, Hunan, Macao, Taiwan, Yunnan; Japan, Thailand) ..... ***S. sauteri***
- 17 With head in full-face view, the fully closed mandibles triangular, with teeth present along entire length of exposed inner margin (Fig. 39A); proximal half or inner margin dentate, without a long diastema between basal tooth and basal lamella; without a large space basally through which the apices of the labral lobes are visible (Brunei Darussalam, China, India, Indonesia, Malaysia, New Guinea, Philippines, Thailand, Vietnam) ..... ***S. mitis***
- With head in full-face view, the fully closed mandibles narrow or elongate-triangular, with teeth present only on distal half of exposed length of inner margin (Fig. 40A); proximal half of inner margin edentate and forming a long diastema between basal tooth and basal lamella; a large space present basally between the opposed mandibles through which the apices or the labral lobes are visible (China: Guangxi, Hunan, Hong Kong; Japan, South Korea, Taiwan) ..... ***S. mutica***
- 18 Antenna with 4 segments (Figs 41, 42A); first funicular segment not separated from the 2-segmented apical club (Pantropical distribution) ..... ***S. emmae***
- Antenna with 6 segments (Fig. 42B); first funicular segment separated from the 2-segmented apical club by two small segments (11 spp.) ..... **19**

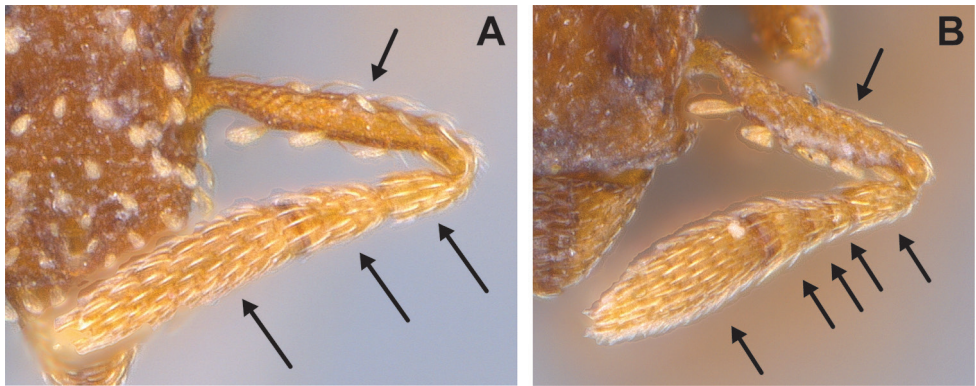
- 19 Fully closed mandibles in full-face view very broad proximally and strikingly tapered distally, obviously not linear or curvilinear (Figs 43, 44C). Outer margin of mandible flared outwards near base and with a strongly projecting prebasal angle (China: Hong Kong ; Indonesia: Java ; Thailand, Vietnam).....***S. sydorata***
- Fully closed mandible in full-face view not very broad proximally nor strikingly tapered distally, linear (Fig. 44A) or curvilinear (Fig. 44B). Outer margin of mandible not flared outwards near base, without a strongly projecting prebasal angle (10 spp.) ..... **20**
- 20 Preapical dentition of each mandible with 2 preapical teeth (Fig. 45A) (*Native*: Afrotropical region ; *Introduced*: widespread) ..... ***S. rogeri***
- Preapical dentition of each mandible either absent or of a single article; when present with either a single tooth or a single denticle (9 spp.) ..... **21**
- 21 With head in full-face view mandible without preapical dentition (Figs 46A, 47A), no trace of a projecting preapical tooth or denticle (China: Hong Kong) ..... ***S. heteropha***
- With head in full-face view mandible with preapical dentition, a projecting preapical tooth (Fig. 47B) or denticle present (8 spp.) ..... **22**
- 22 With mesosoma in profile the propodeal declivity equipped with a broad and conspicuous spongiform lamella (Fig. 48A); the propodeal tooth may be replaced by the lamella or completely buried in the lamella, or lamella may subtend the ventral margin of the tooth for most or all of its length (3 spp.) ..... **23**
- With mesosoma in profile view the propodeal declivity equipped with a simple carina or at most a narrow cuticular flange (Fig. 48B); carina or narrow flange does not subtend the ventral margin of the tooth for most or all of its length (5 spp.) ..... **24**
- 23 Pronotal humeral hair stiff, straight, relatively short (Figs 49, 50A) (Guangdong, Taiwan) ..... ***S. hispida***
- Pronotal humeral hair flagellate, long and slender (Fig. 50B) (2 spp.) ..... **25**
- 24 Dorsal surface of petiole node and disc of postpetiole both smooth and shining, the two surfaces not contrasting. With petiole in dorsal view the node without a truncated anterior face. Smaller ant (TL = 2), with shorter head (HL = 0.52–0.54) and antennae (SL = 0.28–0.30) (Figs 51, 53A) (China: Hong Kong, Macao, Taiwan; Japan) ..... ***S. minutula***
- Dorsal surface of petiole node sharply punctate or reticulate-punctate, disc of postpetiole smooth or with very scattered faint sculptural vestiges, the two surfaces contrasting. With petiole in dorsal view the node with a short truncated anterior face; lateral margins not converging to a triangular anteromedian point. Larger ant (TL = 2.2–2.6), with longer head (HL = 0.58–0.71) and antennae (SL = 0.34–0.42) (Figs 52, 53B) (Bhutan, China: Hong Kong, Taiwan; India, Indonesia, Malaysia, Thailand) ..... ***S. nanzanensis***
- 25 Preapical tooth of mandible spiniform and shallowly curved (Figs. 54, 55A), its length ca. one-third greater than the maximum width of the mandible (China: Hong Kong; Vietnam) ..... ***S. rallarbina***

- Preapical tooth of mandible varying from a denticle to a triangular tooth but not spiniform, the tooth shorter than the maximum width of the mandible, usually distinctly shorter (Fig. 55B) (4 spp.)..... 26
- 26 Preapical tooth very small, in full-face view its length one-quarter or less of the width of the mandible at the point where the tooth arises (Figs 56, 57A) (China: Hong Kong, Macao; Myanmar, Indomalaya) ..... *S. feae*
- Preapical tooth larger, in full-face view its length half or more of the width of the mandible at the point where the tooth arises (Fig. 57B) (3 spp.) ..... 27
- 27 In full-face view, external margin of mandibles straight (Figs. 58, 59A) (China: Guangdong; Japan) ..... *S. stenorhina*
- In full-face view, external margin of mandibles curvilinear (Fig. 59B) (2 spp.) ..... 28

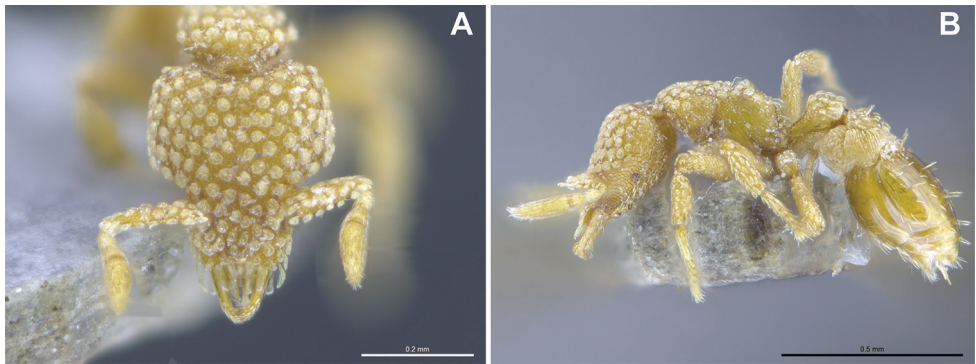


**Figure 14.** Examples of short, not kinetic, mandibles in *S. elegantula* (**A** MAC\_S04\_LLSP\_sp.9, photograph by IBBL), relatively long and kinetic in *S. feae* (**B** MAC\_S15\_LLSP\_sp.8, photograph by IBBL), curvilinear and kinetic in *S. emmae* (**C** MAC\_S20\_LLSP\_sp.7, photograph by IBBL), and with outer margin flared outwards near base and with strongly projecting basal angle in *S. sydorata* (**D** RHL003404, photograph by IBBL).

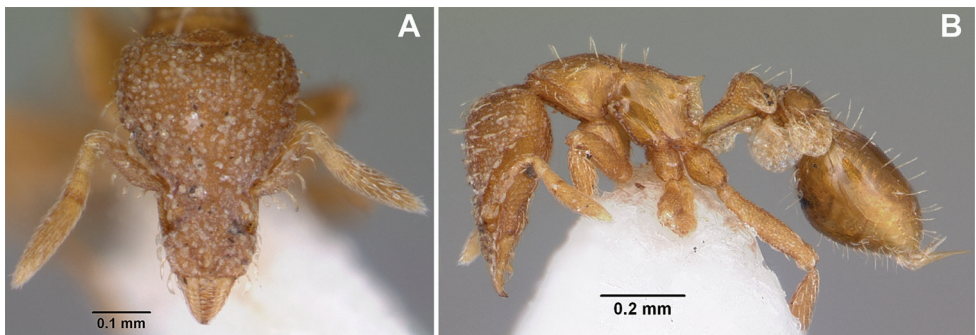




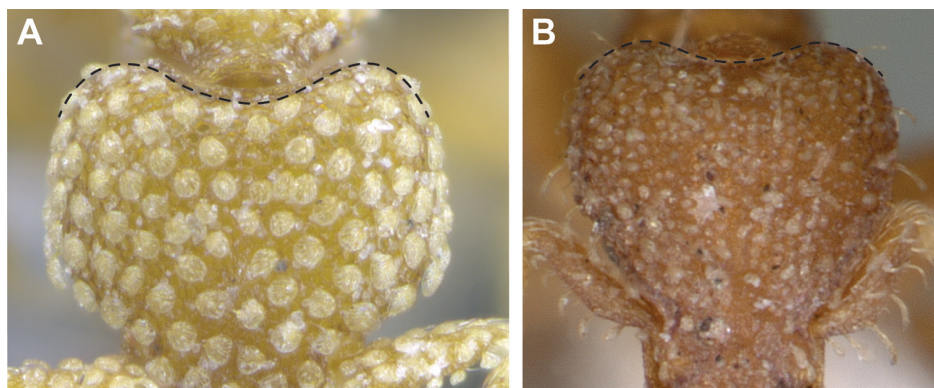
**Figure 15.** Examples of antenna with 4 segments in *S. nepalensis* (**A** MAC\_S19\_LLSP\_sp.3, photograph by IBBL) and antenna with 6 segments in *S. membranifera* (**B** MAC\_S21\_LLSP\_sp.2, photograph by IBBL).



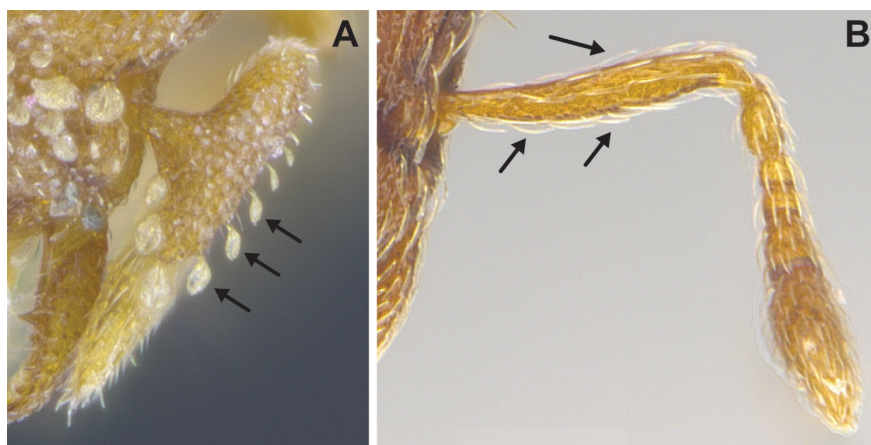
**Figure 16.** *Strumigenys lantau* (ANTWEB1009620, photographed by IBBL) in full-face **A** and profile view **B**.



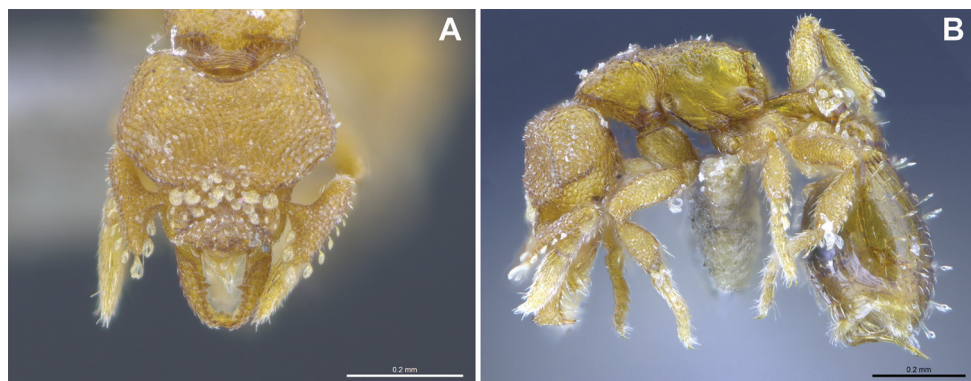
**Figure 17.** *Strumigenys nepalensis* (ANTWEB0102623, photographed by April Nobile) in full-face **A** and profile view **B**.



**Figure 18.** Examples of prominent vertexal corners in *S. lantau* (**A** ANTWEB1009620, photographed by IBBL) and less prominent vertexal corners in *S. nepalensis* (**B** ANTWEB0102623, photographed by April Nobile).

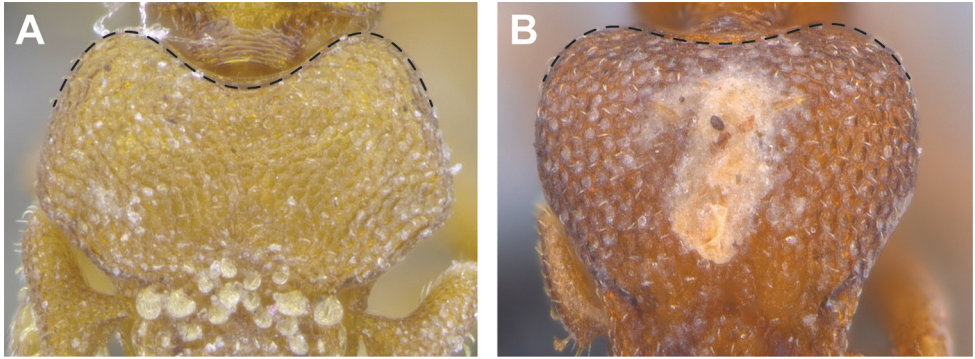


**Figure 19.** Examples of leading edge of scape with conspicuous hairs curving towards the base of the scape in *S. formosa* (**A** RHL003476, photographed by IBBL) and of leading edge of scape lacking projecting hairs that curve toward the base of the scape in *S. elegantula* (**B** MAC\_S04\_LLSP\_sp.9, photographed by IBBL).

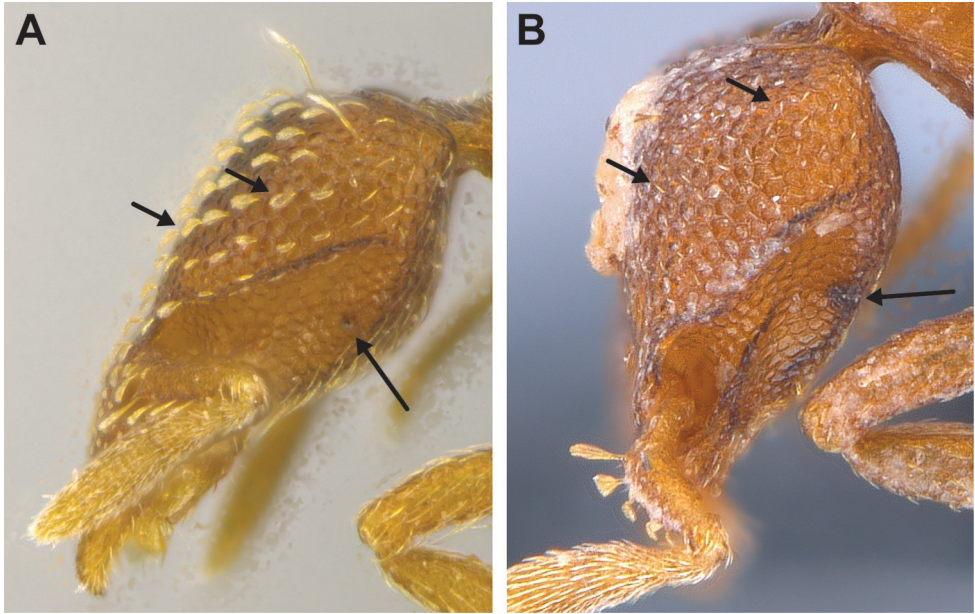


**Figure 20.** *Strumigenys formosa* (RHL003476, photographed by IBBL) in full-face **A** and profile view **B**.





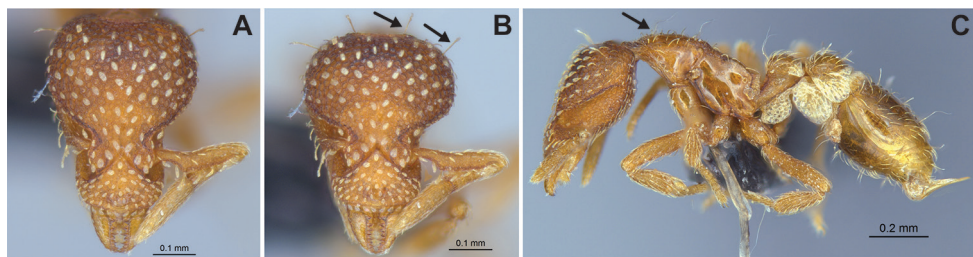
**Figure 21.** Examples of vertexal margin strongly concave in *S. formosa* (**A** RHL003476, photographed by IBBL) and of vertexal margin weakly concave in *S. membranifera* (**B** MAC\_S21\_LLSP\_Sp.2, photographed by IBBL).



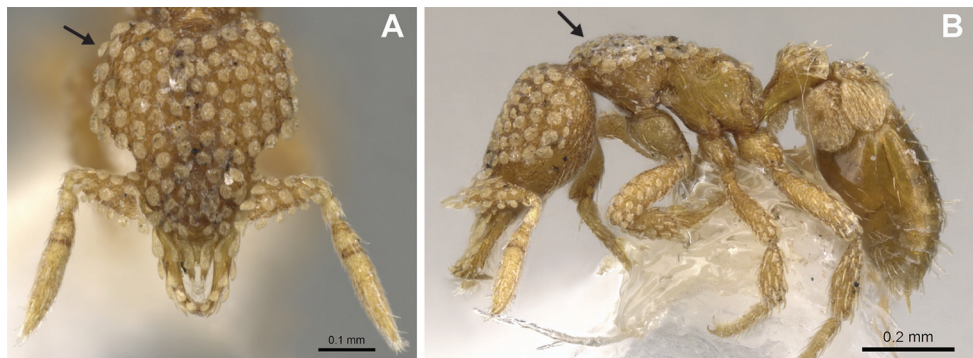
**Figure 22.** Examples of spatulate hairs on head and eye with a single ommatidium in *S. subterranea* sp. nov. (**A** ANTWEB1010847, photographed by François Brassard) and of small appressed simple hairs on head with eye composed of more than one ommatidium in *S. membranifera* (**B** MAC\_S21\_LLSP\_sp.2, photographed by IBBL).



**Figure 23.** *Strumigenys membranifera* (BMW02021, photographed by IBBL) in full-face **A** and profile view **B**.

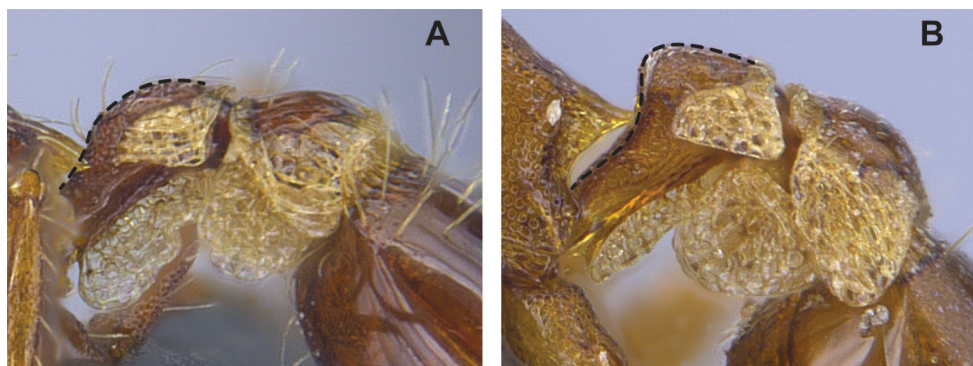


**Figure 24.** *Strumigenys subterranea* (ANTWEB1010847, photographed by François Brassard) in full-face **A**, **B** and profile view **C**.

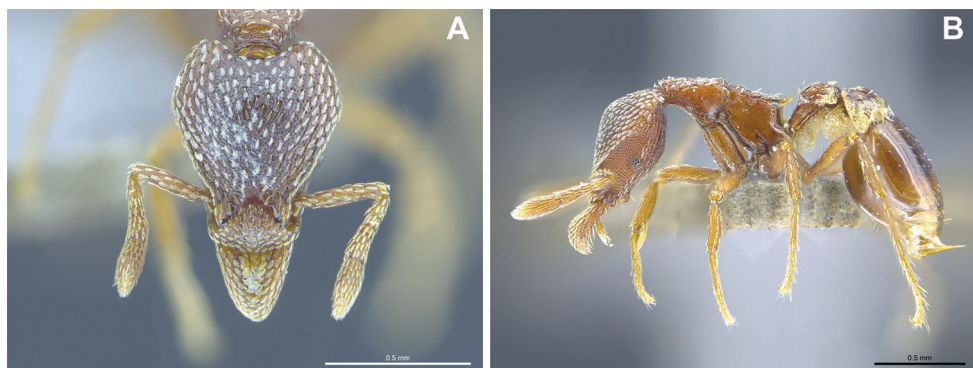


**Figure 25.** *Strumigenys lachesis* (ANTWEB0900156, photographed by Will Ericson) in full-face **A** and profile view **B**.

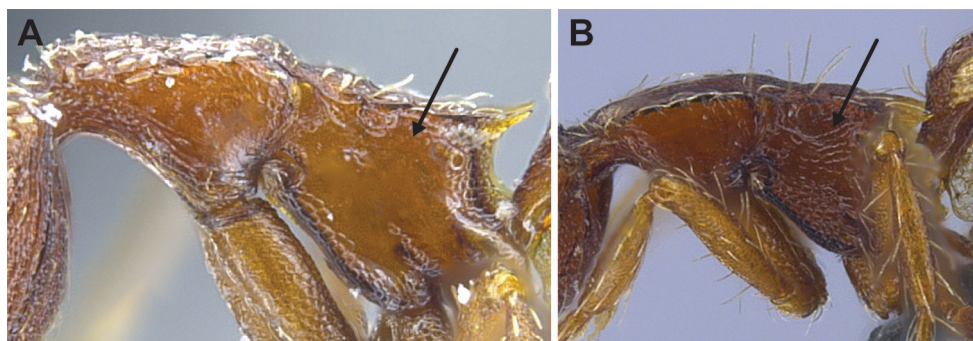




**Figure 26.** Examples of long and relatively flat petiole in *Strumigenys elegantula* (**A** ; MAC\_S04\_LLSP\_sp.9), and short with a dorsal protrusion in *Strumigenys sauteri* (**B** ; MAC\_S04\_LLSP\_sp.2).

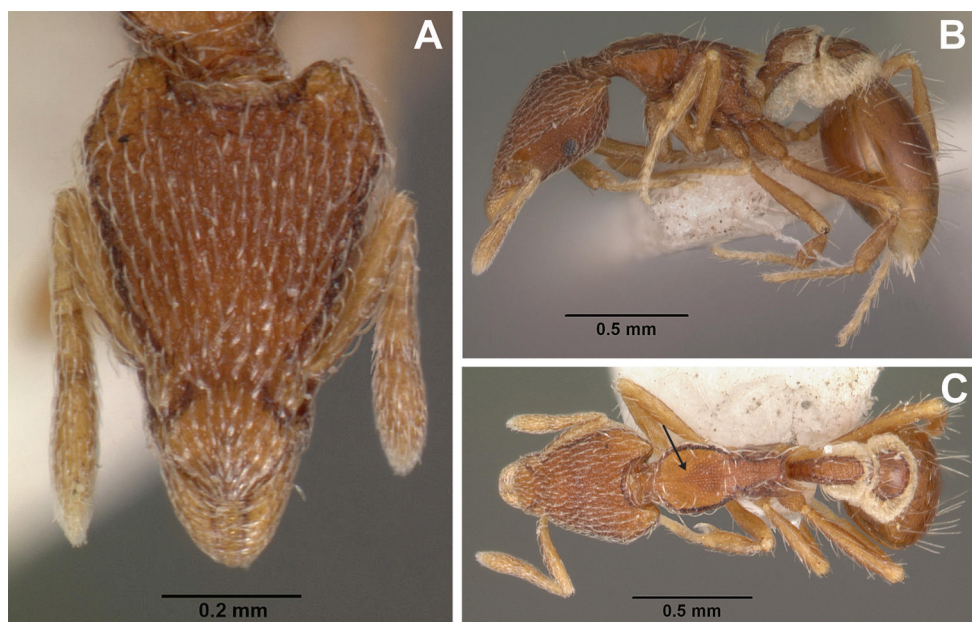


**Figure 27.** *Strumigenys nathistorisoc* (ANTWEB1016948, photographed by IBBL) in full-face **A** and profile view **B**.

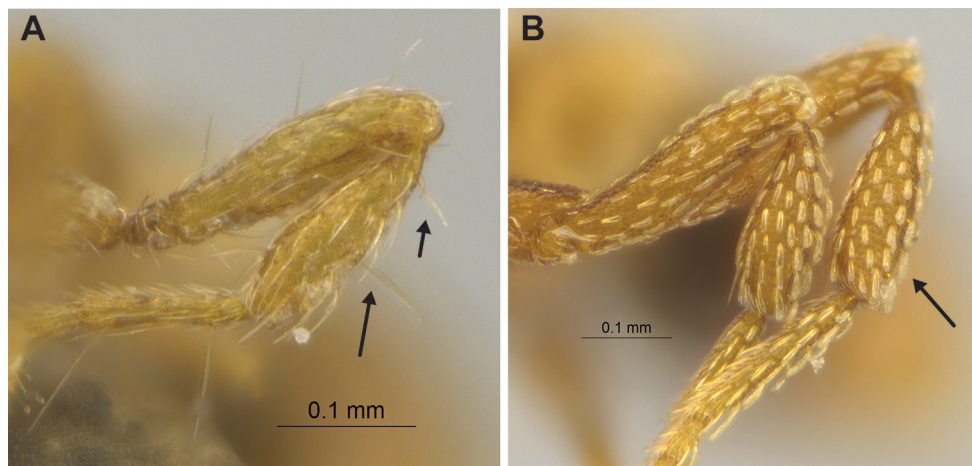


**Figure 28.** Examples of smooth and shiny mesopleuron and metapleuron in *S. nathistorisoc* (**A** ANTWEB1016948, photographed by IBBL), and of sculptured mesopleuron and metapleuron in *S. elegantula* (**B** MAC\_S04\_LLSP\_sp.9, photographed by Siu Yiu).

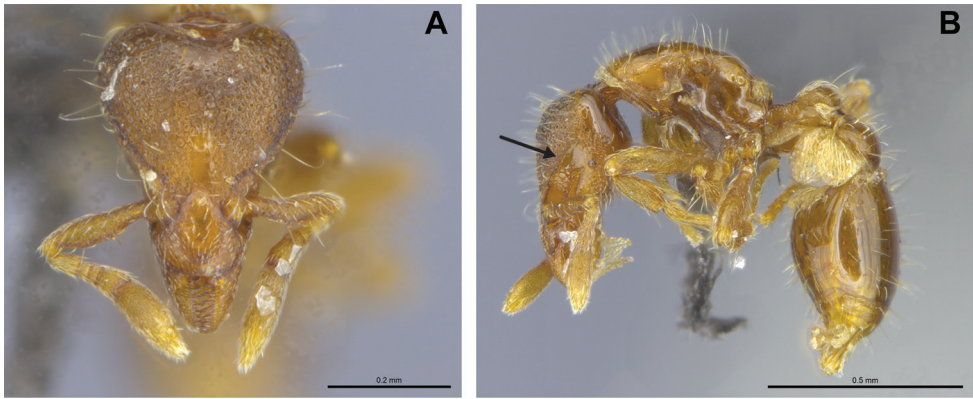




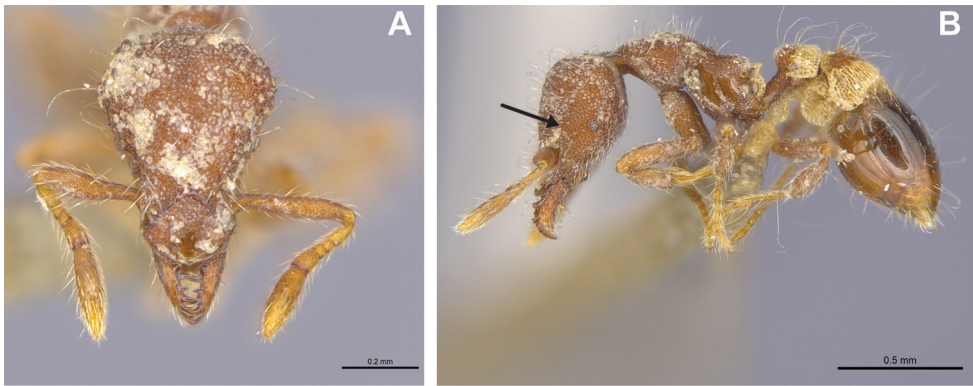
**Figure 29.** *Strumigenys elegantula* (ANTWEB0102542, photographed by April Nobile) in full-face **A**, profile **B**, and dorsal view **C**.



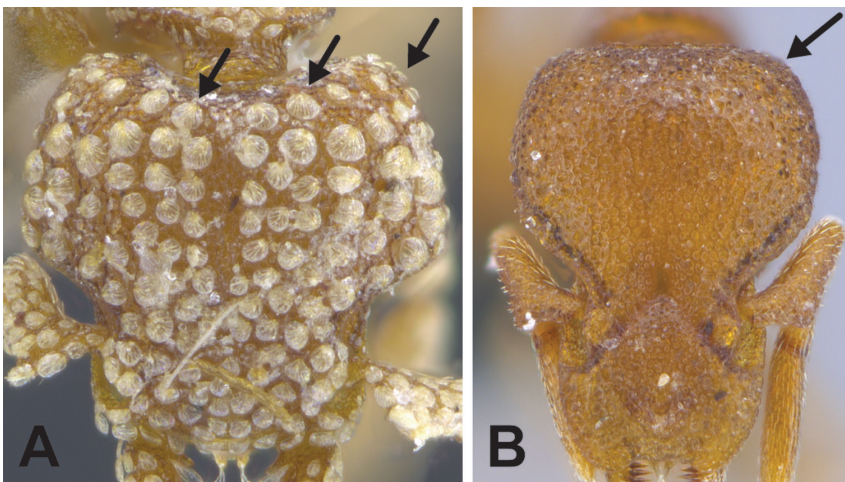
**Figure 30.** Examples of conspicuous laterally projecting hairs on middle and hind tibiae *S. mazu* (**A** ANTWEB01017070, photographed by IBBL) and of small appressed hairs in *S. tisiPHONE* (**B** RHL02818, photographed by IBBL).



**Figure 31.** *Strumigenys mazu* (TT00985, photographed by IBBL) in full-face **A** and profile view **B**.

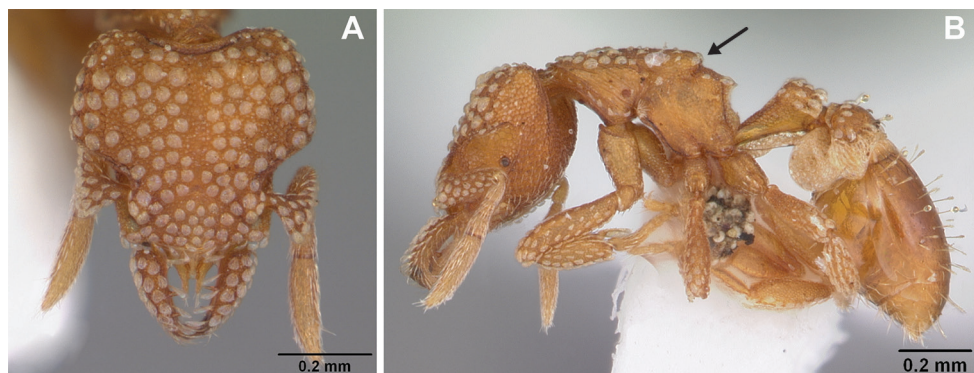


**Figure 32.** *Strumigenys kichijo* (RHL003471, photographed by IBBL) in full-face **A** and profile view **B**.

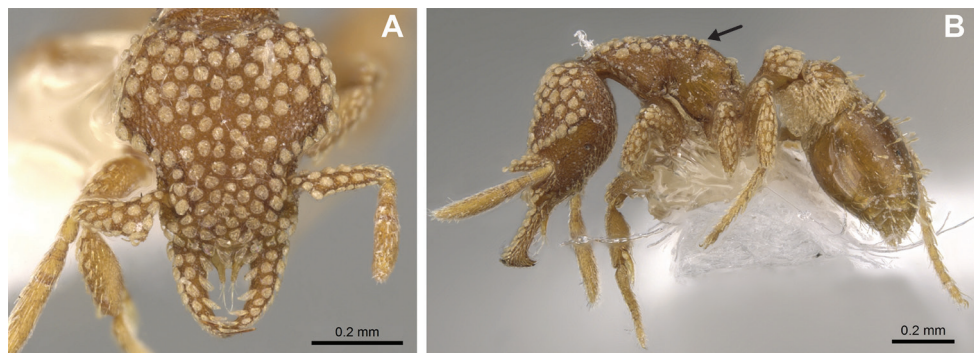


**Figure 33.** Examples of head with dorsum clothed with ground pilosity of conspicuous pale orbicular hairs in *S. hexamera* (**A** RHL003477, photographed by IBBL) and of dorsum of head without hairs in *S. sauteri* (**B** MAC\_S04\_LLSP\_sp.2, photographed by IBBL).

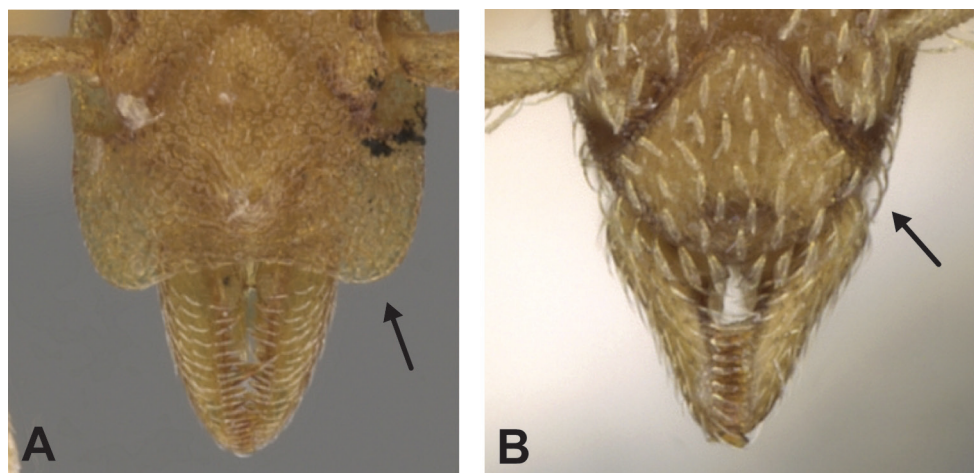




**Figure 34.** *Strumigenys hexamera* (ANTWEB0103819, photographed by April Nobile) in full-face **A** and profile view **B**.



**Figure 35.** *Strumigenys tisiphone* (ANTWEB0900154, photographed by Will Ericson) in full-face **A** and profile view **B**.



**Figure 36.** Examples of anterior clypeal margin projecting laterally beyond the outer line of the mandible in *S. canina* (**A** ANTWEB0900124, photographed by Will Ericson) and of anterior clypeal margin not projecting beyond the outer line of the mandible in *S. mutica* (**B** ANTWEB0280715, photographed by Shannon Hartman).



**Figure 37.** *Strumigenys canina* (ANTWEB0900124, photographed by Will Ericson) in full-face **A** and profile view **B**.

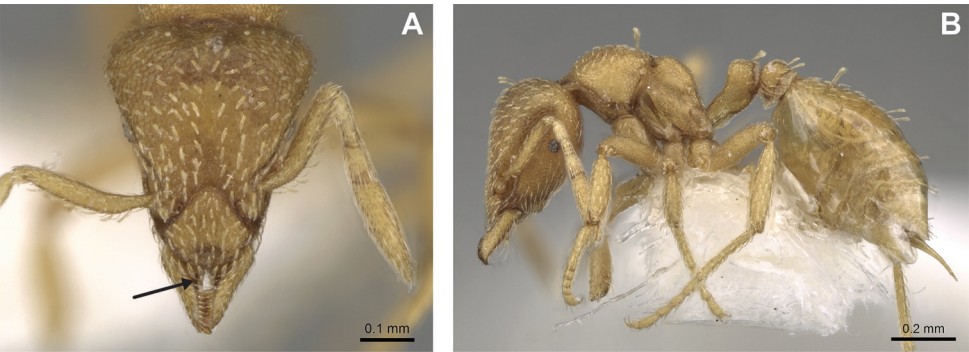


**Figure 38.** *Strumigenys sauteri* (ANTWEB0280702, photographed by Shannon Hartman) in full-face **A** and profile view **B**.

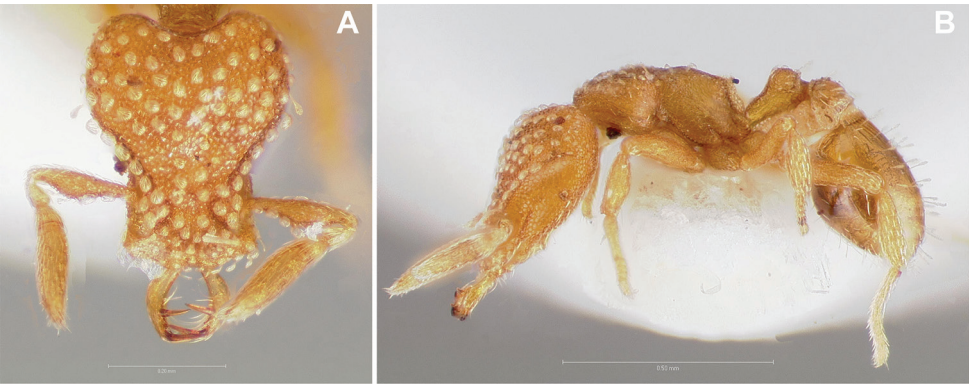


**Figure 39.** *Strumigenys mitis* (ANTWEB0900120, photographed by Will Ericson) in full-face **A** and profile view **B**.

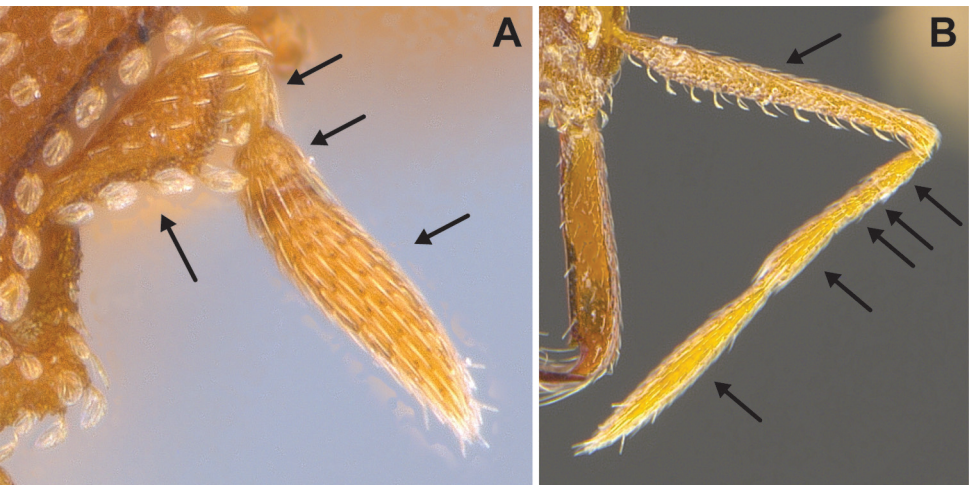




**Figure 40.** *Strumigenys mutica* (ANTWEB0280715, photographed by Shannon Hartman) in full-face **A** and profile view **B**.



**Figure 41.** *Strumigenys emmae* (CASENT000589, photographed by April Nobile) in full-face **A** and profile view **B**.



**Figure 42.** Examples of antenna with 4 segments in *S. emmae* (**A** MAC\_S20\_LLSP\_sp.7, photographed by IBBL) and of antenna with 6 segments in *S. feae* (**B** ANTWEB1017082, photographed by IBBL).

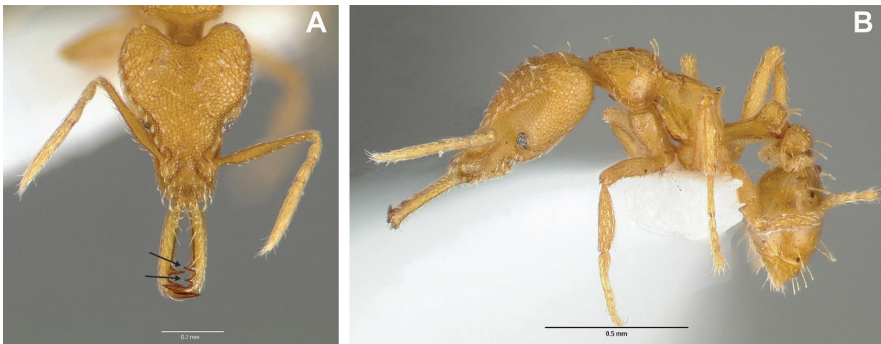




**Figure 43.** *Strumigenys sydorata* (ANTWEB0102619, photographed by April Nobile) in full-face **A** and profile view **B**.



**Figure 44.** Examples of mandibles of different shape: linear mandibles in *S. minutula* (**A** MAC\_S01\_LLSA\_Sp.3, photographed by François Brassard), curvilinear mandibles in *S. feae* (**B** MAC\_S15\_LLSP\_Sp.8, photographed by François Brassard), and broad proximally and mandibles strikingly tapered distally in *S. sydorata* (**C** ANTWEB0102619, photographed by April Nobile).



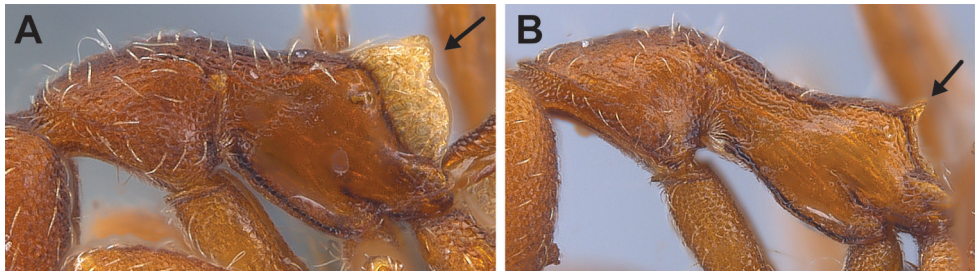
**Figure 45.** *Strumigenys rogeri* (CASENT0005897, photographed by April Nobile) in full-face **A** and profile view **B**.



**Figure 46.** *Strumigenys heteropha* (CASENT0005897, photographed by Will Ericson) in full-face **A** and profile view **B**.

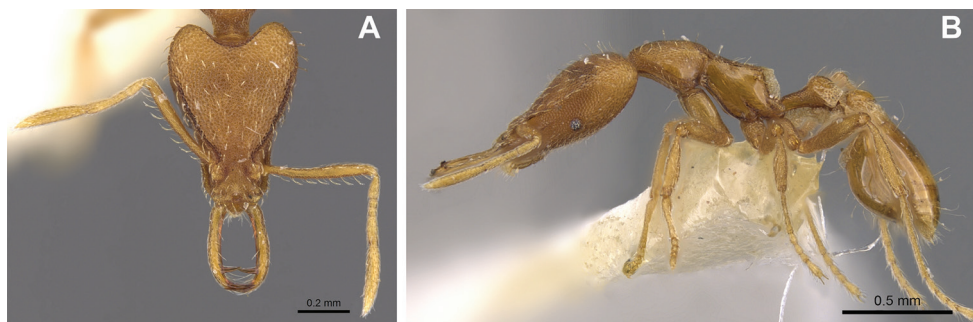


**Figure 47.** Examples of mandible without preapical dentition in *S. heteropha* (**A** CASENT0005897, photographed by Will Ericson) and of mandible with preapical dentition in *S. minutula* (**B** MAC\_S14\_LLSP\_sp.4, photographed by François Brassard).

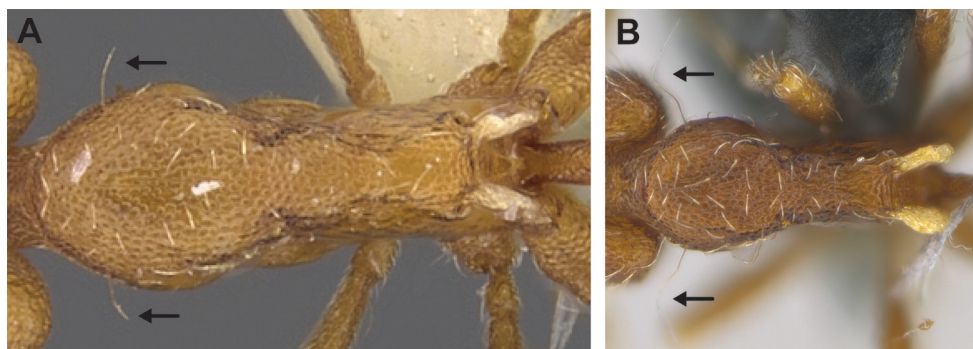


**Figure 48.** Propodeal declivity equipped with a broad and conspicuous lamella (**A** MAC\_S14\_LLSP\_Sp.4, photographed by François Brassard) and propodeal declivity equipped with a simple carina in *S. feae* (**B** MAC\_S15\_LLSP\_Sp.8, photographed by François Brassard).

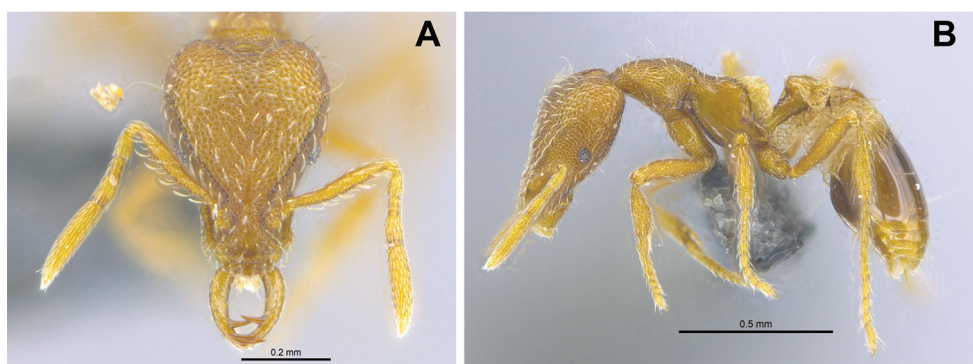




**Figure 49.** *Strumigenys hispida* (CASENT0900821, photographed by Will Ericson) in full-face **A** and profile view **B**.



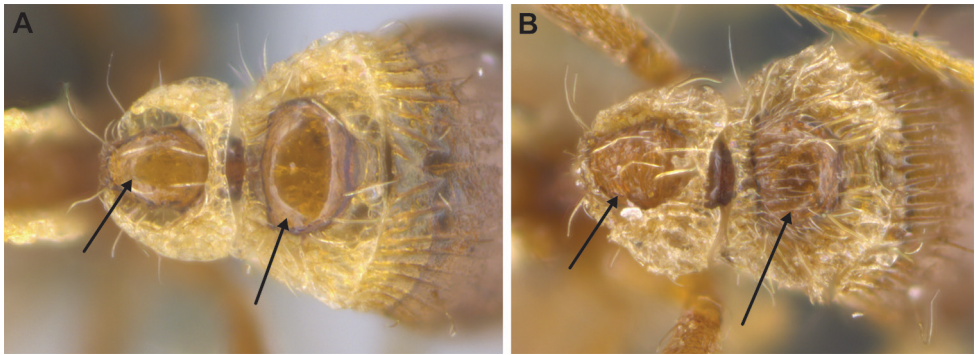
**Figure 50.** Examples of relatively short and straight, stiff pronotal humeral hairs in *S. hispida* (**A** CASENT0900821, photographed by Will Ericson) and of long and slender flagellate pronotal hairs in *S. minutula* (**B** MAC\_LLSA\_S06\_sp.6, photographed by François Brassard).



**Figure 51.** *Strumigenys minutula* (MAC\_S11\_GN3\_H4\_n1, photographed by François Brassard) in full-face **A** and profile view **B**.



**Figure 52.** *Strumigenys nanzanensis* (CASENT02807, photographed by Shannon Hartman) in full-face **A** and profile view **B**.

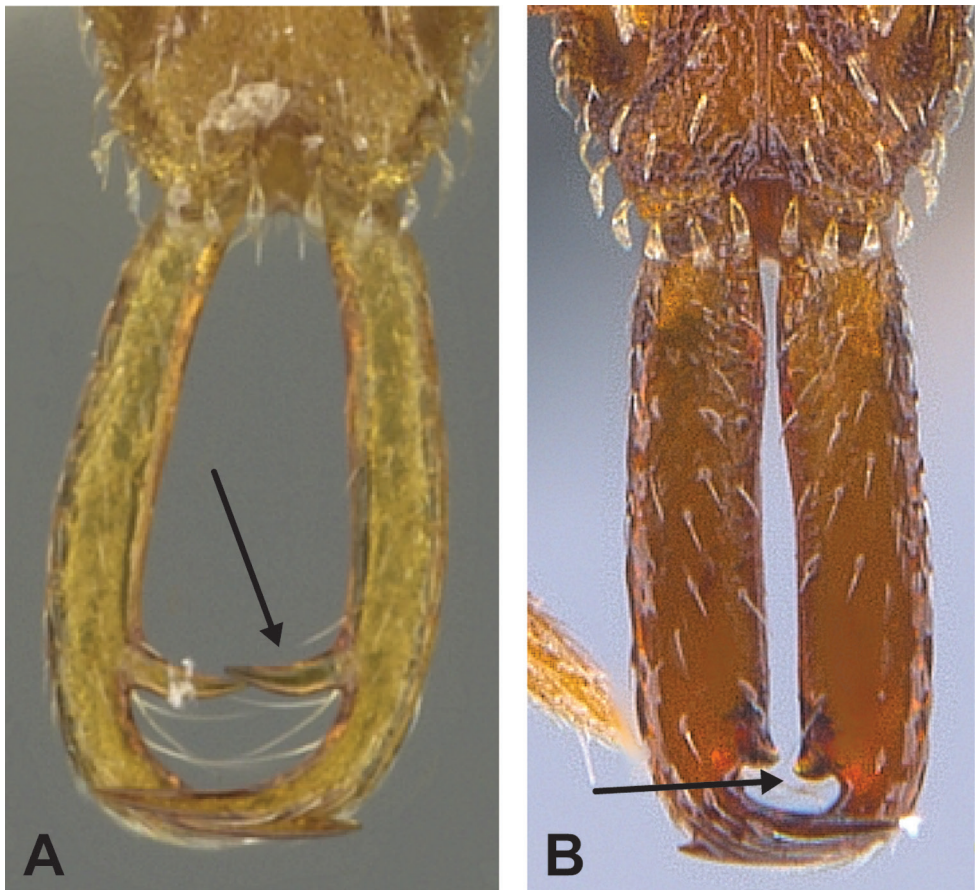


**Figure 53.** Examples of smooth dorsal surface of petiole node and disc of postpetiole in *S. minutula* (**A** MAC\_LLSA\_S06\_sp.6, photographed by François Brassard) and of reticulate-punctate dorsal surface of petiole node and postpetiole smooth with very scattered faint sculptural vestiges in *S. nanzanensis* (**B** BMW00846, photographed by François Brassard).

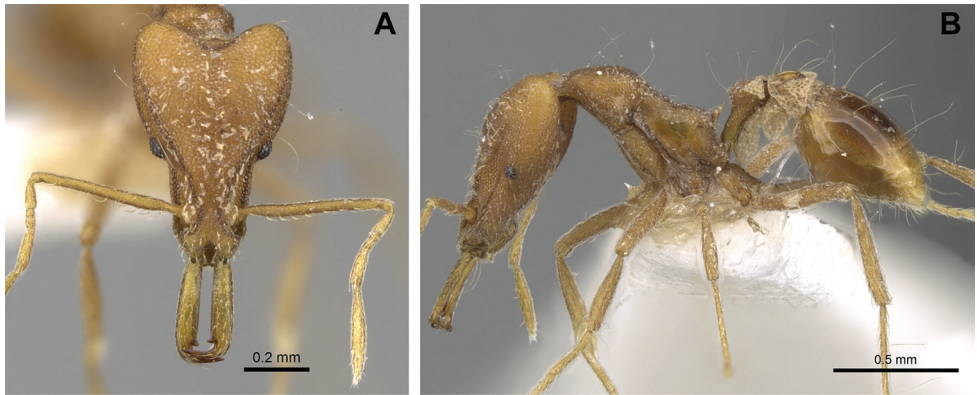


**Figure 54.** *Strumigenys rallarhina* (CASENT0900839, photographed by Ryan Perry) in full-face **A** and profile view **B**.

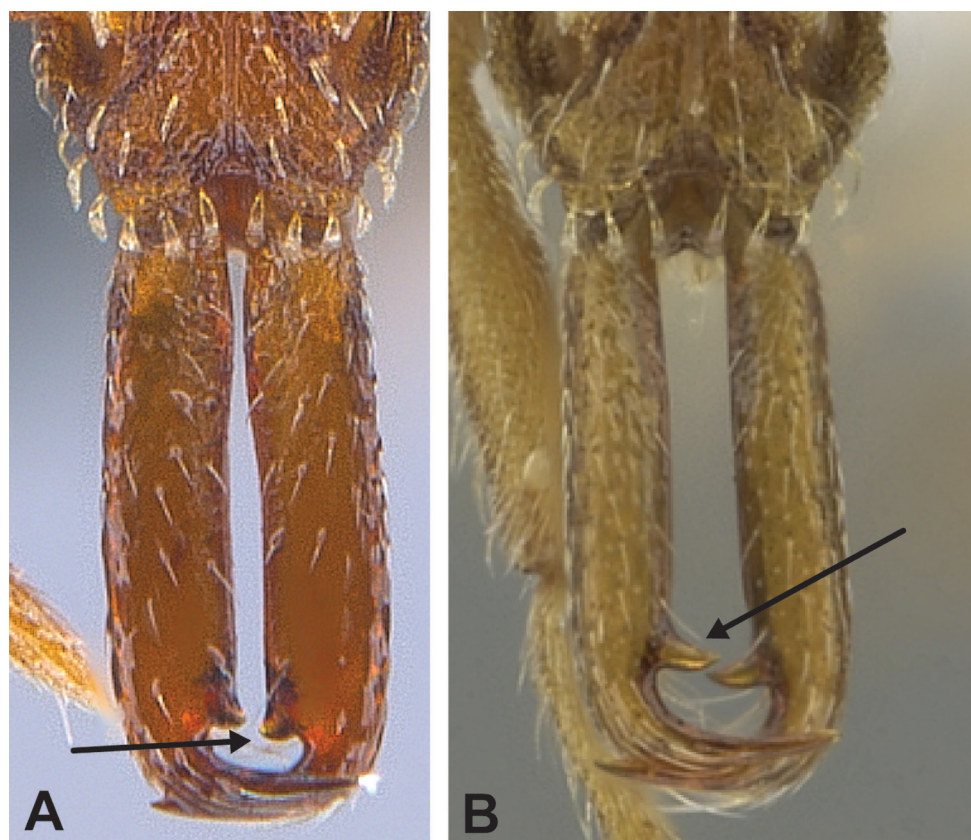




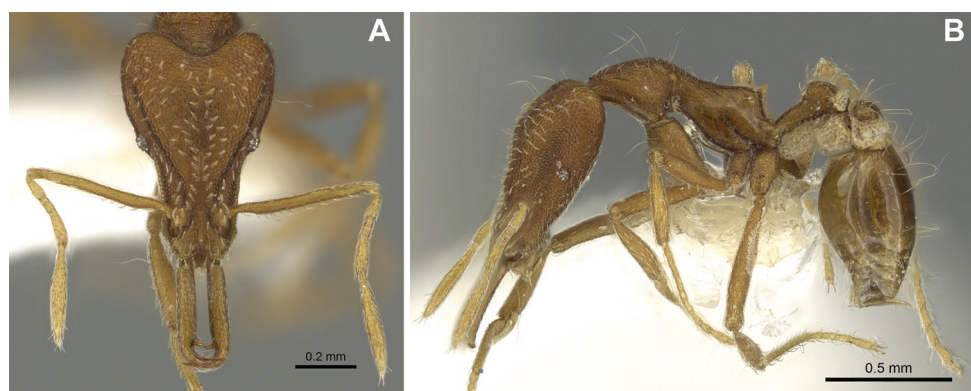
**Figure 55.** Example of spiniform and shallowly curved preapical tooth in *S. rallarhina* (**A** CASENT0900839, photographed by Ryan Perry) and of short triangular tooth in *S. feae* (**B** MAC\_S15\_LLSP\_sp.8, photographed by IBBL).



**Figure 56.** *Strumigenys feae* (CASENT0280748, photographed by Shannon Hartman) in full-face **A** and profile view **B**.

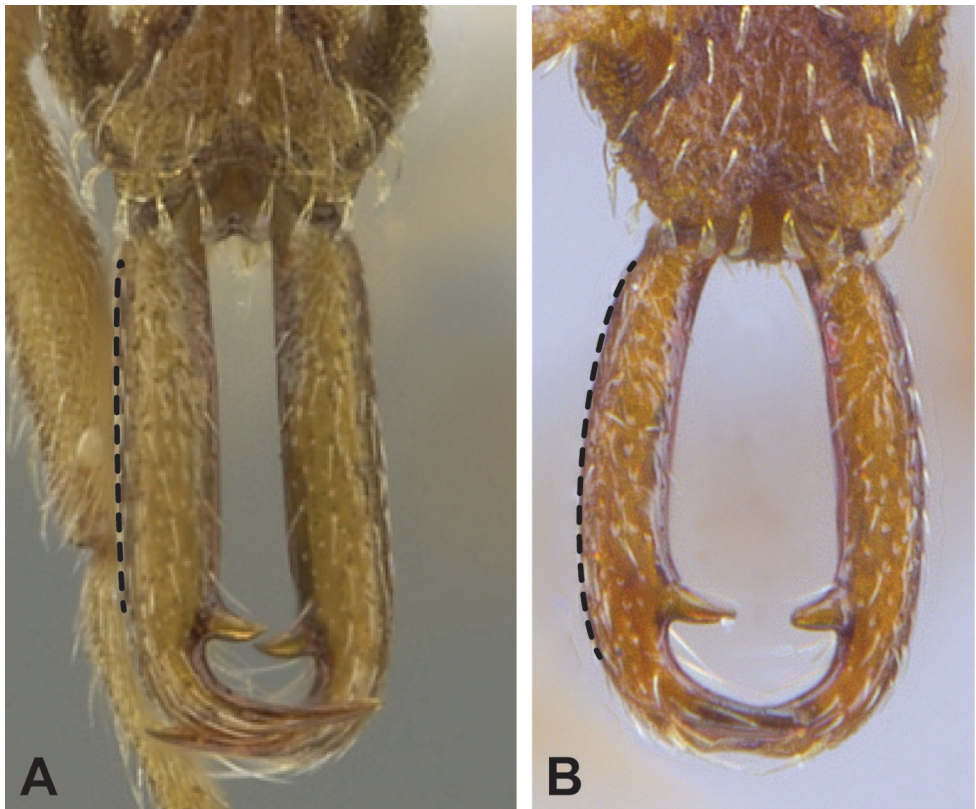


**Figure 57.** Examples of small preapical tooth in *S. feae* (**A** MAC\_S15\_LLSP\_sp.8, photographed by IBBL) and of larger preapical tooth in *S. stenorhina* (**B** CASENT0900840, photographed by Ryan Perry).

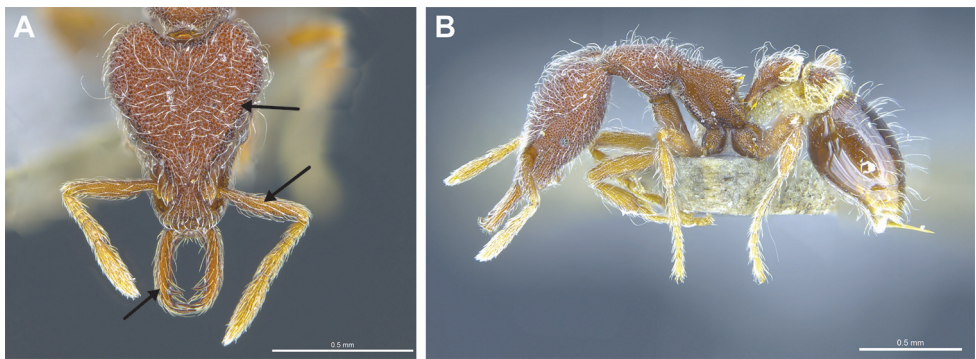


**Figure 58.** *Strumigenys stenorhina* (CASENT0900840, photographed by Ryan Perry) in full-face **A** and profile view **B**.

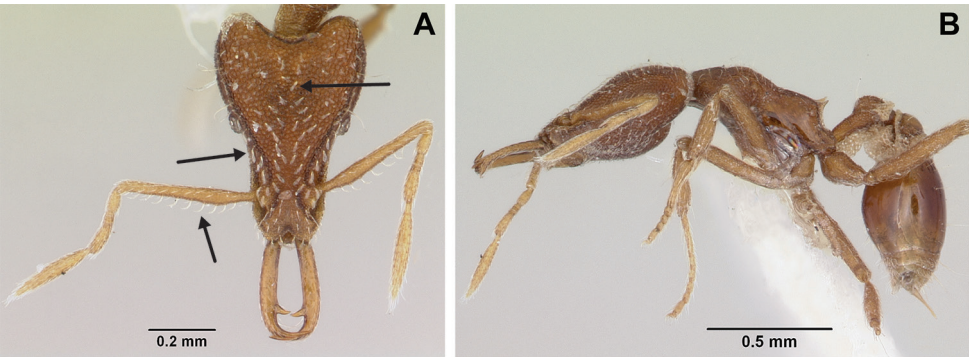




**Figure 59.** Examples of mandible with straight external margin in *S. stenorhina* (**A** CASENT0900840, photographed by Ryan Perry) and of mandible with curvilinear external margin in *S. exilirhina* (**B** MAC\_S01\_LLSA\_sp.3, photographed by IBBL).



**Figure 60.** *Strumigenys hirsuta* (ANTWEB1009855, photographed by IBBL) in full-face **A** and profile view **B**.



**Figure 61.** *Strumigenys exilirhina* (CASENT0102650, photographed by April Nobile) in full-face **A** and profile view **B**.

- 28      In full-face view, long appressed simple hairs abundant on head, antennae and mandibles (Fig. 60A). Metapleuron partly smooth, with the majority of its surface punctate (*Native*. China: Hong Kong) .....*S. hirsuta*
- In full-face view, pilosity on head and antennae consisting mostly of relatively slender appressed spatulate hairs (Fig. 61A). Pilosity on mandibles consisting of short appressed simple hairs. Metapleuron completely smooth and shining (Bhutan, China: Hong Kong, Macao; India, Japan, Nepal, Thailand) .....  
..... *S. exilirhina*

**Discussion**

Traditionally, *Strumigenys* species have been collected through the extraction of arthropods present in the leaf litter, which is here confirmed with the capture of eight out of nine species through this method. However, the addition of subterranean traps allowed the collection of an undescribed species: *Strumigenys subterranea* sp. nov. If the majority of *Strumigenys* species are not considered subterranean, but rather leaf-litter foragers or even arboreal (Longino and Nadkarni 1990; Lattke et al. 2018), a few exceptions occur. For instance, the species *Strumigenys hexamera* Brown, 1958 (Masuko 1984) and *Strumigenys mitis* Brown, 2000 (Mezger and Pfeiffer 2010) are considered subterranean, while other records suggest a potential subterranean lifestyle in other species such as in *Strumigenys* sp. nr. *sutrix* Bolton, 2000, for which 2 individuals were collected with subterranean traps at a depth of 5 cm (Andersen and Brault 2010).

Subterranean ants have adaptations, such as specific morphological characteristics, to live within the particular environmental conditions that define the underground habitat (Wong and Guénard 2017). Among those, the absence of eyes or the presence of reduced eyes, while not strictly limited to subterranean ants (e.g., some epigaeic army ants), represent an adaptation to this obscure environment. Indeed, visual ori-



entation underground should be limited if non-existent, thus rendering obsolete the need for large eyes providing a more acute vision. The presence of short mandibles, presumably easier to maneuver underground than the long and snapping mandibles of certain trap-jaw *Strumigenys*, potentially represents another adaptation. For instance, *S. hexamera* is a sit and wait predator that uses its short mandibles to hunt preys within tunnels (Masuko 1984), while the short triangular mandibles of the subterranean *S. mitis* have been proposed as a subterranean adaptation in contrast to the long and wide-opening mandibles of the epigaeic *S. rotogenys* (Mezger & Pfeiffer, 2010). Since *Strumigenys subterranea* sp. nov. possesses both characteristics (i.e., reduced eyes and short triangular mandibles) and was detected at 12.5 cm below ground, this would suggest a subterranean lifestyle. Nevertheless, mentions of subterranean *Strumigenys* are still rare, which may be due to very limited sampling efforts within this stratum (Wong and Guénard 2017).

To collect subterranean *Strumigenys*, other techniques than subterranean traps exist. For instance, *Strumigenys louisianae* Roger, 1863, *Strumigenys* nr. *epinotalis* Weber, 1934 and *Strumigenys denticulata* Mayr, 1887 were retrieved using soil monoliths at a depth of 0–10 cm (Martins et al. 2020), while the holotype worker of *Strumigenys fuarda* Bolton, 2000 was collected within a soil core (Bolton 2000). However, soil sampling, if done without removing the upper soil layer, does not preclude the collection of leaf litter ants foraging on the upper surface of a core or monolith. This is potentially the case for *S. louisianae* or *S.* nr. *epinotalis* (Martins et al. 2020), and as such further observations are required to establish if they are hypo- or epigaeic.

Another sampling method that can potentially collect subterranean *Strumigenys* is nest excavation, which has been used to collect nests of the subterranean *S. hexamera* (Masuko, 2013). Moreover, excavations under the litter-fermentation-humidification horizon up to a depth of 25 cm found nests of *Strumigenys kumadori* Yoshimura & Onoyama, 2007 (Masuko 2010). However, nest excavations do not ensure that the species collected are subterranean, because even though these species may nest underground, their foraging activity could be mainly occurring above ground. As such, labeling an ant as subterranean solely because it was collected during an excavation is not fully satisfactory. As an example, *S. kumadori*, which has relatively large eyes and long snapping mandibles, does not match the morphology of an hypogaeic species. Thus, to collect subterranean *Strumigenys* species, subterranean traps or the careful excavation of soil monoliths (of which the top soil layers would be excluded) seem to be preferential solutions.

## Conclusions

Although cities and the nature parks within them (i.e., patches of secondary forests) are rarely viewed as a refuge for biodiversity, recent work using diverse sampling approaches have shown that urban habitats can host high numbers of both native and exotic ant species (Guénard et al. 2015; Leong et al. 2017). This study in Macao, as well as recent work in Hong Kong (Tang et al. 2019) – two heavily urbanized regions –

shows that both regions support a high diversity of *Strumigenys* species, with nine and 24 species recorded respectively. Recent work in other parts of the world, such as in the USA, also showed that the discovery of new *Strumigenys* species within urban habitats is possible (Longino and Booher 2019). Alarming, further urbanization threatens several of these habitats, including the type locality of the species described here. Indeed, a construction project is planned in proximity of where the only specimen of *Strumigenys subterranea* sp. nov. was found, which could potentially impact key habitats for this species. In summary, the current study supports both the ideas that urban areas can hold a surprisingly high biodiversity for particular taxa as well as to contain species novel to science. As such, it is worth protecting forest patches within cities, and using extensive sampling methods to discover and describe what lurks amongst our dwellings.

## Acknowledgments

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## Supplementary material I

### Figure S1. Map of Coloane Island showcasing the 21 sites sampled

Authors: François Brassard, Chi-Man Leong, Hoi-Hou Chan, Benoit Guénard

Data type: occurrence

Explanation note: White dots mark sites where the full protocol was done (i.e., leaf litter extraction, ground baiting, ground nests, subterranean traps and arboreal traps), whereas grey dots mark preliminary sites where only ground baiting and leaf litter extraction were done. Hand collection was also opportunistically used at each site.

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Link: <https://doi.org/10.3897/zookeys.970.54958.suppl1>



## Supplementary material 2

### Figure S2. Schematic representation of the subterranean sampling protocol used in the study

Authors: François Brassard, Chi-Man Leong, Hoi-Hou Chan, Benoit Guénard

Data type: measurement

Explanation note: For a site, 4 different quadrats each had four traps placed 1 m apart at each of their corners ( $n = 16$ ). Within a quadrat, traps were distributed at four different depths: 12.5, 25, 37.5, and 50 cm (A). Traps consisted of a 15 mL falcon tube containing 70 % ethanol at its bottom (B). To attract ants, a bait consisting of tuna mixed with honey was placed at the top of the trap. To allow ants to enter the trap, four holes were drilled on the wall of the tube.

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Link: <https://doi.org/10.3897/zookeys.970.54958.suppl2>

## Supplementary material 3

### Figure S3. Schematic representation of ground nests used in the study

Authors: François Brassard, Chi-Man Leong, Hoi-Hou Chan, Benoit Guénard

Data type: measurement

Explanation note: Four nests blocks, each containing two entrances of the same size (1.588, 1.984, 2.381 or 3.175 mm), were placed in a bundle. A nest bundle is represented with a top view in (A) and a sideview in (B). Details of the nest and an inside chamber are shown in (C). A zoomed in inset of a nest chamber containing a queen, a worker, a larva, eggs and pupae is shown in (D). For each site, 8 nests bundles ( $n = 64$  nests) were placed.

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Link: <https://doi.org/10.3897/zookeys.970.54958.suppl3>

## Supplementary material 4

### Figure S4. Transect design used for ground baiting

Authors: François Brassard, Chi-Man Leong, Hoi-Hou Chan, Benoit Guénard

Data type: measurement

Explanation note: Each bait ( $n = 11$ ) were placed 5 m apart along a 50 m transect.

The baits, placed for 45 to 60 minutes, consisted of a 4 mm-thick slice of sausage previously dipped in honey.

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Link: <https://doi.org/10.3897/zookeys.970.54958.suppl4>

## Supplementary material 5

### Table S5. List of the sampling sites visited in 2019, with their associated number, name and geolocation

Authors: François Brassard, Chi-Man Leong, Hoi-Hou Chan, Benoit Guénard

Data type: species data

Explanation note: The date refers to the first sampling event made at a site, which corresponded to the leaf litter extraction and placement of subterranean traps. Sampling protocols are defined as follows: the letter (P) signifies a partial sampling protocol (i.e., leaf litter extraction, ground baiting and hand collection), whereas the letter (F) signifies a full protocol (i.e., leaf litter extraction, ground baiting, ground nests, subterranean traps, arboreal traps and hand collection).

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Link: <https://doi.org/10.3897/zookeys.970.54958.suppl5>

# Exotic-looking Neotropical Tischeriidae (Lepidoptera) and their host plants

Jonas R. Stonis<sup>1</sup>, Arūnas Diškus<sup>1</sup>, Andrius Remeikis<sup>1</sup>,  
M. Alma Solis<sup>2</sup>, Liliana Katinas<sup>3</sup>

**1** Institute of Ecology, Nature Research Centre, Akademijos St. 2, Vilnius LT-08412, Lithuania **2** Systematic Entomology Laboratory, Beltsville Agriculture Research Center, Agriculture Research Center, U.S. Department of Agriculture, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20013-7012, USA **3** División Plantas Vasculares, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

Corresponding author: Jonas R. Stonis ([stonis.biotaxonomy@gmail.com](mailto:stonis.biotaxonomy@gmail.com))

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## Abstract

Seven new species of Tischeriidae are described from the Neotropics: *Astrotischeria jociui* Diškus & Stonis, **sp. nov.** (feeding on *Wissadula excelsior* (Cav.) C. Presl., Malvaceae), *A. atlantica* Diškus & Stonis, **sp. nov.** (feeding on *Baccharis spicata* (Lam.) Baill., Asteraceae), *A. cornuata* Diškus & Stonis, **sp. nov.** (host plant unknown), *Paratischeria guarani* Diškus & Stonis, **sp. nov.** (feeding on *Elephantopus mollis* Kunth, Asteraceae), *P. mesoamericana* Diškus & Stonis, **sp. nov.** (feeding on *Montanoa hibiscifolia* Benth., Asteraceae), *P. suprafasciata* Diškus & Stonis, **sp. nov.** (feeding on *Allophyllus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl., Sapindaceae), and *P. braziliensis* Diškus & Stonis, **sp. nov.** (host plant unknown). Additionally, an updated distribution map of *Paratischeria neotropicana* (Diškus & Stonis, 2015), which currently has the broadest distribution range among the Neotropical Tischeriidae is provided along with new host-plant data, a list of all recorded host plants in the Neotropics, and a brief discussion on trophic relationships of Tischeriidae. It is hypothesized that host-plant distribution ranges can provide clues to potential distribution ranges of these specialized, monophagous or oligophagous, leaf miners. All new taxa are illustrated with photographs of the adults, their genitalia, and, if available, leaf mines.

## Keywords

*Astrotischeria*, distribution range, leaf mines, new species, *Paratischeria*

## Introduction

Biodiversity inventories provide knowledge about nature and are of utmost importance to understand the complicated mechanisms of the global biota. It is also essential for providing tools for prompt measures in the preservation of biodiversity in the face of a biodiversity crisis and climate change. Along with other organisms, trumpet moths (Tischerioidae: Tischeriidae) can provide data in support of hypotheses about the earlier genesis of the Earth's biota. They also been used as an express tool for monitoring biodiversity, rapid assessment of biodiversity plots of critical value, and determining priority areas from the environmental point of view in the tropical America (Stonis, unpublished). However, tischeriids are not well-known or very common in museum holdings worldwide and are probably among the least studied lepidopteran groups in tropical and subtropical areas worldwide, including the Neotropics (Stonis et al. 2019b, 2020b). Nevertheless, they are a distinct family from the oldest (monotrysian) lineages of extant Lepidoptera (see Regier 2015 for a phylogenetic discussion) and very peculiar morphologically (Stonis et al. 2020b). Larvae of Tischeriidae are leaf miners of wild and cultivated plants; they mine inside green tissues during all instars and produce irregular, usually blotch-like leaf mines (Figs 5–9, 11–14, 17–21, 25–31, 35–37), but sometimes these are slender and sinuous or have another shape. Pupation occurs inside the leaf mine, often in a round, silken-lined nidus (Figs 31, 131, 137). Adults of trumpet moths (Figs 38–49) are very small, 5–10 mm in wingspan, with the 3<sup>rd</sup> antennal segment greatly enlarged (see Stonis et al. 2017: Fig. 67). Males possess long antennal sensillae trichodea, which usually exceed the width of the flagellum by more than 4.5–10 times and have strongly recurved, sometimes thickened bases (see Stonis et al. 2017: Fig. 67). In the male genitalia, the phallus is strongly narrowed and usually bifurcated or with spines at its apex. In the female genitalia, the ovipositor lobes are covered with short, dark, thickened peg-like setae; along the stout anterior and posterior apophyses, there are three additional pairs of unique, rod-like or plate-like projections collectively referred as prela. For detailed morphological and biological characterization of this group of tiny leaf miners, we refer to Braun (1972), Puplesis and Diškus (2003), Stonis et al. (2018a); and for generic diagnostics we recommend Puplesis and Diškus (2003), Stonis et al. (2017, 2018a), and Xu et al. (2017). The phylogenetic position of Tischeriidae was discussed by Regier et al. (2015).

The study of the Tischeriidae fauna in the Neotropics began with descriptions of two species from the Caribbean (Walsingham 1897), one from southwestern Mexico (Walsingham 1914), one species from Guyana, and three species from Ecuador and Peru (Meyrick 1915c). After a long break, Bourquin (1962) added one more species from Argentina. The study of Neotropical Tischeriidae has become more resolute and dynamic with targeted, additional fieldwork during the last two decades (Puplesis and Diškus 2003; Landry and Roque-Albelo 2004; Stonis and Diškus 2007, 2008; Stonis et al. 2008, 2016, 2017, 2018a, 2019b, 2019c, 2019d, 2020a, 2020b; Navickaitė et al. 2011; Diškus et al. 2014; Diškus and Stonis 2015).



In this current study, the expertise and specific interest in the documentation of leaf-mining Tischerioidea and Nepticuloidea of AD, JRS, AR, and MAS's interest in large-scale Microlepidoptera taxonomy of the Americas and global faunas, and LK's botanical expertise, particularly of Asteraceae taxonomy were combined.

The main goal of this publication is to describe seven new species of trumpet moths, possessing unusual genitalic characters, in order to have their names and biological data available for further analysis. We also identified previously unidentified Neotropical material from the collection holdings of the National Museum of Natural History (USNM). Further, we discovered that *Paratischeria neotropicana* (Diškus and Stonis 2015), which was already known to possess the broadest distribution among the Neotropical Tischeriidae, has an even broader distribution in Central and South America. We provide new host-plant data for Neotropical Tischeriidae, as well as a record of Sapindaceae, a new host-plant family for Tischeriidae worldwide, and, for the first time, a full list of host plants of the Neotropical Tischeriidae. We hypothesize that host-plant ranges predict a much broader distribution for host-specific leaf miners treated here through their host-plant distribution. Finally, we provide a short review on the history of Tischeriidae species descriptions in the Neotropics. We hope that this publication will stimulate further studies in Neotropical Tischeriidae and will contribute to a more detailed account of the diversity of the Neotropical leaf-mining insects.

## Materials and methods

The description of *Paratischeria brasiliensis* sp. nov. is based on material deposited in the collection of the National Museum of Natural History (NMNH), formerly the U.S. National Museum of Natural History, Washington D.C., U.S.A. (USNM). The type series of six new species will be deposited at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN). New distribution data of *Paratischeria neotropicana* are based on the material from the collections of USNM, ZIN, the Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Copenhagen (ZMUC), and the Natural History Museum, London, U.K. (NHMUK).

Detailed techniques of rearing adults from mining larvae are provided by Diškus and Stonis (2012) and Stonis et al. (2018a). Protocols for species identification and description were outlined in Puplesis and Diškus (2003) and Stonis et al. (2014, 2018a). Permanent mounts on microscope slides were photographed and studied using a Leica DM2500 microscope and Leica DFC420 digital camera. Adults were photographed using a Leica S6D stereoscopic microscope with attached Leica DFC290 digital camera.

The descriptive terminology of morphological structures follows Puplesis and Diškus (2003), except for the term “aedeagus”, which is referred to here as “phallus”, and the term “cilia”, which is referred to here as “fringe”.

## Taxonomic accounts

### *Astrotischeria jociui* Diškus & Stonis, sp. nov.

<http://zoobank.org/FB1D5882-9D68-4613-9E67-6CFDABED85F8>

Figs 15–18, 38, 39, 50–67

**Holotype.** male, pinned, with genitalia slide AD999. Labels: Peru, Urubamba Province, near Machu Picchu, 13°9'48"S, 72°32'10"W, elevation 2160 m, mining larva on *Wissadula* sp. (Malvaceae), 19 Oct 2008, field card no. 4945, A. Diškus (ZIN).

**Diagnosis.** Externally, this new species can be confused with some other speckled *Astrotischeria* species, including the species described below. In the male genitalia, the unique shape of the bifid dorsal processes of valva (Figs 51, 56, 57) and the unusually complex, angular apex of phallus with ventral spines (Figs 52–55, 59) distinguishes *A. jociui* sp. nov. from all known congeneric species. In the female genitalia, the combination of wide processes of the prela (Figs 61, 63) and proximally very long and slender corpus bursae differentiate the new species from other *Astrotischeria* taxa. This species is also distinctive because no other species in this genus is known to feed on *Wissadula* Medik. (Malvaceae), except for the South American *Astrotischeria ochrimaculosa* Diškus, Stonis & Vargas, which possesses very different male genitalia (see Stonis et al. 2019b).

**Description. Male** (Fig. 38). Forewing length 3.5–3.8 mm; wingspan 7.7–8.1 mm ( $n = 2$ ). Head: frons and pecten ochre; frontal tuft and collar comprised of ochre and grey, ochre-tipped scales; antenna longer than one half the length of forewing; flagellum ochre, annulated with grey scales in proximal quarter, but grey distally. Tegula and thorax covered with ochre and grey, ochre-tipped scales. Forewing ochre to pale ochre, apically speckled with grey, ochre-tipped scales; fringe grey; forewing underside dark brown-grey, without spots or androconia. Hindwing and fringe grey on upper side and underside, without androconia. Legs dark brownish grey, with some ochre scales, especially numerous on underside and tarsi. Abdomen grey with some green and purple iridescence on upper side, brownish grey, with some pale ochre scales on underside; genital plates pale grey; anal tufts long, dark grey.

**Male genitalia** (Figs 50–60) with capsule 870–950  $\mu\text{m}$  long, 500–510  $\mu\text{m}$  wide. Uncus (Figs 50, 56) comprised of two long, slender lobes. Socii small, paired, membranous. Valva (Figs 50, 51, 56–58) ca. 610–620  $\mu\text{m}$  long (excluding the basal process); dorsal lobe (Figs 51, 56) greatly developed, bifid, curved dorsally; ventral lobe of valva with a unique spine-like process (Figs 56, 57, 60). Anellus mostly membranous, thickened only laterally (Fig. 51). Vinculum rounded distally (Fig. 50). Phallus (Fig. 59) ca. 505–520  $\mu\text{m}$  long, apically very complex, angular (Fig. 55), with a pair of spine-like processes (Figs 52–54).

**Female** (Fig. 39). Forewing length 2.8–3.1 mm; wingspan 6.2–6.8 mm ( $n = 2$ ). Head similar to male, but frons and palpus pale ochre. Thorax similar to male, but thorax and forewing tend to be slightly darker and dark scales less contrast to main color of forewing. Abdomen similar to male, but without anal tufts, and with a protruding slender ovipositor.

**Female genitalia** (Figs 61–67) ca. 2550  $\mu\text{m}$  long. Ovipositor lobes large (Figs 63–65), clothed with peg-like setae. Posterior apophyses slightly shorter than anterior ones

(Figs 61, 63); prela comprised of three pairs of unique projections (Figs 61, 63). Corpus bursae with very slender and long (1020  $\mu\text{m}$ ) proximal part (Fig. 62) and oval main body (Fig. 67); pectination indistinctive. Ductus spermathaecae with many large coils (Fig. 66).

**Bionomics.** (Figs 15–18). Host plant is *Wissadula excelsior* (Cav.) C. Presl., Malvaceae (Fig. 15). Larvae mine leaves in October. The blotch-like mine (Figs 17, 18) is irregular, usually white, fully transparent, without frass. Adults occur in late October – November.

**Distribution.** This species is known from a single locality in Peru, Urubamba Province, near Machu Picchu, at the elevation 2000–2200 m (Fig. 16), but the host plants have a much wider distribution (see Discussion).

**Etymology.** The species is named in honor of Mr. Modestas Jocius (Vilnius, Lithuania), recognizing his understanding, continued support, and enthusiasm for biodiversity inventories in tropical countries.

**Other material examined.** 4 ♂, 4 ♀, paratypes: Peru, Urubamba Province, near Machu Picchu, 13°9'48"S, 72°32'10"W, elevation 2160 m, mining larvae on *Wissadula* sp. (Malvaceae), 19 Oct 2008, field card no. 4945, A. Diškus, genitalia slide nos AD922♂ (from adult in pupal skin, no moths preserved), AD976♂ (from adult in pupal skin, no moths preserved), AD997♀ (from adult in pupal skin, no moths preserved), AD977♂ (from adult in pupal skin, no moths preserved), AD978♀ (ZIN).

***Astrotischeria atlantica* Diškus & Stonis, sp. nov.**

<http://zoobank.org/24A33F1D-005A-4BB1-AF77-56D5543BD528>

Figs 1–9, 40, 41, 68–80

**Holotype.** male, pinned, with genitalia slide no. AD969. Labels: Uruguay, Rocha Department, La Paloma, 34°39'41"S, 54°13'4"W, elevation 5 m, mining larva on *Baccharis spicata* (Lam.) Baill., Asteraceae, 26 Feb 2019, field card no. 5303, A. Diškus (ZIN).

**Diagnosis.** Externally, this new species can be confused with some other speckled *Astrotischeria* species, including the species described in this paper. *Astrotischeria atlantica* sp. nov. can be distinguished from similar *A. jociui* sp. nov. (see described above) by the significantly paler color of forewing: in *A. atlantica* forewing is cream to pale yellowish ochre, in *A. jociui* is ochre. In the male genitalia, the shape of dorsal processes of the valva with unique folds (Fig. 75) and the presence of additional lobes on the uncus (Figs 68, 69) distinguish *A. atlantica* sp. nov. from all known congeneric species. In the female genitalia, the presence of a highly modified ovipositor (Fig. 78) differentiates this new species from other *Astrotischeria* taxa. This species is also distinctive because no other species in this genus is known to feed on *Baccharis spicata* (Lam.) Baill. (Asteraceae).

**Description. Male** (Fig. 40). Forewing length 3.6–4.2 mm; wingspan 7.7–9.3 mm ( $n = 2$ ). Head: frons and pecten golden cream; frontal tuft glossy cream distally, ochre-grey proximally; collar ochre-grey; antenna slightly longer than one half the length of forewing; flagellum yellowish cream proximally, pale yellowish grey distally. Tegula yellowish grey, distally cream; thorax yellowish cream. Forewing cream to pale yellowish ochre, irregularly speckled with grey and pale grey scales, apically also with some black





**Figures 1–9.** Bionomics of *Astrotischeria atlantica* sp. nov. **1** habitat, elevation 5 m, La Paloma, Rocha Department, Uruguay **2–4** host plant *Baccharis spicata* (Lam.) Baill., Asteraceae **5–9** leaf mines.

scales; fringe pale grey, with fringe line comprised of black scales; forewing underside pale ochre-grey to brownish cream, without spots or androconia. Hindwing glossy greyish cream to cream on upper side, pale grey on underside, without androconia, but some-



times with a dark line of grey scales along one third of the fold; fringe cream. Foreleg pale grey or blackish grey on upper side, midleg and hindleg ochre cream to cream, with some pale grey scales on upper side and spurs. Abdomen yellow cream, distally pale grey on upper side, pale ochre with some grey scales on underside; genital plates large, covered with long, yellow cream scales; anal tufts long, merged into one, cream.

**Male genitalia** (Figs 68–76) with capsule 1120  $\mu\text{m}$  long, 730  $\mu\text{m}$  wide. Uncus (Figs 68–71) comprised of two short, triangular lobes (Fig. 71) and two long, slender lobes (Fig. 70); the latter possess a unique lobe-like process (Figs 68, 69). Socii small, paired, membranous. Valva (Figs 72, 75) ca. 730  $\mu\text{m}$  long; dorsal lobe (Figs 72, 75) greatly developed, with folds distally (Fig. 75); ventral lobe of valva slender. Anellus mostly membranous, thickened only laterally (Fig. 75). Vinculum rounded distally (Fig. 72). Phallus ca. 970  $\mu\text{m}$  long, apically bifid, with hook-like apices (Fig. 73).

**Female** (Fig. 41). Forewing length 3.6–4.3 mm; wingspan 7.7–9.4 mm ( $n = 2$ ). Similar to male, but thorax and forewing tend to be paler, i.e., less speckled with grey scales. Anal tuft long, ochre cream; ovipositor slightly protruding. Otherwise, identical with male.

**Female genitalia** (Figs 77–80) ca. 3410  $\mu\text{m}$  long. Ovipositor lobes modified into a unique (among Tischeriidae) plate-like ovipositor without peg-like setae (Fig. 78); second pair of ovipositor lobes large, with numerous long setae. Posterior apophyses shorter than anterior ones (Fig. 79); prela comprised of three pairs of unique projections (Fig. 79). Corpus bursae with very slender and long proximal part and small main body without pectination (Fig. 77). Ductus spermathaeae with three large coils (Fig. 77).

**Bionomics.** (Figs 1–9). Host plant is *Baccharis spicata* (Lam.) Baill., Asteraceae (Figs 1–4). Larvae mine leaves in February. The blotch-like mine (Figs 5–9) is irregular, but elongated, pale brown or pale green, without frass. Adults occur in March.

**Distribution.** This species is known from a single locality on the Atlantic coast in Uruguay, Rocha Department, La Paloma (Fig. 1), at sea level, but the host plant has a much wider distribution (see Discussion).

**Etymology.** The species is named after the Atlantic Ocean, in reference to its occurrence on the Atlantic coast of Uruguay.

**Other material examined.** 2 ♂, 3 ♀, paratypes: Uruguay, Rocha Department, La Paloma, 34°39'41"S, 54°13'4"W, elevation 5 m, mining larvae on *Baccharis spicata* (Lam.) Baill., Asteraceae, 26 Feb 2019, field card no. 5303, A. Diškus, genitalia slide nos AD970♂ (from adult in pupal skin, no moths preserved), AD968♀ (ZIN).

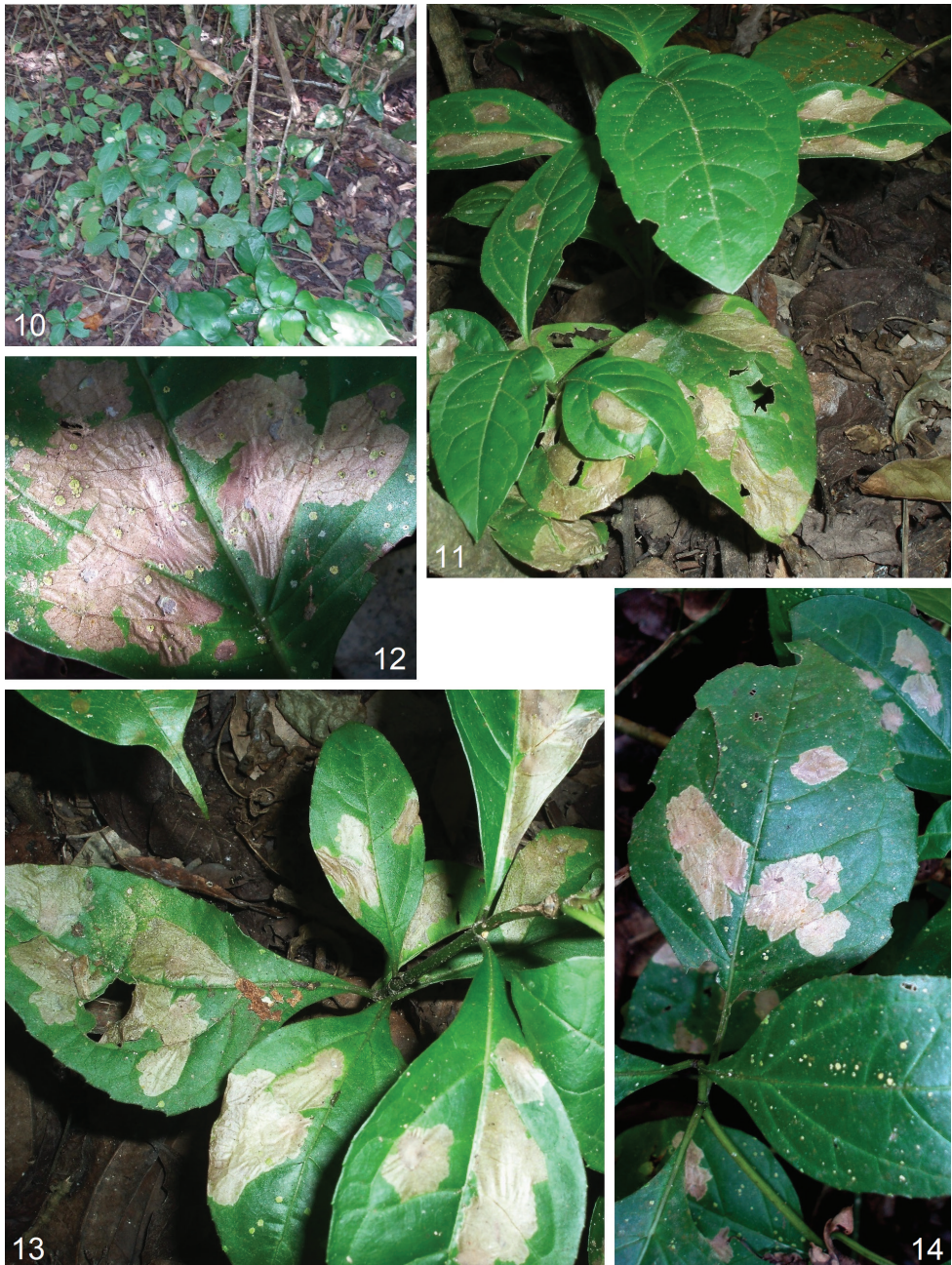
### *Astrotischeria cornuata* Diškus & Stonis, sp. nov.

<http://zoobank.org/3ECCBA77-7B14-44F4-9A81-0331ADABAB6C>

Figs 10–14, 42, 43, 81–91

**Holotype.** male, pinned, with genitalia slide no. AD522. Labels: Honduras, Copán Department, Copán, 14°50'13"N, 89°8'37"W, elevation 620 m, from feeding larva (Asteraceae host plant unidentified), 15 Feb 2012, field card no. 5090, A. Diškus (ZIN).

**Diagnosis.** Externally, this new species can be confused with some other dark speckled Tischeriidae species, including *Paratischeria mesoamericana* sp. nov. (described



**Figures 10–14.** Bionomics of *Astrotischeria cornuata* sp. nov. **10** habitat, elevation 620 m, Copán, Copán Department, Honduras **11–14** leaf mines on unidentified Asteraceae host plant.

below). In the male genitalia, the presence of pseudotranstilla (Figs 83, 87) and a unique, four-furcated phallus (Figs 85, 86) distinguish *A. cornuata* sp. nov. from all known congeneric species. In the female genitalia, the combination of large ovipositor

lobes, densely covered with peg-like setae (Fig. 90) and a very small corpus bursae (Fig. 89) distinguish the new species from other *Astrotischeria* taxa.

**Description. Male** (Fig. 42). Forewing length 2.8–3.2 mm; wingspan 6.0–7.2 mm ( $n = 3$ ). Head: frons grey cream to yellow-ochre; pecten golden pale grey to ochre cream; frontal tuft glossy, metallic grey, distally yellow-ochre; collar yellow-ochre; antenna slightly to distinctly longer than one half the length of forewing; flagellum glossy grey. Tegula grey; thorax grey-ochre medially, grey laterally and distally. Forewing densely irrorated with dark grey scales (in apical half of the forewing majority of these scales are ochre-tipped) and with irregular, oblique patches of bright yellow-ochre scales; fringe dark grey, apically ochre; fringe line distinctive, comprised of dark grey scales; forewing underside blackish grey, without spots or androconia. Hindwing dark grey or black-grey depending on angle of view, without androconia; fringe dark grey with some ochreous-purple tint. Legs dark grey or black-grey, irregularly annulated with ochre cream scales on upper side. Abdomen glossy dark grey-brown on upper side and underside, sometimes with some purple iridescence; genital plates ochreous cream; anal tufts cream to grey cream: two dorsal tufts large, almost merged in one, lateral tufts shorter.

**Male genitalia** (Figs 81–88) with capsule 880–920  $\mu\text{m}$  long, 410–445  $\mu\text{m}$  wide. Uncus (Figs 81–83) comprised of two short, widely rounded lobes (Fig. 81) and two long, slender lobes (Figs 82, 83). Socii small, paired, membranous. Valva (Figs 83, 84) ca. 780–790  $\mu\text{m}$  long; dorsal lobe (Fig. 83) greatly developed, slender, curved inwardly (Fig. 88); ventral lobe of valva very slender and straight (Figs 83, 84). Valvae connected with a unique transverse band which we call here a pseudotranstilla (Figs 83, 87). Anellus mostly membranous, indistinctive (Fig. 83). Vinculum rounded distally (Fig. 83). Phallus (Fig. 86) ca. 475–485  $\mu\text{m}$  long, apically split in two short, weakly chitinized, median lobes and two pointed, lateral lobes, the latter each with an apical spine (Fig. 85).

**Female** (Fig. 43). Forewing length 3.0–3.5 mm; wingspan 6.6–7.6 mm ( $n = 4$ ). Similar to male, but with a yellow-ochre postmedian area of forewing, usually larger and often resembling a fascia. Abdomen dark grey on upper side, yellow-ochre with some grey scales on underside. Ovipositor not protruding.

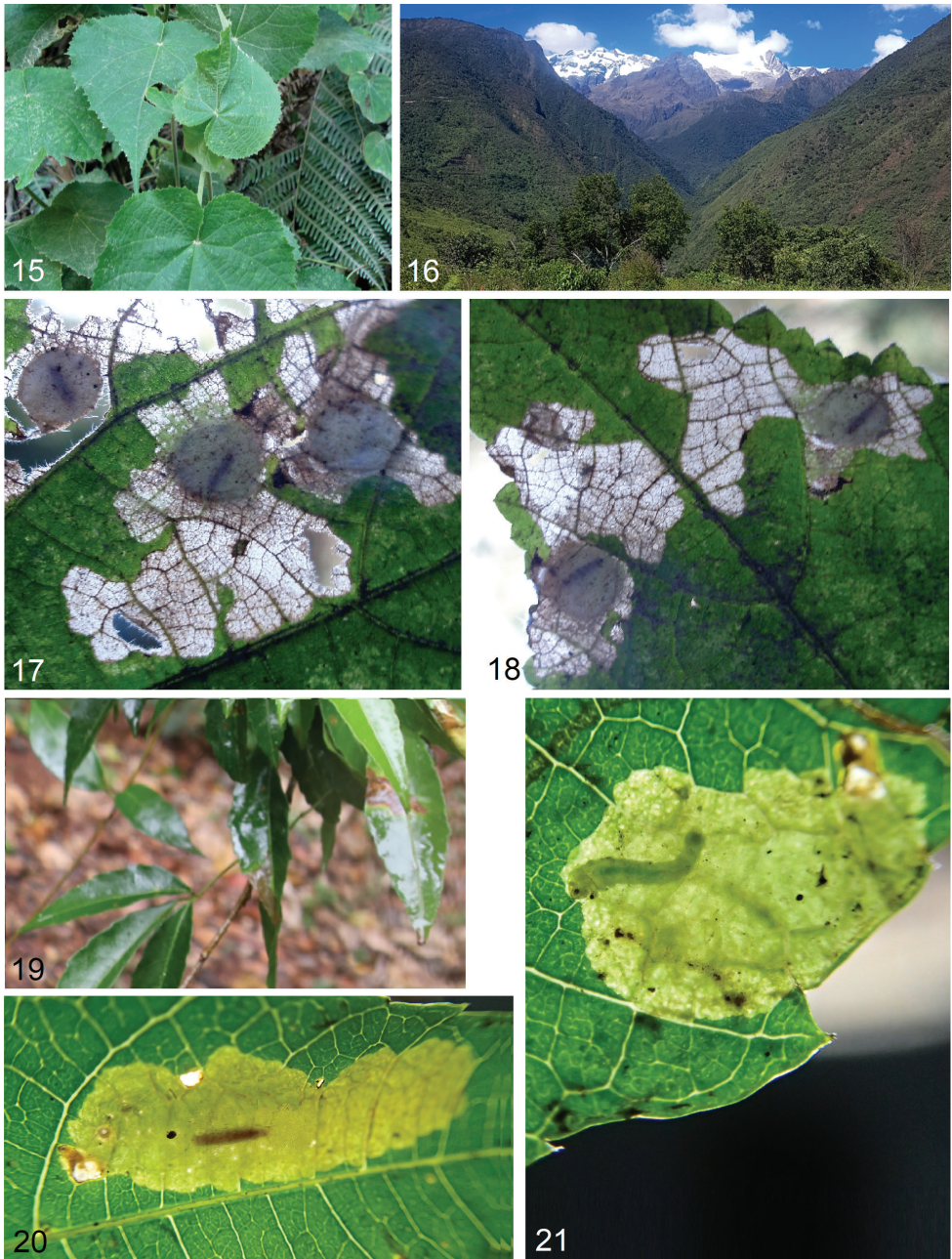
**Female genitalia** (Figs 89–91) ca. 3150  $\mu\text{m}$  long. Ovipositor lobes unusually large, rounded, densely covered with peg-like setae (Fig. 90); second pair of ovipositor lobes very small and slender, with numerous long setae. Anterior and posterior apophyses equal in length (Fig. 90); prela comprised of three pairs of unique, rod-like projections (Fig. 91). Corpus bursae very long, with a slender proximal part and very small main body without distinctive pectination (Fig. 89). Ductus spermathecae sinuous, without distinctive coils (Fig. 89).

**Bionomics.** (Figs 10–14). Host plant is an Asteraceae, genus and species unidentified (Figs 10, 11). Larvae mine leaves in February. The mine is blotch-like (Figs 11–14), irregularly shaped, whitish grey, not transparent, without frass. Adults occur in March.

**Distribution.** This species is known from a single locality in Honduras, Copán Department, Copán, at the elevation of 620 m.

**Etymology.** The species name is derived from Latin *cornuatus* (horned), in reference to the large, horn-like lobes of the uncus and valva in the male genitalia.





**Figures 15–21.** Bionomics of new species. **15** *Astrotischeria jociui* sp. nov., host plant *Wissadula excelsior* (Cav.) C. Presl., Malvaceae **16** same, habitat, elevation 2160 m, near Machu Picchu, Urubamba Province, Peru **17, 18** same, leaf mines on *Wissadula excelsior* **19** *Paratischeria suprafasciata* sp. nov., host plant *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl., Sapindaceae **20** leaf mine with a pupa **21** leaf mine with a feeding larva.



**Other material examined.** 2 ♂, 4 ♀, paratypes: Honduras, Copán Department, Copán, 14°50'13"N, 89°8'37"W, elevation 620 m, from feeding larvae (Asteraceae host plant unidentified), 15 Feb 2012, field card no. 5090, A. Diškus, genitalia slide nos AD975♂, AD981♀ (ZIN).

***Paratischeria guarani* Diškus & Stonis, sp. nov.**

<http://zoobank.org/D3990BF8-93B3-4843-BEC8-A38F06888465>

Figs 22–31, 44, 45, 92–96

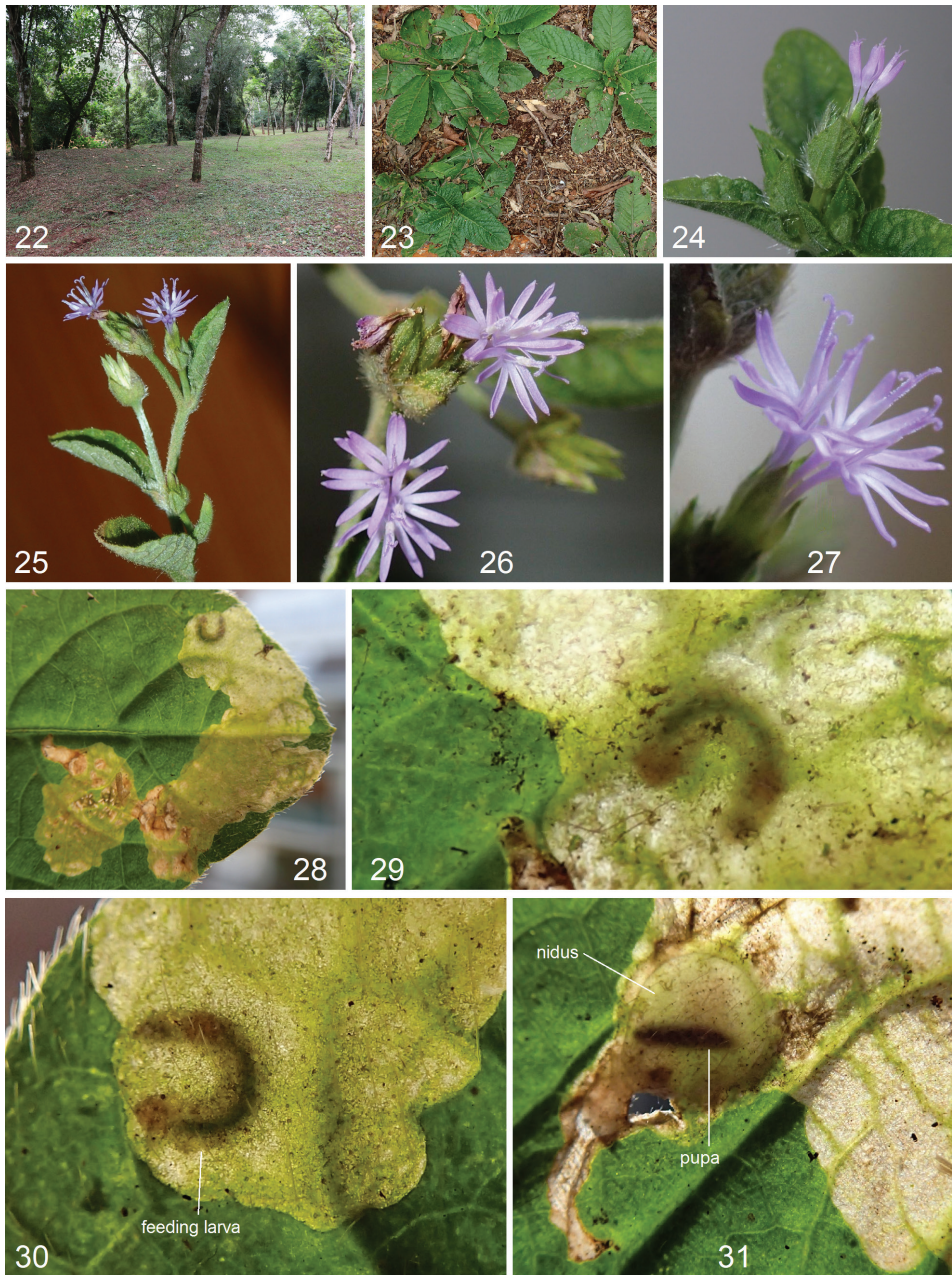
**Holotype.** male, pinned, with genitalia slide no. AD988. Labels: Paraguay, Departamento de Itapúa, Hohenau, 27°5'6"S, 55°40'22"W, elevation 115 m, mining larva on *Elephantopus mollis* Kunth, Asteraceae, 14 Feb 2019, field card no. 5293, A. Diškus (ZIN).

**Diagnosis.** Externally, this new species can be confused with some other brightly colored species, including *A. cornuata* sp. nov. (described above) or Central American *A. guatemalica* Diškus & Stonis, and Ecuadorian *A. bachariphaga* Diškus & Stonis (see Stonis et al. 2019). However, these externally similar *Astrotischeria* species possess a well-developed dorsal lobe of valva, but all *Paratischeria* species have no dorsal lobe. In the male genitalia, the combination of very long and slender uncus and a laterally strongly thickened anellus distinguish *Paratischeria guarani* sp. nov. from all known congeneric species. The characters of the female genitalia are not informative, and, therefore, are of very limited use for species differentiation. This species is also distinctive because no other tischeriid species is known to feed on *Elephantopus mollis* Kunth, Asteraceae.

**Description. Male** (Fig. 44). Forewing length 2.8–3.1 mm; wingspan 6.1–6.8 mm (n = 4). Head: frons ochre-grey, pecten pale ochre; frontal tuft glossy grey proximally, pale ochre distally; collar ochre-grey; antenna slightly longer than one half length of forewing; flagellum greyish cream, irregularly annulated with dark grey scales. Tegula and thorax grey-ochre. Forewing variable, pale ochre irregularly speckled with dark grey, apically with black scales; fringe dark grey, with fringe indistinctive or absent; forewing underside brown-black, without spots or androconia. Hindwing grey on upper side and underside, without androconia; fringe grey. Legs grey on upper side, ochre cream on underside. Abdomen black on upper side, glossy ochre with some dark brown scales on underside; genital plates pale ochre to pale grey; anal tufts grey-ochre.

**Male genitalia** (Figs 92–94) with capsule 760 µm long, 315 µm wide. Uncus (Fig. 93) with two very long and slender lateral lobes. Socii small, paired, membranous. Valva (Fig. 92) ca. 615 µm long. Anellus strongly thickened laterally, constricted at the middle (Fig. 92). Vinculum small, rounded distally (Fig. 92). Phallus ca. 670 µm long, apically bifid (Fig. 94).

**Female** (Fig. 45). Forewing length 3.0–3.3 mm; wingspan 6.5–7.1 mm (n = 2). Similar to male, but sometimes darker, with bright ochre thorax and forewing more intensively speckled with black scales. Abdomen black, ochre only distally; ovipositor very short, but protruding. Otherwise, identical with male.



**Figures 22–31.** Bionomics of *Paratischeria guarani* sp. nov. **22** habitat, elevation 115 m, Hohenau, Departamento de Itapúa, Paraguay **23–27** host plant *Elephantopus mollis* Kunth, Asteraceae **28–30** leaf mines with a feeding larva **31** leaf mine with a pupa.

**Female genitalia** (Figs 95–97) 680  $\mu$ m long. Ovipositor lobes oval-shaped, covered with peg-like setae; second pair of ovipositor lobes small, with long setae (Fig. 96). Anterior and posterior apophyses equal in length (Fig. 96); prela comprised of three pairs of rod-like

projections (Fig. 96). Corpus bursae very slender, with long proximal part and small main body without pectination (Fig. 95). Ductus spermathecae with 7–8 large coils (Fig. 97).

**Bionomics** (Figs 22–31). Host plant is *Elephantopus mollis* Kunth, Asteraceae (Figs 23–27). Larvae mine leaves in February. Larva greenish white, with dark green intestine and brown head. The blotch-like mine (Figs 28–31) is irregular, but often elongated, pale brown or pale green, without frass. Pupation in a round nidus. Adults occur in March.

**Distribution.** This species is known from a single locality in Paraguay, Departamento de Itapúa, Hohenau (Fig. 22), at the elevation of 115 m, but the host plant has a much wider distribution (see Discussion).

**Etymology.** This species is named after the Guaraní, indigenous people of South America, living in present-day Paraguay between the Uruguay River and lower Paraguay River.

**Other material examined.** 5 ♂, 2 ♀, paratypes: Paraguay, Departamento de Itapúa, Hohenau, 27°5'6"S, 55°40'22"W, elevation 115 m, mining larvae on *Elephantopus mollis* Kunth, Asteraceae, 14 Feb 2019, field card no. 5293, A. Diškus, genitalia slide nos AD986♂ (from adult in pupal skin, no pinned moth preserved), AD998♂, AD987♀ (ZIN).

***Paratischeria mesoamericana* Diškus & Stonis, sp. nov.**

<http://zoobank.org/A1306212-7A99-4237-84BB-D2A138A2A013>

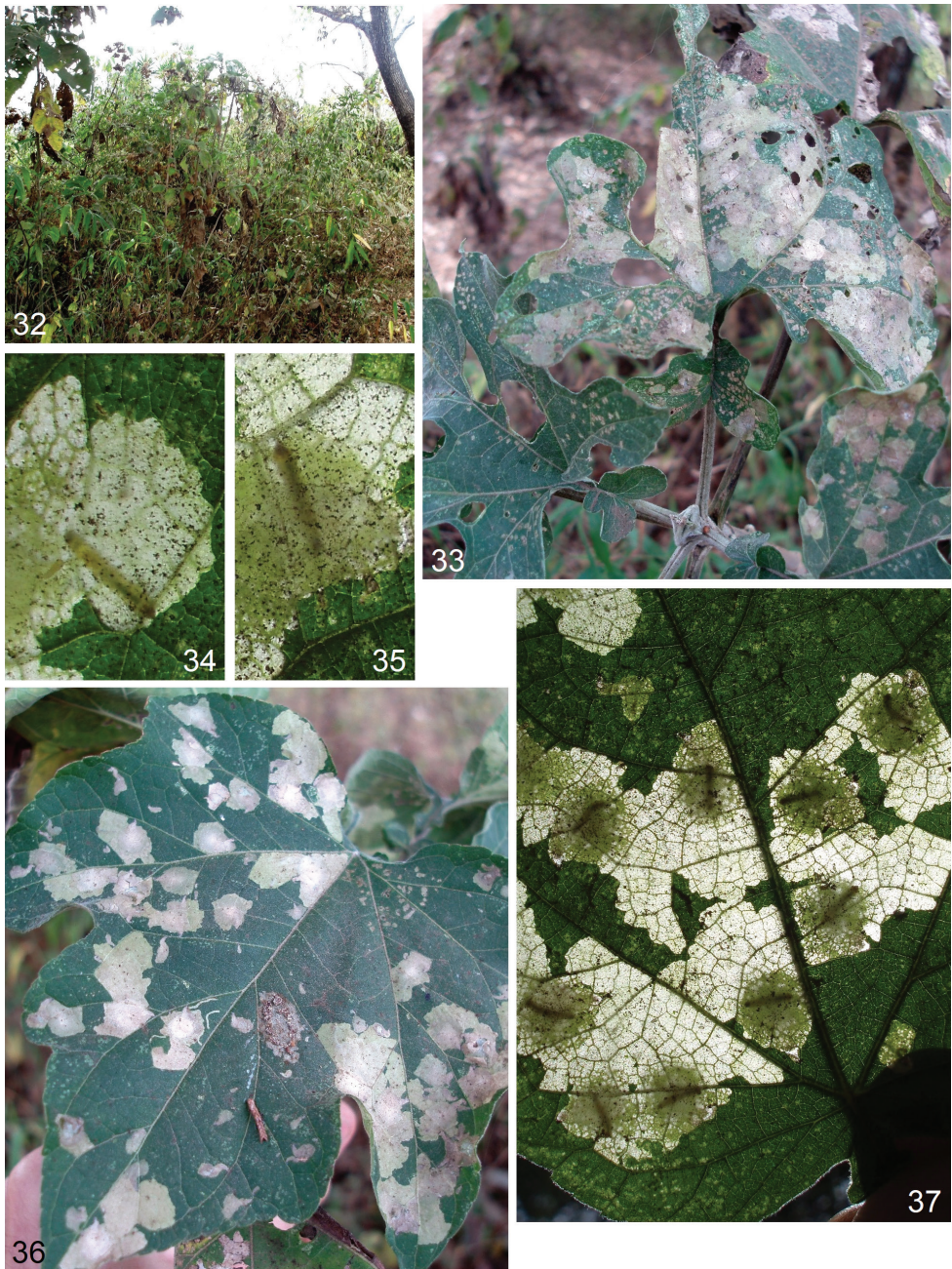
Figs 32–37, 46, 48, 98–110

**Holotype.** male, pinned, with genitalia slide no. AD1005. Labels: Guatemala, Antigua Guatemala, San Juan del Obispo, 14°31'7"N, 90°43'50"W, elevation 1680 m, feeding larva on *Montanoa hibiscifolia* Benth., Asteraceae, 25 Feb 2012, field card no. 5109, A. Diškus (ZIN).

**Diagnosis.** Externally, *P. mesoamericana* sp. nov. can be confused with some brightly speckled *Astrotischeria* Puplesis & Diškus species, including *A. cornuata* sp. nov. (described above) or the Central American *A. guatemalica* Diškus & Stonis, South American *A. bachariphaga* Diškus & Stonis, and *A. truncata* Diškus & Stonis (in Stonis et al. 2019). However, all these externally similar species belong to another genus, *Astrotischeria*, and possess principally different male genitalia with dorsal lobe(s) on the valva. In the male genitalia, the combination of a unique, distally pointed, four-lobed phallus (Fig. 99), medially constricted anellus (Fig. 98), and the presence of bifid cheatae on the valva (Fig. 101) distinguish *P. mesoamericana* sp. nov. from all known congeneric species. This species is also distinctive because no other species in this genus is known to feed on *Montanoa hibiscifolia* Benth., Asteraceae.

**Description. Male** (Fig. 46). Forewing length 2.6–3.8 mm; wingspan 5.7–8.6 mm (n = 10). Head: frons and pecten ochreous cream; frontal tuft ochre cream, distally whitish cream; collar ochre cream; antenna longer than one half the length of forewing; flagellum glossy cream, usually annulated with dark brown or pale brown scales. Tegula ochre cream, densely irrorated with grey-brown scales; thorax ochre cream. Forewing yellow-ochre with irregular patches of dark scales: most of these scales are cream but

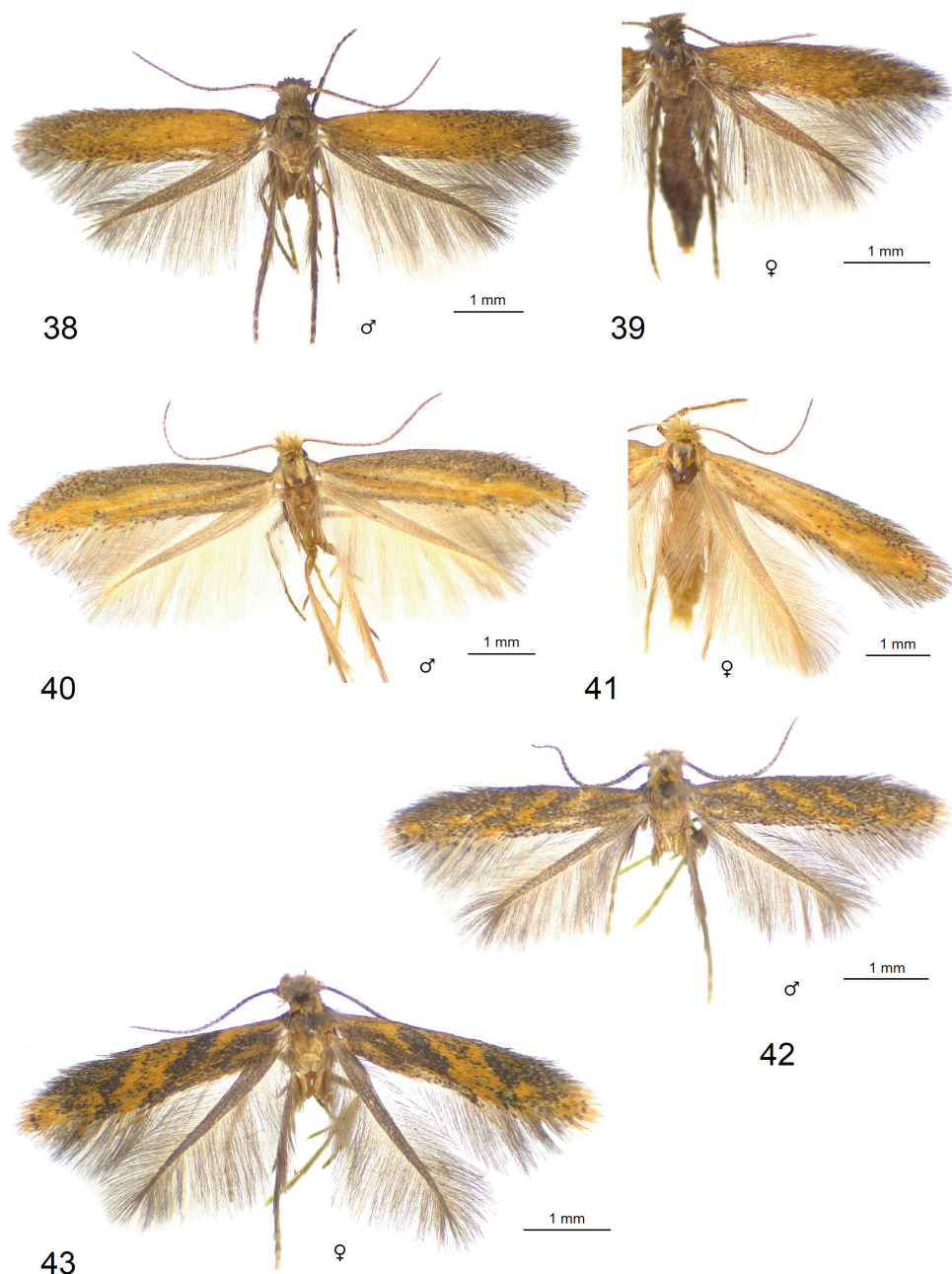




**Figures 32–37.** Bionomics of *Paratischeria mesoamericana* sp. nov. **32** habitat and host plant *Montanoa hibiscifolia* Benth., Asteraceae, elevation 1680 m, San Juan del Obispo, Antigua Guatemala, Guatemala **33–37** leaf mines with feeding larvae.

black-tipped, others are plain brown; fringe grey, apically ochre; fringe line present, sometimes ill-defined, comprised of brown and black-tipped cream scales; forewing underside ochre-brown, apically sometimes brownish cream, without spots or androconia. Hind-





**Figures 38–43.** Adults of *Astrotischeria* spp. **38** *A. jociui* sp. nov., male, holotype **39** same, female, paratype **40** *A. atlantica* sp. nov., male, holotype **41** same, female, paratype **42** *A. cornuata* sp. nov., male, holotype **43** same, female, paratype (ZIN).

wing glossy, pale grey on upper side and underside, at base cream; fringe pale grey. Legs covered with grey-brown scales on upper side, ochreous cream on underside. Abdomen glossy, pale grey to grey-brown depending on angle of view, with some purple iridescence

on upper side, ochre cream, densely speckled with grey-brown or ochre-brown scales on underside; genital plates ochre cream; anal tufts long, dorsally paired, cream.

**Male genitalia** (Figs 98–104) with capsule 890  $\mu\text{m}$  long, 450  $\mu\text{m}$  wide. Uncus comprised of two short, rounded lobes (Fig. 100) and two long, slender lobes (Fig. 104). Socii small, paired, membranous. Valva (Figs 98, 102) ca. 660  $\mu\text{m}$  long, with bifid chaetae. Anellus thickened laterally and constricted medially (Figs 98, 103). Vinculum small, rounded distally (Fig. 102). Phallus (Fig. 99) ca. 675  $\mu\text{m}$  long, apically split into four pointed lobes.

**Female** (Fig. 43). Forewing length 3.2–4.0 mm; wingspan 7.0–8.7 mm ( $n = 8$ ). Scaling similar to male, but sometimes can be darker; frontal tuft ochre cream to ochre-brown. Thorax ochre cream to ochre-brown. Forewing sometimes darker than in males. Abdomen ochre-brown to brown, with some purple iridescence on upper side, ochre cream densely covered with brown or dark brown scales on underside. Ovipositor protruding.

**Female genitalia** (Figs 105–110) 2520–2680  $\mu\text{m}$  long. Ovipositor lobes unusually small, rounded, with peg-like setae (Fig. 109); second pair of ovipositor lobes only slightly smaller. Anterior apophyses slightly shorter than posterior apophyses (Fig. 107); prela with three pairs of long, rod-like projections (Figs 109, 110). Corpus bursae with a very slender but very long proximal part, and a small, oval, main body (Fig. 107); pectination indistinctive. Ductus spermathecae with many large coils (Fig. 108).

**Bionomics.** (Figs 32–37). Host plant is *Montanoa hibiscifolia* Benth., Asteraceae (Figs 32, 33). Larvae mine leaves in February. Larva is greenish yellow with a brownish green intestine and brown head. The mine is blotch-like (Figs 33–37), usually slightly angular, fully transparent, without frass. Adults occur in March.

**Distribution.** This species is known from a single locality in Guatemala: Antigua Guatemala, San Juan del Obispo, at the elevation 1680 m, but the host plant has a much wider distribution (see Discussion).

**Etymology.** The species named after Mesoamerica, a historical region of North America.

**Other material examined.** 14 ♂, 27 ♀, paratypes: Guatemala, Antigua Guatemala, San Juan del Obispo, 14°31'7"N, 90°43'50"W, elevation 1680 m, feeding larvae on *Montanoa hibiscifolia* Benth., Asteraceae, 25 Feb 2012, field card no. 5109, A. Diškus, genitalia slide nos AD871♂, AD887♀, AD1006♀ (ZIN).

### *Paratischeria suprafasciata* Diškus & Stonis, sp. nov.

<http://zoobank.org/DA9C53D0-66CB-4FDB-B116-711B7AECF3B3>

Figs 19–21, 47, 111–115

**Holotype.** female, pinned, with genitalia slide no. AD967. Labels: Argentina, Misiones Province, Puerto Iguazú, 25°41'8"S, 54°26'47"W, elevation 160 m, mining larva on *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl., Sapindaceae, 10 Feb 2019, field card no. 5291, A. Diškus (ZIN).

**Diagnosis.** Externally, this new species can be differentiated from all congeneric species by the distinct forewing pattern with an ochre, oblique, postmedian fascia and ochre subap-

ical spot (Fig. 47). Male unknown. In the female genitalia, the new species is characterized by the unique, oval-shaped widening of slender part of corpus bursae proximally (Fig. 111). This species is also distinctive because no other species in Tischeriidae is known to feed on *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. (Sapindaceae).

**Description. Male.** Unknown.

**Female** (Fig. 47). Forewing length 3.2 mm; wingspan 6.9 mm ( $n = 1$ ). Head: frons and pecten ochre cream to pale ochre; golden cream; collar glossy ochre-grey; antenna slightly longer than one half the length of forewing; flagellum dark grey on upper side, pale grey on underside. Tegula and thorax glossy ochre-grey. Forewing slender, glossy grey-ochre in basal half, with bright ochre, oblique postmedian fascia and bright ochre subapical spot widely surrounded by black and cream-tipped scales with purple iridescence; fringe black-grey, without fringe line. Hindwing and fringe grey on upper side and underside, without androconia. Legs grey to blackish grey on upper side, ochre cream on underside. Abdomen blackish grey on upper side, glossy pale ochre with some grey scales (especially prominent proximally) on underside; anal tufts absent; ovipositor slightly protruding.

**Female genitalia** (Figs 111–115) 1310  $\mu\text{m}$  long. Ovipositor lobes large, rounded, clothed with short, modified peg-like setae; area between ovipositor lobes slender, with tiny papillae and some short setae. Second pair of lobes, lateral and anterior to the ovipositor lobes, slightly smaller, triangular, with long slender setae. Posterior apophyses slightly shorter than anterior ones (Fig. 115); prela comprised of three pairs of rod-like projections (Fig. 115); inner pair of these rod-like projections very long (as long as anterior apophyses). Corpus bursae folded, oval-shaped proximally, bulbous distally (Fig. 111), without pectination or signum on wide, basal part, but with some tiny spines proximally (Fig. 113). Ductus spermathecae very slender, with many coils (Fig. 112).

**Bionomics.** (Figs 19–21). Host plant is *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl., Sapindaceae (Fig. 19). Larvae mine leaves in February. Larva very pale green with a bright green intestine and very pale brown head. The mine is blotch-like (Figs 20, 21), fully transparent, without frass. Adults occur in March.

**Distribution.** This species is known from a single locality in northern Argentina, Misiones Province, Puerto Iguazú, at the elevation ca. 160 m, but the host plant has a much wider distribution (see Discussion).

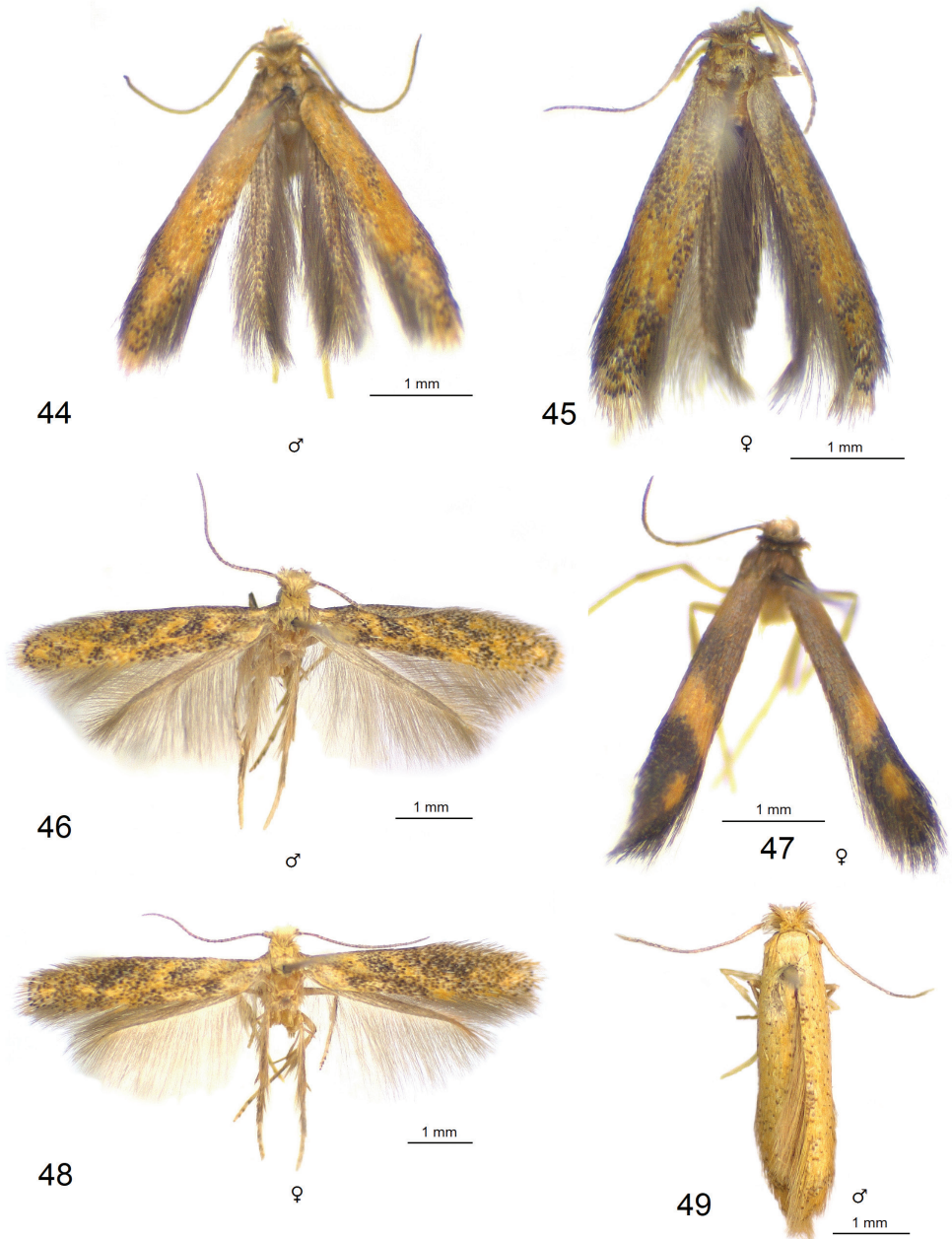
**Etymology.** The species name is derived from Latin *fasciatus* (banded, with a fascia) with the prefix *supra*, in reference to the unusual (in Tischeriidae), forewing pattern with a distinctive postmedian fascia.

***Paratischeria braziliensis* Diškus & Stonis, sp. nov.**

<http://zoobank.org/E51DF3A6-2756-44EB-B824-14FF97EAC647>

Figs 49, 116–126

**Holotype.** male, pinned, with genitalia slide no AD1004. Label: Brazil, Nova Teutônia, 27°11'S, 52°23'W, Oct 1944, Fritz Plaumann (USNM).



**Figures 44–49.** Adults of *Paratischeria* spp. **44** *P. guarani* sp. nov., male, holotype (ZIN) **45** same, female, paratype (ZIN) **46** *P. mesoamericana* sp. nov., male, holotype (ZIN) **47** *P. suprafasciata* sp. nov., female, holotype (ZIN) **48** *P. mesoamericana* sp. nov., female, paratype (ZIN) **49** *P. braziliensis* sp. nov., male, holotype (USNM).

**Diagnosis.** External characters are not informative for species identification: this new species can be confused with many other pale speckled *Paratischeria* Diškus & Stonis, *Coptotriche* Walsingham, and *Astrotischeria* Puplesis & Diškus species. In the



male genitalia, the unique, unusually long, rod-like process of vinculum (Figs 120, 121), absence of transtilla, and the unique, spiny phallus (Figs 124–126) easily differentiate *P. braziliensis* sp. nov. from all known Tischeriidae species (also see Discussion).

**Description. Male** (Fig. 38). Forewing length 3.9 mm; wingspan 8.4 mm ( $n = 1$ ). Head: frons and pecten glossy whitish cream; frontal tuft ochre cream, but distally glossy whitish over the frons, laterally with some brown-tipped scales; collar ochre cream; antenna only longer than one half the length of forewing; flagellum glossy yellow cream. Tegula pale ochre-yellow; thorax ochre cream. Forewing pale ochre yellow, with irregularly scattered ochre-brown scales; fringe indistinct or absent; forewing underside pale ochre-brown. Hindwing and fringe yellow-ochre. Legs pale yellow ochre, with some ochre-brown scales on upper side. Abdomen ochre cream on upper side and underside; genital plates cream; anal tufts long, cream.

**Male genitalia** (Figs 116–126) with capsule 550  $\mu\text{m}$  long, 450  $\mu\text{m}$  wide. Uncus (Fig. 118) comprised of two large, strongly thickened, lateral lobes. Socii membranous, unpaired, unusually large (Fig. 116). Valva (Figs 117, 119, 120) 500  $\mu\text{m}$  long (excluding the basal process), wide (Fig. 119). Transtilla absent. Anellus indistinctive. Vinculum with unusually slender but very long (785  $\mu\text{m}$ ), rod-like process (Figs 120, 121). Phallus (Figs 122–126) 1185  $\mu\text{m}$  long, apically with three lobes and some large spines laterally (Figs 124, 126).

**Female.** Unknown.

**Bionomics.** Adults fly in October. Otherwise, biology is unknown.

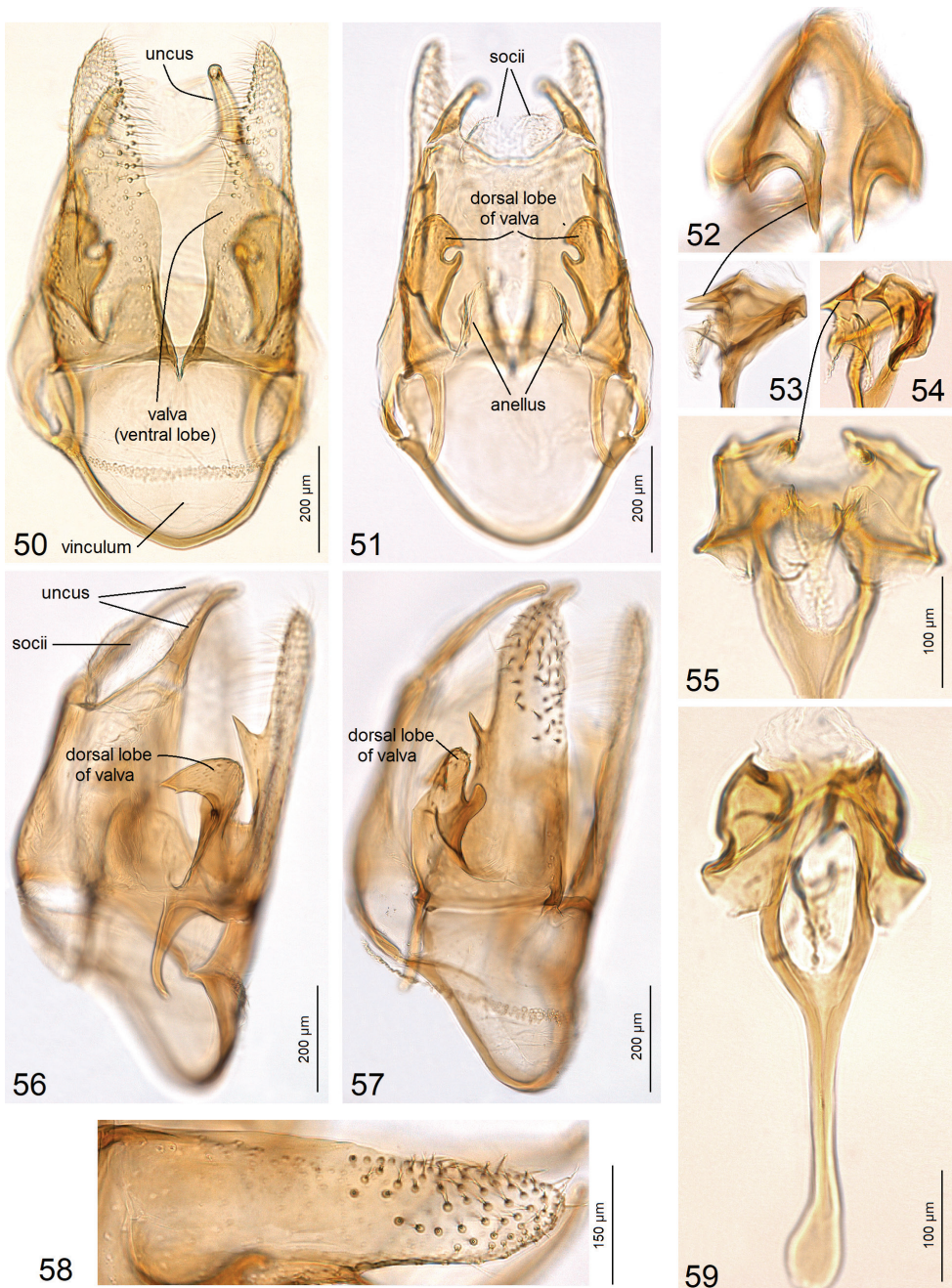
**Distribution.** This species is known from a single locality in southeastern Brazil, Santa Catarina: Nova Teutônia.

**Etymology.** The species is named after Brazil, the country where it was found.

### Extended distribution range of *Paratischeria neotropicana* (Diškus & Stonis, 2015)

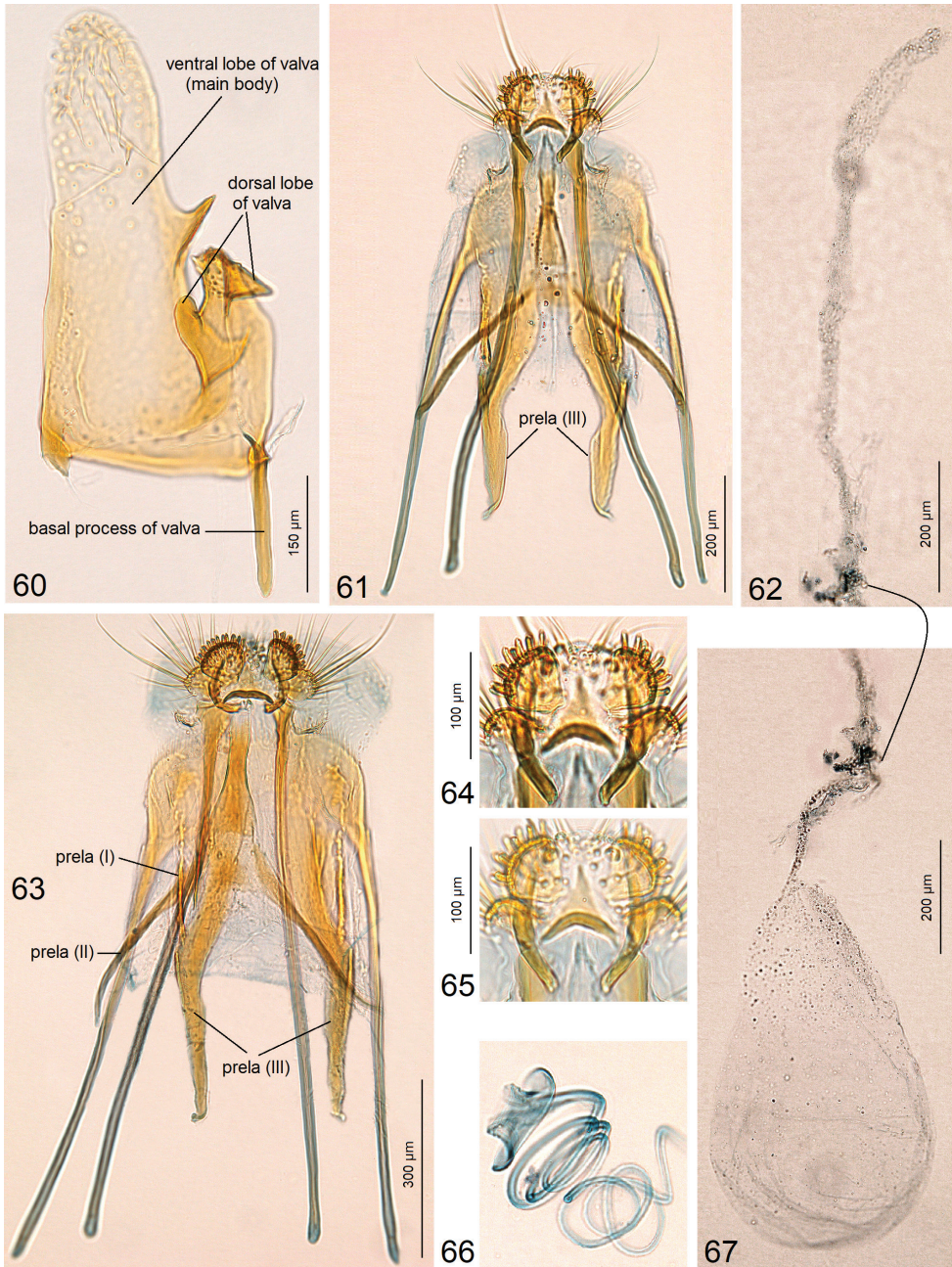
The majority of the Neotropical Tischeriidae are known only from their type localities, due to insufficient sampling efforts. *Paratischeria neotropicana* is a leaf miner on *Sida* L., Malvaceae (Fig. 128): larvae produce blotch-like leaf mines (Figs 130–137). In the male genitalia, it is characterized by the unique lobes of the anellus (Fig. 127). Recently this species was recorded as possessing the broadest distribution among the Neotropical Tischeriidae (Diškus and Stonis 2015), with a range from Belize to Peru. However, our study of new, unidentified material expanded the distribution range of this species from Mexico to Bolivia (Fig. 129).

**New material examined.** 2 ♂, 5 ♀: **Mexico**, Veracruz, Boca Del Rio, 19°06'N, 96°06'W (Mexican Field Station), 13–28 Jul 1994, reared from *Sida acuta*, *S. rhombifolia*, and *S. spinosa*, P. Juarez, R. Segura and M. Martinez, genitalia slide no. RA1037♂ (USNM); 1 ♂: **Guatemala**, Petén Region, Rio Dulce, 15°38'N, 89°00'W, elevation 300 m, mining larva on *Sida* sp., Malvaceae, 14 Feb 2012, LT-GT Scie. Exp. 2012, genitalia slide no. RA492 (USNM); 18 ♂, 15 ♀: **Belize**, Cayo District, Chiquibul Forest Reserve, Las Cuevas Research Station, 16°43'53"N, 88°59'11"W, 550 m, mining larvae on *Sida* sp., 17 Sep – 17 Nov 1997 and 6 Feb – 13 Jun 1998, O. T. Lewis, genitalia slide nos 010316205♂, 010316206♂, 010316207♂, 010316208♂,



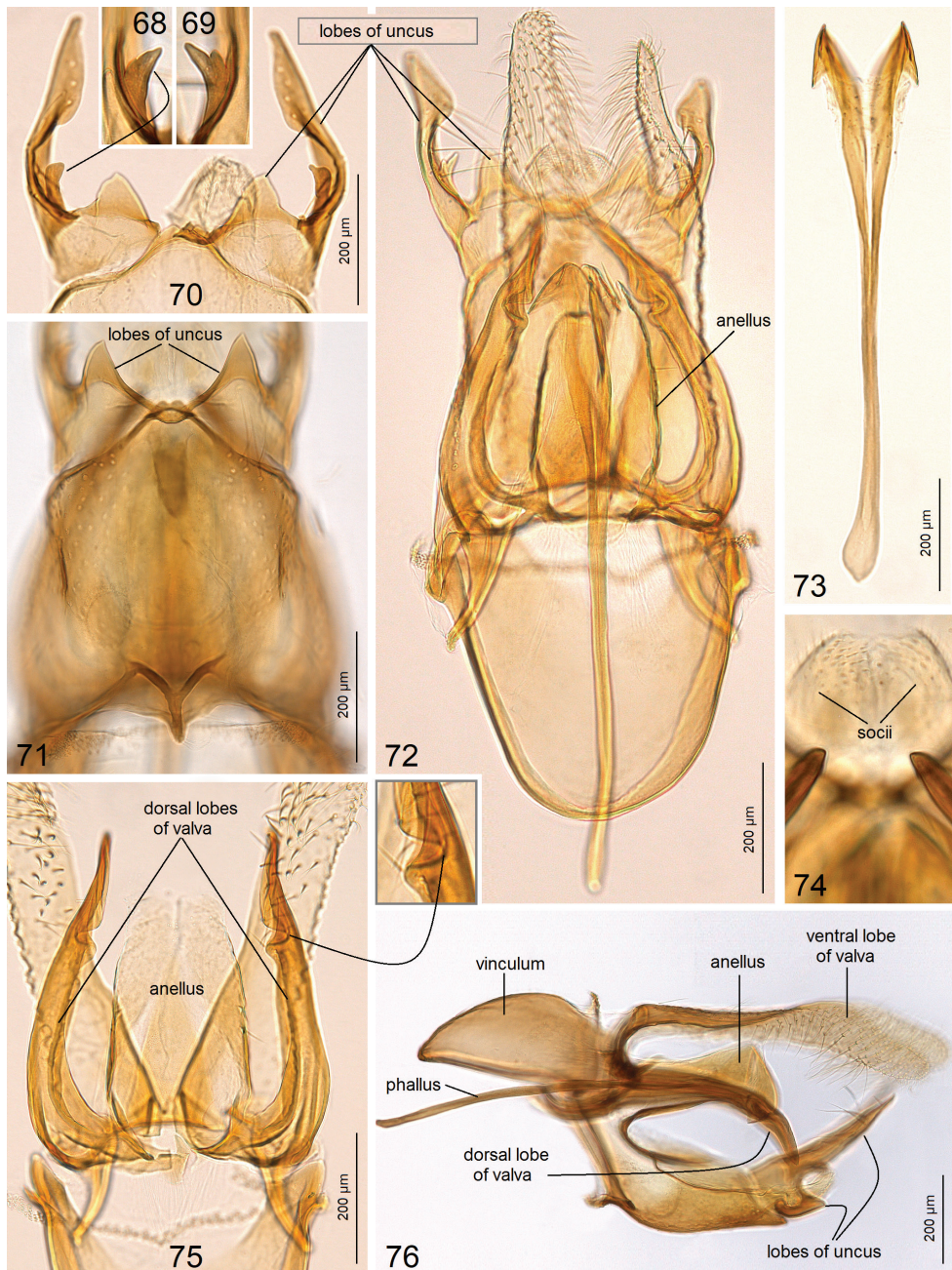
**Figures 50–59.** Male genitalia of *Astrotischeria jociui* sp. nov. **50, 51** capsule with phallus removed, holotype, genitalia slide no. AD999 **52, 53** apex of phallus, paratype, genitalia slide no. AD977 **54** same, genitalia slide no. AD976 **55** same, genitalia slide no. AD922 **56–58** lateral view of capsule, paratype, genitalia slide no. AD977 **59** phallus, general view, paratype, genitalia slide no. AD977 (ZIN).





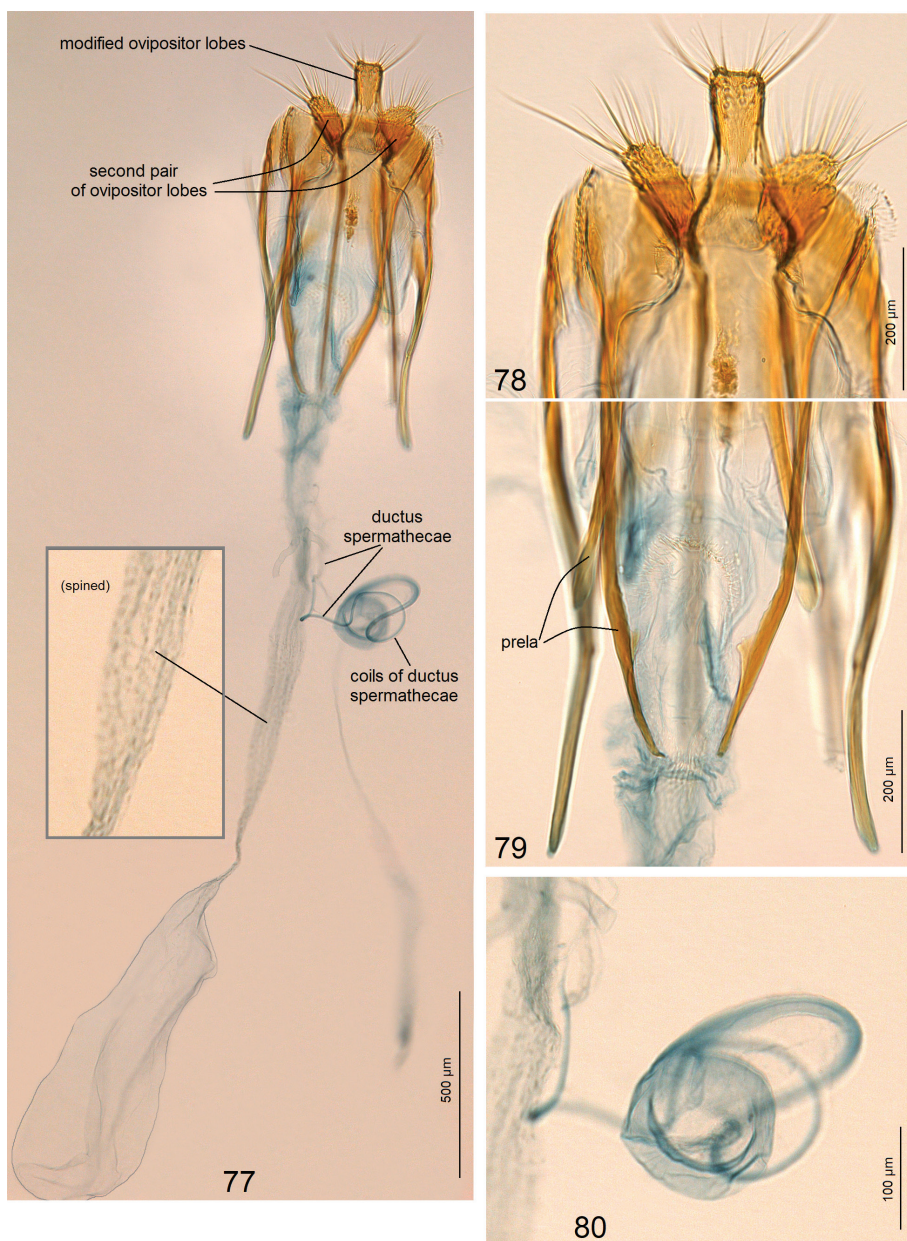
**Figures 60–67.** Genitalia of *Astrotischeria jociui* sp. nov. **60** male genitalia, valva, lateral view, paratype, genitalia slide no. AD976 **61, 63** female genitalia, paratype, genitalia slide no. AD978, ovipositor lobes and apophyses **62** same, slender part of corpus bursae **64, 65** same, details of ovipositor lobes **66** same, coils of ductus spermathecae **67** same, main body of corpus bursae (ZIN).





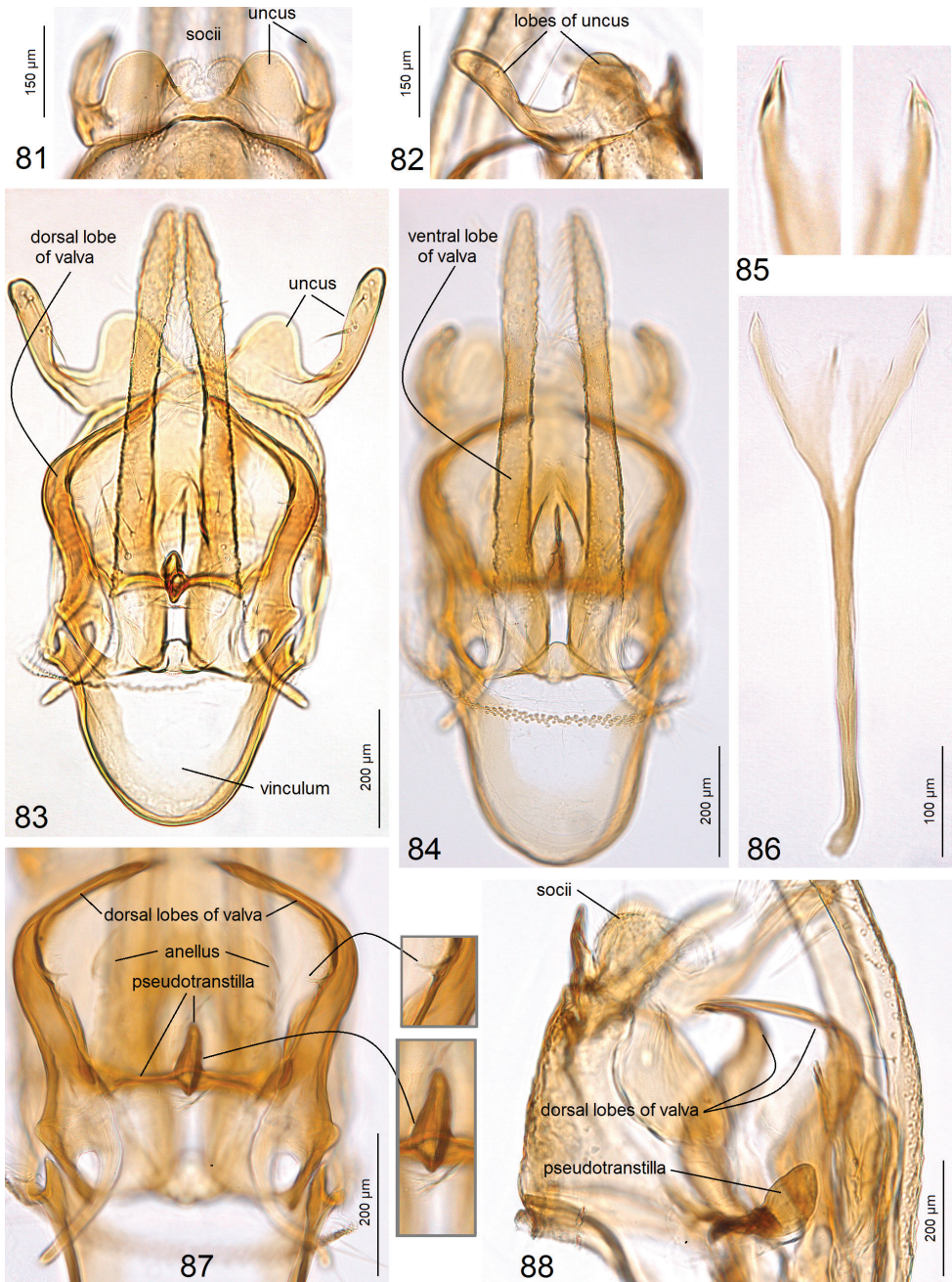
**Figures 68–76.** Male genitalia of *Astrotischeria atlantica* sp. nov. **68, 69** inner process of uncus, holotype, genitalia slide no. AD969 **70** uncus, paratype, genitalia slide no. AD970 **71** smaller lobes of uncus and tegumen, holotype, genitalia slide no. AD969 **72** general view of capsule with phallus inside, holotype, genitalia slide no. AD969 **73** phallus, paratype, genitalia slide no. AD970 **74** socii, holotype, genitalia slide no. AD969 **75** dorsal lobes of valvae and anellus, paratype, genitalia slide no. AD970 **76** lateral view of capsule with phallus inside, holotype, genitalia slide no. AD969 (ZIN).





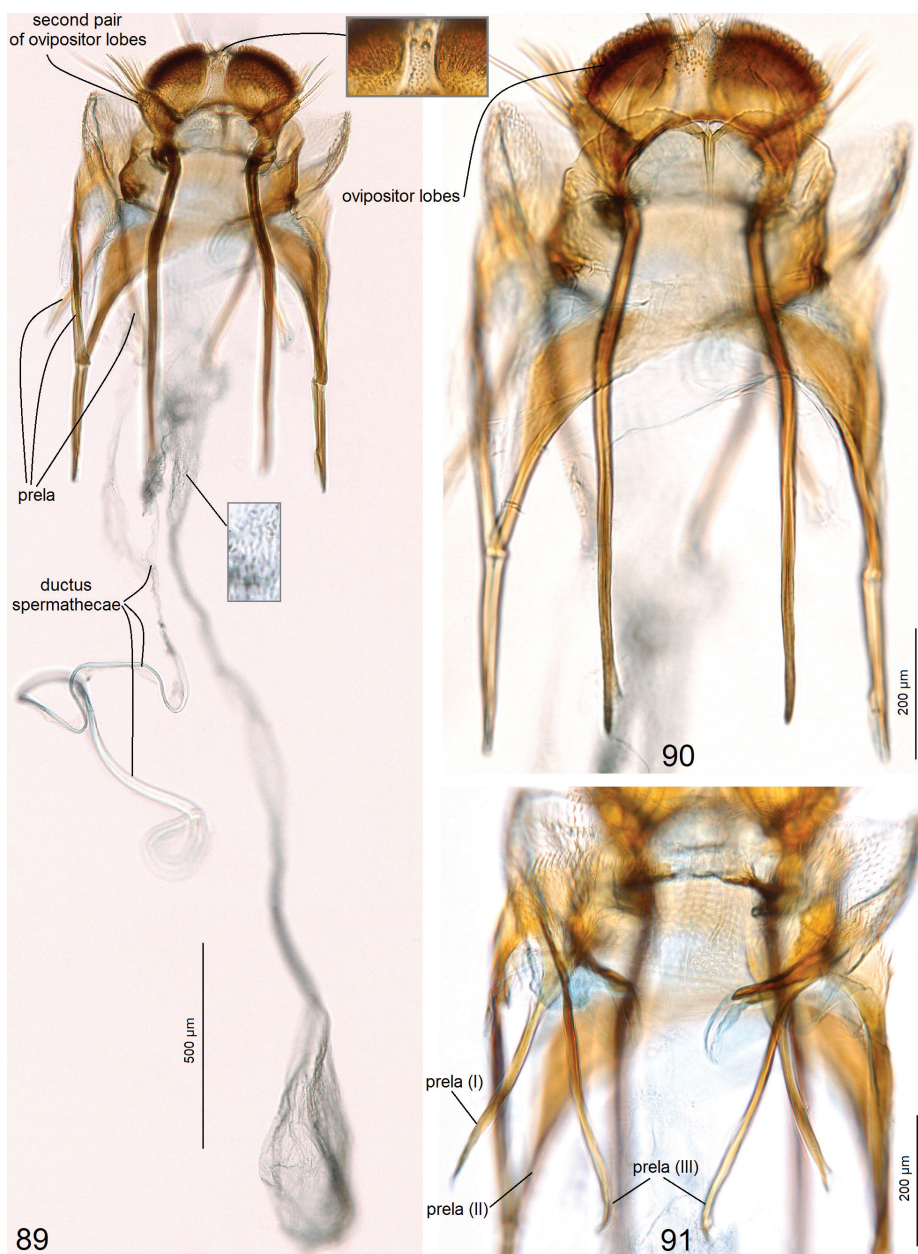
**Figures 77–80.** Female genitalia of *Astrotischeria atlantica* sp. nov. **77** paratype, genitalia slide no. AD968, general view **78** same, ovipositor lobes **79** same, apophyses and prela **80** same, coils of ductus spermathecae (ZIN).

010316209♂, 010316210♂, 010316211♀ (NHMUK); 3 ♂, 5 ♀: **Bolivia**, Nor Yungas Province, Coroico, 16°12'24"S, 67°43'54"W, elevation 1650 m, mining larvae on *Sida* sp., 7–11 Jun 2018, A. Diškus and J. R. Stonis (ZIN).



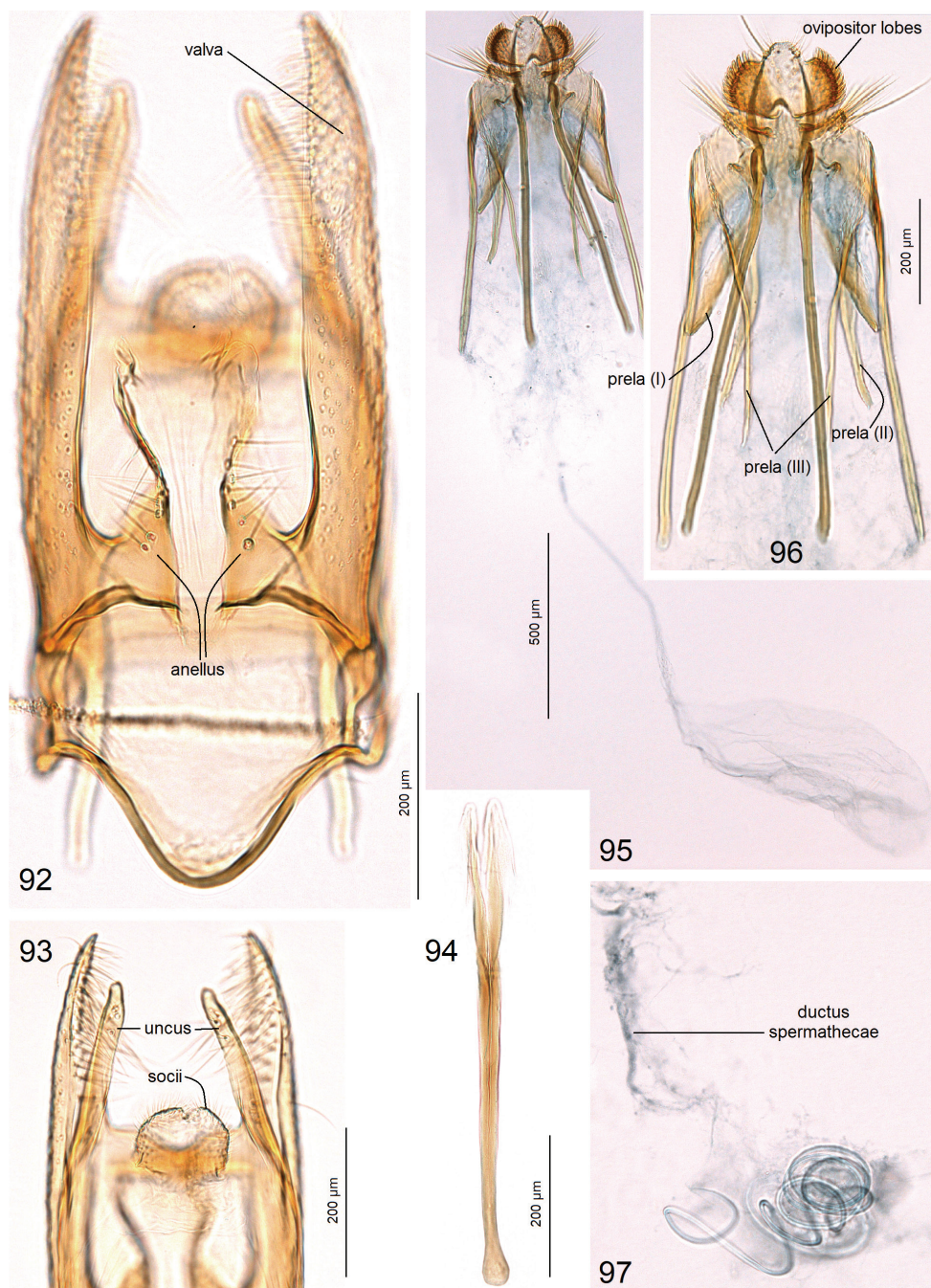
**Figures 81–88.** Male genitalia of *Astrotischeria cornuata* sp. nov. **81** uncus, paratype, genitalia slide no. AD975, ventral view **82** same, lateral view **83** general view of capsule with phallus removed, holotype, genitalia slide no. AD522 **84** same, focused on valvae, paratype, genitalia slide no. AD975 **85** apex of phallus, paratype, genitalia slide no. AD975 **86** general view of phallus, holotype, genitalia slide no. AD522 **87** dorsal processes of valvae and pseudotranstilla, paratype, genitalia slide no. AD975, ventral view **88** same, lateral view (ZIN).





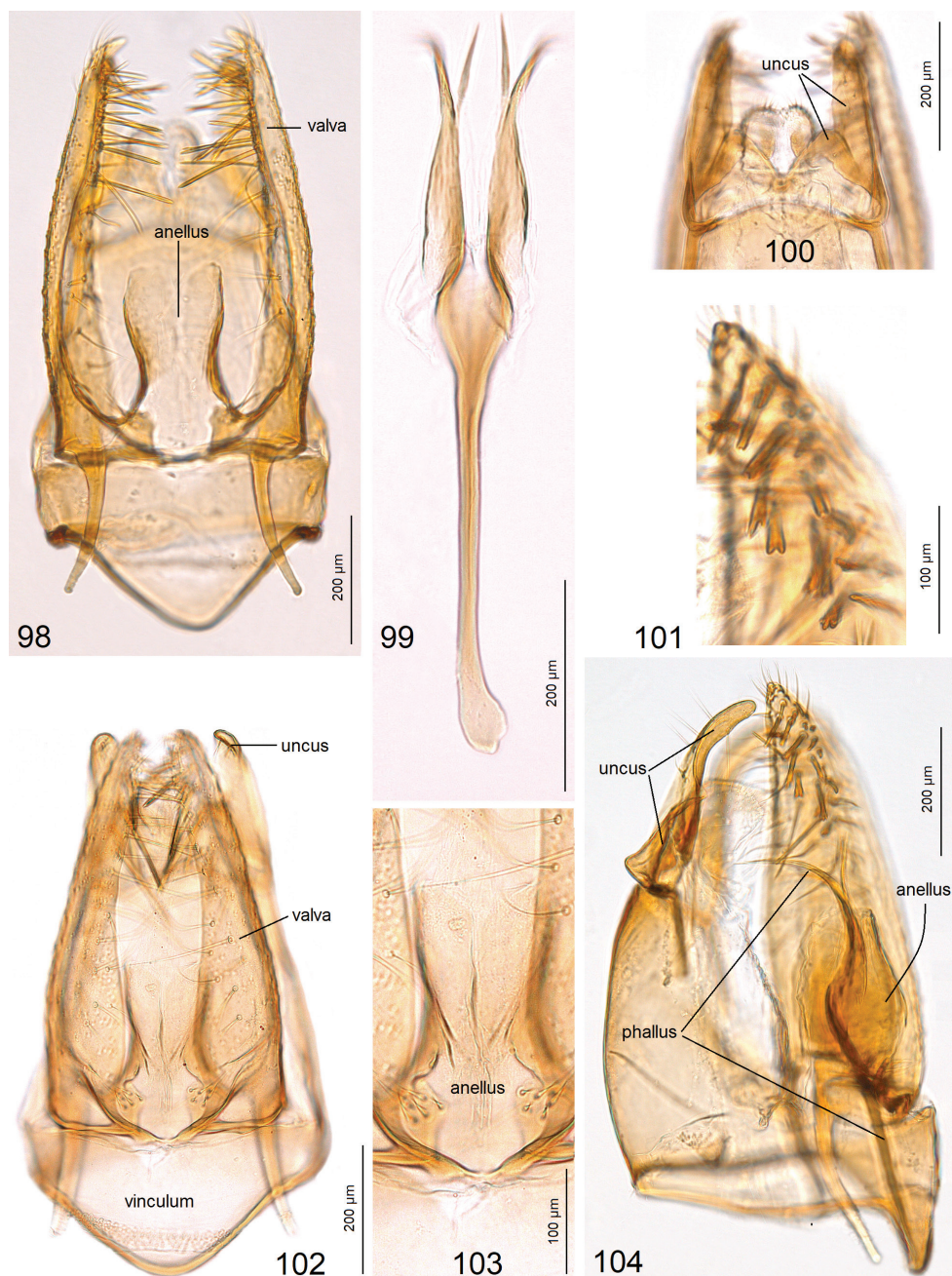
**Figures 89–91.** Female genitalia of *Astrotischeria cornuata* sp. nov. **89** paratype, genitalia slide no. AD981, general view **90** same, ovipositor lobes and apophyses **91** same, prela (ZIN).

**Other material examined.** (published by Diškus and Stonis 2015). 4 ♂, 2 ♀, holotype and paratypes: **Peru**, Tambopata Province, Puerto Maldonado, 12°35'33"S, 69°10'29"W, elevation 195 m, on *Sida rhombifolia* 16 Oct 2008,

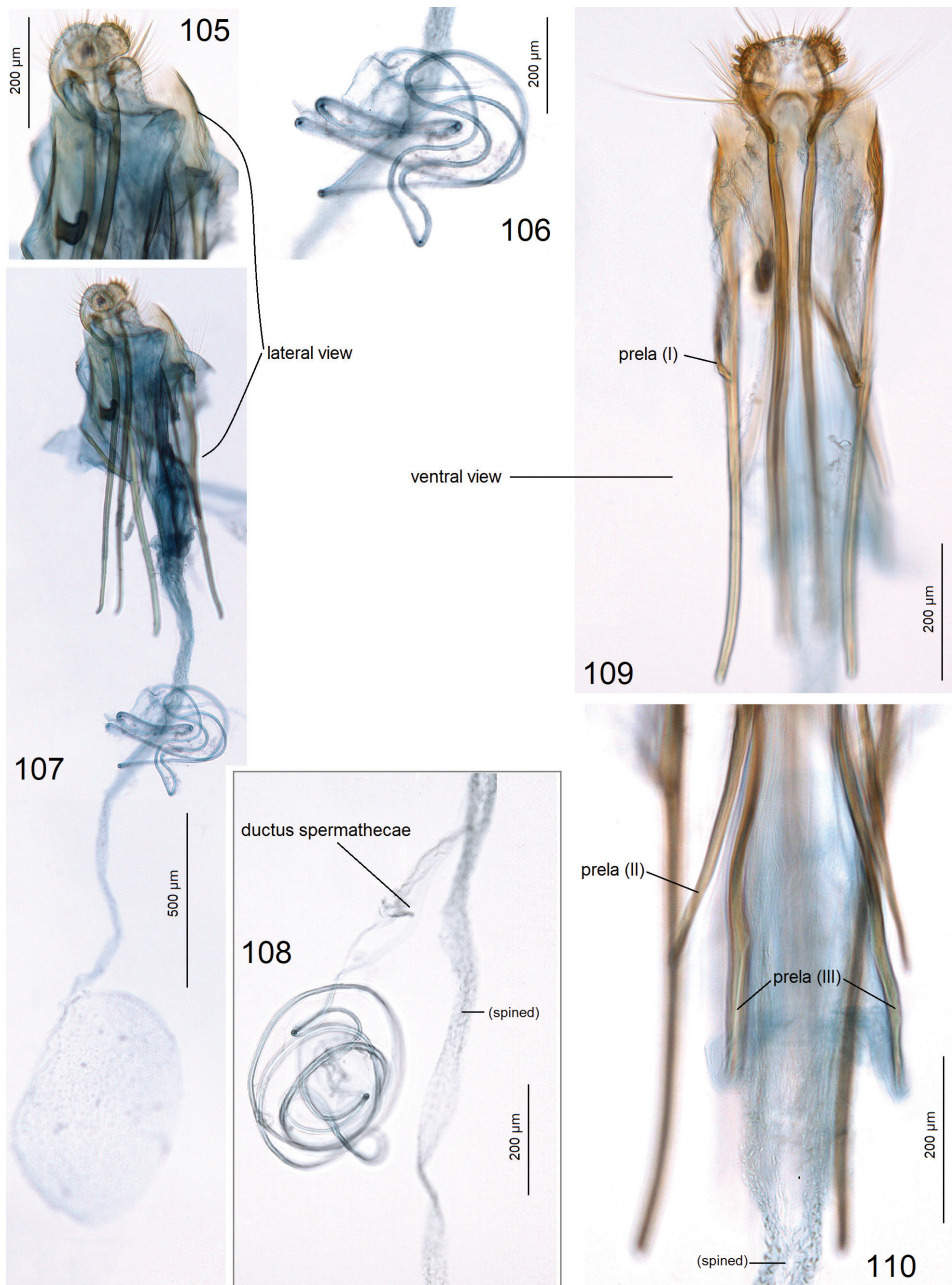


**Figures 92–97.** Genitalia of *Paratischeria guarani* sp. nov. **92** holotype, slide no. AD988, male genitalia, general view of capsule with phallus removed **93** same, uncus and socii **94** same, phallus **95** paratype, slide no. AD987, female genitalia, general view **96** same, ovipositor lobes and apophyses **97** same, coils of ductus spermathecae (ZIN).





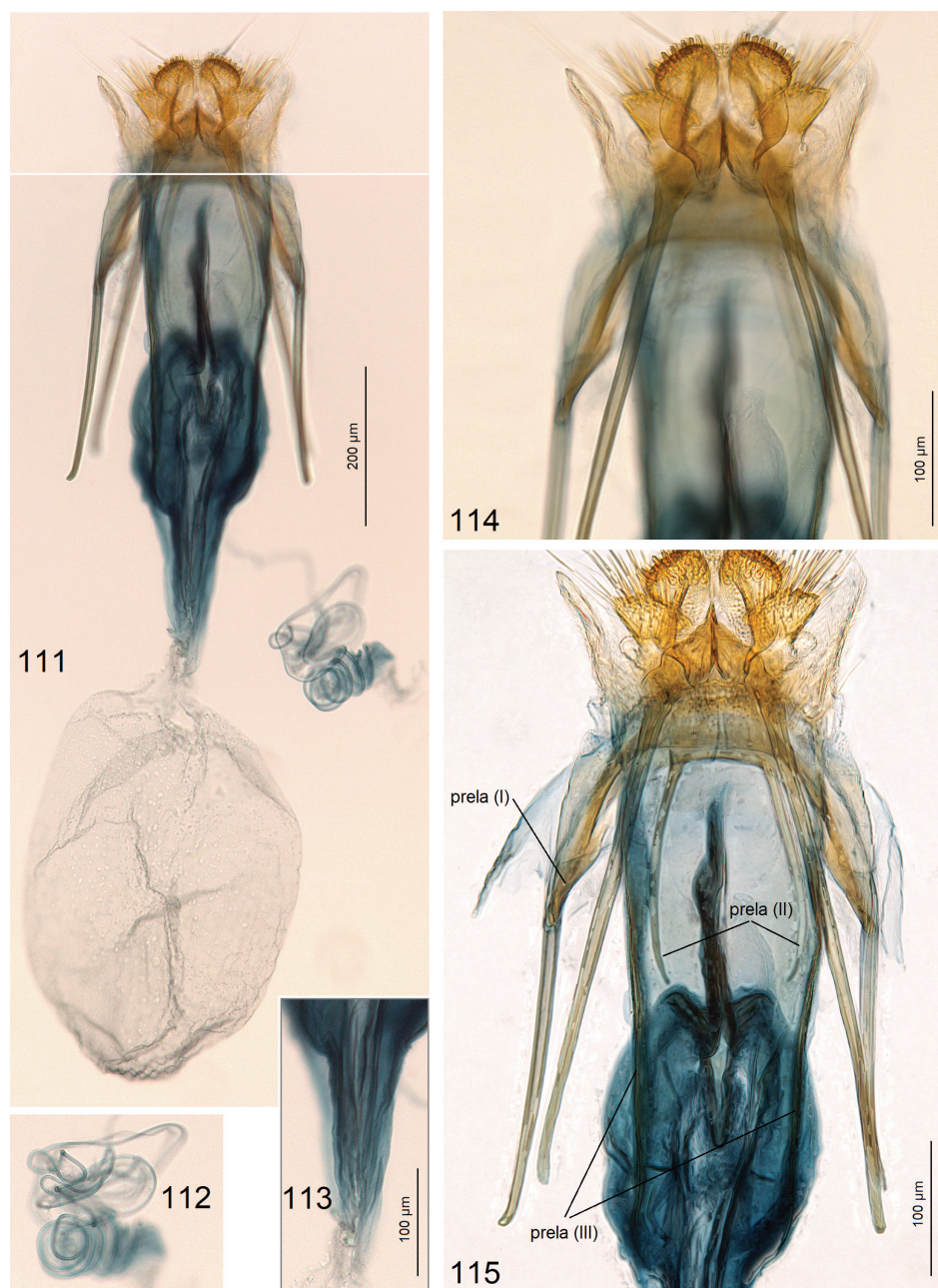
**Figures 98–104.** Male genitalia of *Paratischeria mesoamericana* sp. nov. **98** holotype, slide no. AD1005, general view of capsule with phallus removed **99** same, phallus **100** same, uncus and socii **101** same, thickened bifid chaetae of valva **102**, **103** capsule with phallus removed, ventral view, paratype, genitalia slide no. AD871 **104** same, lateral view with phallus inside, holotype, genitalia slide no. AD1005 (ZIN).



**Figures 105–110.** Female genitalia of *Paratischeria mesoamericana* sp. nov. **105** paratype, genitalia slide no. AD1006, ovipositor, lateral view **106** same, coils of ductus spermathecae **107** same, general view **108** same, coils of ductus spermathecae **109** same, ovipositor lobes and apophyses **110** same, prela (ZIN).

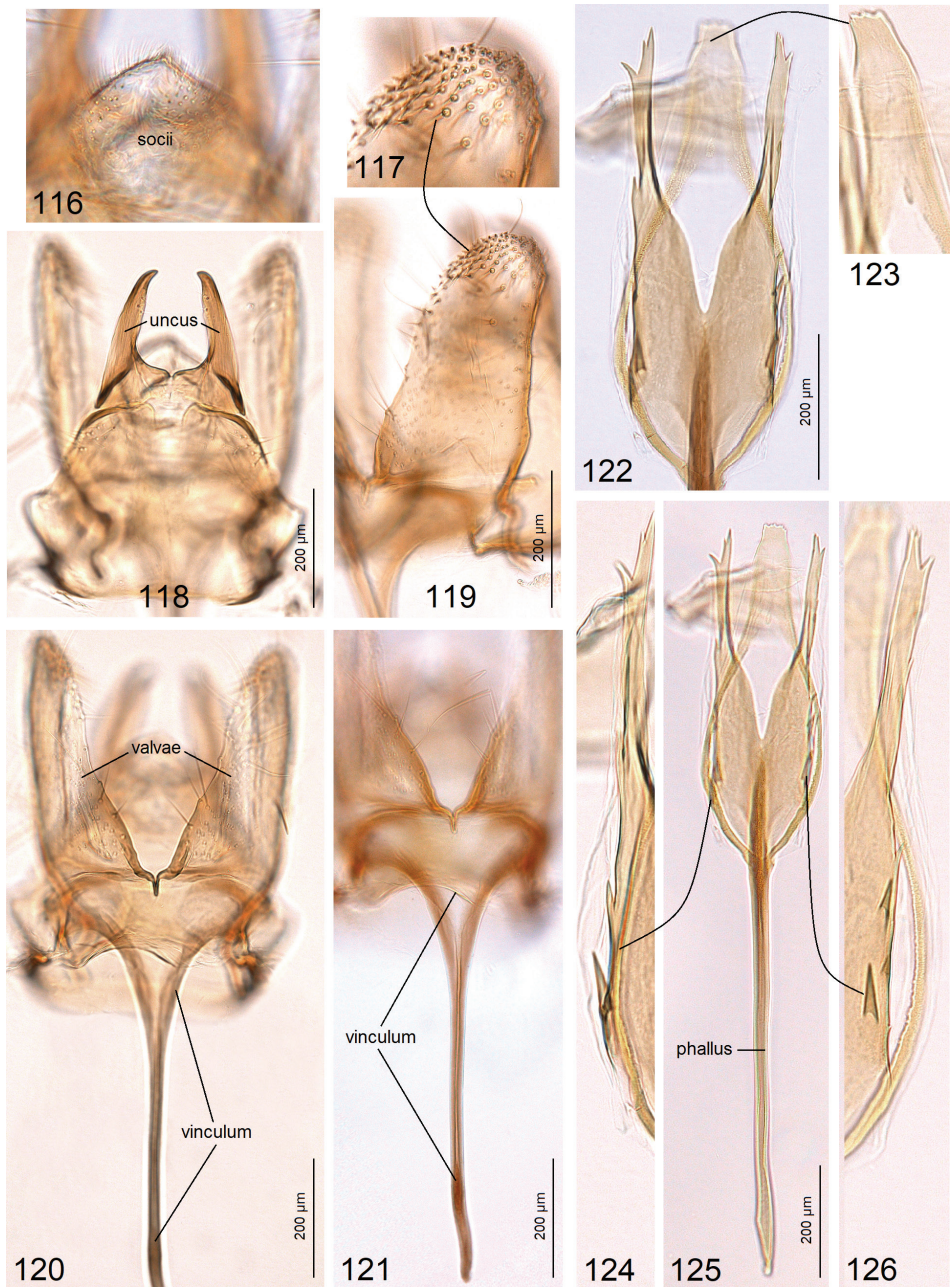
A. Diškus, genitalia slide no. AD711♂ (holotype), AD710♂, AD714♀ (paratypes) (ZMUC); 3 ♂, 4 ♀, paratypes: **Ecuador**, Napo Province, SE Tena, Puerto Misahuallí, 1°2'06"S, 77°40'09"W, elevation 400 m, mining larvae on *Sida rhombifolia*,





**Figures 111–115.** Female genitalia of *Paratischeria suprafasciata* sp. nov. **111** holotype, genitalia slide no. AD967, general view **112** same, coils of ductus spermathecae **113** same, fragment of corpus bursae **114** same, ovipositor lobes **115** same, apophyses and prela (ZIN).

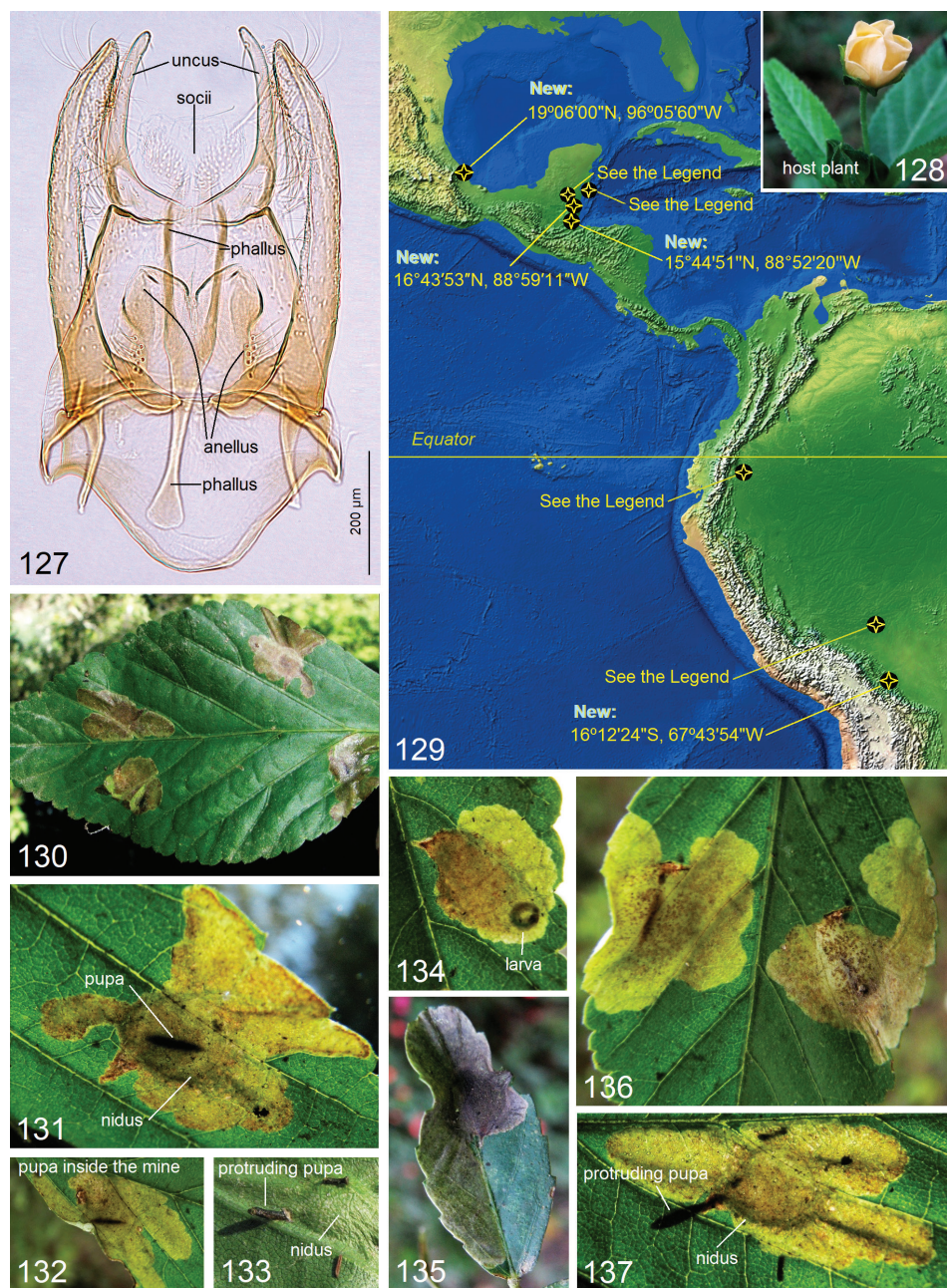
6 Feb 2007, A. Diškus, genitalia slide no. AD715♂ (ZMUC); 1 ♂ (genitalia from adult in pupal skin, no pinned moth preserved), 4 ♀, paratypes, 1°2'03"S, 77°39'54"W, elevation 395 m, mining larvae on *Sida rhombifolia*, 7 Nov 2007,



**Figures 116–126.** Male genitalia of *Paratischeria braziliensis* sp. nov. **116** holotype, slide no. AD1004, **socii 117** same, apex of valva **118** same, uncus and tegumen **119** same, valva **120, 121** same, vinculum **122–126** same, phallus (USNM).

A. Diškus, genitalia slide nos. AD712♂, AD713♀, AD719♀ (ZMUC); 2 ♂, 1 ♀, paratypes: **Guatemala**, Petén region, El Remate, Tikal, 17°13'22"N, 89°37'24"W, elevation 320 m, mining larvae on *Sida rhombifolia* 06 Feb 2012, LT-GT Scien-





**Figures 127–137.** *Paratischeria neotropicana* (Diškus & Stonis, 2015). **127** male genitalia, capsule with phallus inside, Rio Dulce, Guatemala, genitalia slide no. RA492 (USNM) **128** host plant *Sida* L., Malvaceae **129** distribution map (for the localities see Material examined) **130–137** leaf mines, Coroico, Bolivia.

tific Expedition, genitalia slide no. AD716♂ (ZMUC); 1 ♀, paratype: **Belize**, Orange Walk District, Orange Walk, 18°04'40"N, 88°33'28"W, elevation ca. 5 m, mining larva on *Sida rhombifolia*, 9 Feb 2012, LT-GT Scientific Expedition; 2 ♂,

2 ♀, paratypes: Caribbean Archipelago, Ambergris Cay, 17°56'12"N, 87°57'05"W, elevation ca. 5 m, mining larvae on *Sida rhombifolia* 10 Feb 2012, LT-GT Scientific Expedition, genitalia slide no. AD718♂ (ZMUC).

## Discussion

The word “exotic” in this article’s title was borrowed from Edward Meyrick (1854–1938), who discovered and described the record number of the new Microlepidoptera taxa and laid the foundations of the modern systematics of the smallest Lepidoptera, or the so-called Microlepidoptera (Hill 1939, Clarke 1955, Robinson 1986). Obviously, there is no professional in the field of Microlepidoptera taxonomy who would not know the volumes “Exotic Microlepidoptera” by Edward Meyrick (Meyrick 1915a, 1915b, 1921, 1934, 1936); some of these volumes also include descriptions of new Tischeriidae (Meyrick 1915b, 1934, 1936).

Our article deals with distinctive new species exhibiting unusual, “exotic” morphology and provides new host plants not known outside of the Neotropics. The smallest Lepidoptera in the tropics and subtropics are still wrapped in mystery: they have been poorly investigated, are not well known, and the variety of their morphological and ecological adaptations is surprising.

## Novel, atypical morphological characters

Usually, in male genitalia of Tischeriidae, the valva is covered with simple, slender chaetae, only occasionally it bears a pectinifer (Stonis et al. 2020a). In *Paratischeria mesoamericana* sp. nov. we found that the valva is covered with unique, thickened and distally bifid chaetae (Fig. 101).

The female ovipositor of Tischeriidae is not of the piercing type. Females are characterized by two distinct, rounded ovipositor lobes, and only in a few Malvaceae-feeding *Astrotischeria* species these ovipositor lobes are greatly or fully reduced (Stonis et al. 2019b, 2020a). In the course of our study, we found that in *A. atlantica* sp. nov. the ovipositor lobes are modified into an extended, plate-like process, which slightly resembles a piercing ovipositor of some other moth families (Fig. 78). Such a specialized ovipositor or distally bifid chaetae in the male genitalia were not previously known in the Tischeriidae. Moreover, females of *A. atlantica* possess no peg-like setae, but these modified setae are among the most distinct apomorphies and diagnostic characters of the family. Males of *Astrotischeria* species usually possess two pairs of uncus lobes. In *A. atlantica*, the ventral lobe of the uncus has a small additional spine-like lobe; such a derived uncus was discovered in Tischeriidae for the first time. Moreover, usually in *Astrotischeria* dorsal lobes are long and slender, while ventral lobes are short and rounded. In *A. atlantica* it is an opposite case: ventral lobe greatly developed, while the dorsal lobe, in contrast to other congeneric species, is small and triangular (see Fig. 76).

Xu et al. (2017) postulated that many large coils of ductus spermathecae in the female genitalia are characteristic exclusively for *Paratischeria* Diškus & Stonis, and it

was expected that species of *Astrotischeria* Puplesis & Diškus would possess only a few, small coils. During our study we discovered that, in contrast to other *Astrotischeria*, *A. jociui* sp. nov. possesses many large coils in the ductus spermathecae (Fig. 66). On the other hand, we discovered that females of *A. cornuata* sp. nov. possess a sinuous ductus spermathecae (Fig. 89), but have no distinct coils at all. It is the first species of *Astrotischeria* to be discovered without coils in the ductus spermathecae. Moreover, a strong reduction of the ovipositor lobes is among the most distinct apomorphies and diagnostic characters of the genus; however, we found that in females of *A. cornuata*, the ovipositor lobes are greatly developed, i.e., very large and rounded (Fig. 90).

Previously, within Tischeriidae only species of *Coptotriche* Walsingham were known to possess a transtilla in the male genitalia. The transverse bar that we discovered between the valvae in *A. cornuata* sp. nov. does not seem to be homologous to the transtilla in *Coptotriche*, because in *A. cornuata* it is not attached to the base of the basal process of the valva, and it represents a novel character for *Astrotischeria*; we propose to use the term pseudotranstilla for this structure (Fig. 87).

Usually Tischeriidae species can hardly be differentiated externally from each other because of their simple and very similar forewing pattern. However, the discovered *Paratischeria suprafasciata* sp. nov. possesses a unique, very distinctive forewing pattern (see Fig. 47).

*Paratischeria braziliensis* sp. nov. represents the most bizarre species in the genus: so far there is no known species with a greatly extended, rod-like vinculum and spiny phallus. These characters are novel to *Paratischeria*, and they resemble, but are probably not homologous, to the characters in *Coptotriche*. Moreover, *P. braziliensis* does not have a transtilla that is so characteristic for *Coptotriche*.

## Trophic relationships of global and Neotropical Tischeriidae

Tischeriidae are trophically associated with plants belonging to rosid and asterid I core eudicot angiosperms. Recently, the following seventeen host-plant families were known to be hosts for the Tischeriidae family worldwide: Euphorbiaceae, Hypericaceae (Malpighiales), Fabaceae (Fabales), Rhamnaceae, Rosaceae, Ulmaceae, Urticaceae (Rosales), Betulaceae, Fagaceae (Fagales), Combretaceae (Myrtales), Anacardiaceae (Sapindales), Malvaceae, including the former families Sterculiaceae and Tiliaceae (Malvales), Ericaceae, Theaceae, Symplocaceae (Ericales), Apocynaceae (Gentianales), and Asteraceae (Asterales) (Stonis et al. 2017, Xu et al. 2018). Now, because of our discovery of *P. suprafasciata* sp. nov. feeding on *Allophyllus edulis*, we added one more host-plant family to the list, Sapindaceae (Sapindales).

In the Neotropics, Tischeriidae have been recorded feeding on seven host-plant families: Rhamnaceae, Urticaceae (Rosales), Combretaceae (Myrtales), Sapindaceae (Sapindales), Malvaceae (Malvales), Apocynaceae (Gentianales), and Asteraceae (Asterales). Although we discovered Sapindaceae as a new host-plant family, it is only represented by one tischeriid species, so Asteraceae is still the most utilized host-plant family of the Neotropical Tischeriidae.

It is not known why Tischeriidae have been so successful utilizing Asteraceae in the Americas. However, the estimation of Asteraceae richness and taxonomic diversity



by Katinas et al. (2007) indicates that Central and South America are characterized by the globally highest number of genera. It should be also mentioned that the earliest fossils confidently assigned to Asteraceae suggest a South American-Antarctica origin (Barreda et al. 2010, 2012). Recent studies showed that Asteraceae is also an important host for some other leaf-mining families in South America, notably the Nepticulidae (Stonis et al. 2018b) and Bucculatricidae (Vargas et al. 2012). It is interesting to note, that no Asteraceae-feeding Tischeriidae are known outside the Americas. Similar situation was observed with the Asteraceae-feeding Nepticulidae (for a review see Stonis et al. 2018b). Outside of the Americas, Asteraceae-feeding Nepticulidae were found only in North Africa (a single species) and New Zealand where Nepticulidae fauna is dominated by Asteraceae-feeders and the proportion of Asteraceae miners is at least 54% or higher (R. Hoare, pers. comm.).

Below, for the first time, we provide a full list of Tischeriidae host plants from the Neotropics (Table 1).

### Predicting distribution through host-plant distribution of the host-specific Tischeriidae

Currently, only three Tischeriidae species have been recorded over a broad range in the Neotropics: *Paratischeria neotropicana* (Diškus & Stonis), occurring from Mexico to Bolivia (Fig. 129), *Astrotischeria selvica* Diškus, Carvalho-Filho & Stonis, occurring from Central America to the Atlantic coast of equatorial Brazil (Stonis et al. 2018a), and *A. ochrimaculosa* distributed from Colombia to Peru (Stonis et al. 2019b). All remaining Neotropical species are known from a single locality, or restricted area, which suggests that they are poorly sampled. On the other hand, leaf-mining larvae of Tischeriidae show a great selectivity in their food choice: they are stenophagous (monophagous or oligophagous). Therefore, despite the fact that insect distribution may depend on many more factors than host plant alone, recently we hypothesized that the distribution of the host plants can suggest much broader ranges for these host-specific leaf miners (Stonis et al. 2019c). We discuss potential distribution ranges of the species described in this paper.

*Astrotischeria jociui* sp. nov. is currently known only from a single locality in Peru, and feeds on *Wissadula* Medik., Malvaceae. It is currently estimated that *Wissadula* consists of approximately 32 species. The largest number of species occurs in the Neotropics, with the highest concentration in southeastern Paraguay, northern Argentina, and midwestern Brazil (Fig. 138), and with a few species in North America, Asia, and Africa (Bovini and Baumgratz 2016). We expect this tischeriid species may also occur in other countries in South America and possibly in Central America, and in sunny areas with disturbed vegetation, rarely in forests.

*Astrotischeria atlantica* sp. nov. is currently known only from a single locality in Uruguay, Rocha Department, La Paloma, and feeds on *Baccharis spicata* (Lam.) Baill., Asteraceae. *Baccharis spicata*, “chilca blanca” or “chilca amarga”, is a dioecious, rhizomatous shrub or subshrub native to Bolivia, Paraguay, southern Brazil, Uruguay, and central and northeastern Argentina (Fig. 139); recently it has been reported as an



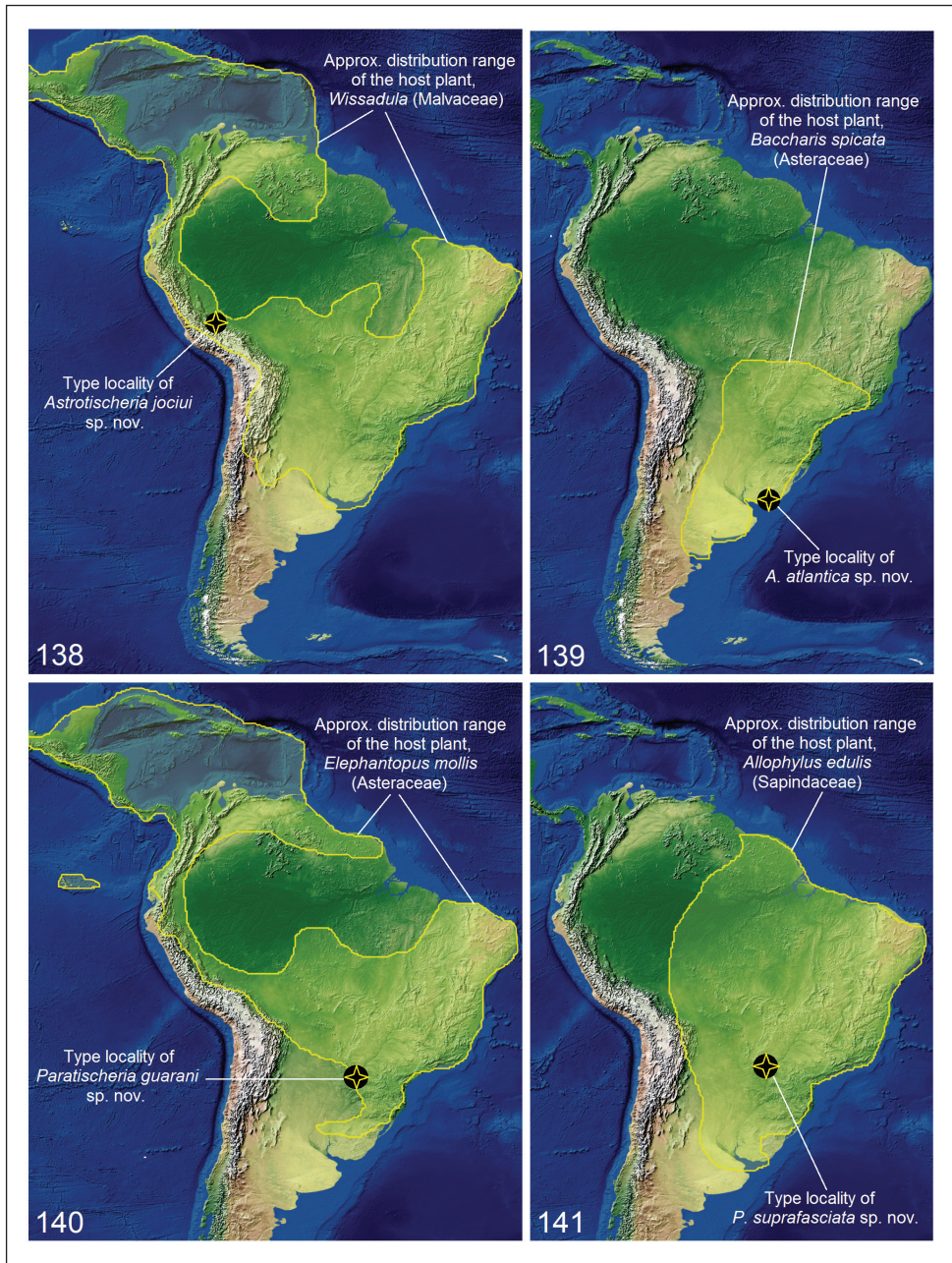
**Table 1.** List of currently known host plants of the Neotropical Tischeriidae.

<b>Rhamnaceae:</b>	
<i>Gouania polygama</i> (Jacq.) Urb.	<i>Tischeria gouaniae</i> (Stonis & Diškus, 2007)
<b>Sapindaceae:</b>	
<i>Allophylus edulis</i> (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl.	<i>Paratischeria suprafasciata</i> sp. nov. (new record)
<b>Malvaceae:</b>	
<i>Sida glabra</i> Mill.	<i>Astrotischeria</i> sp. (Stonis et al. 2020a)
<i>S. rhombifolia</i> L., <i>S. spinosa</i> L., <i>S. acuta</i> Burm.f.	<i>Paratischeria neotropicana</i> (Diškus & Stonis, 2015)
<i>Wissadula</i> sp., possibly <i>W. amplissima</i> (L.) R. E. Fr.	<i>Astrotischeria ochrimaculosa</i> Diškus, Stonis & Vargas (Stonis et al. 2019b)
<i>W. excelsior</i> (Cav.) C. Presl.	<i>Astrotischeria jociui</i> sp. nov. (new record)
<b>Combretaceae:</b>	
<i>Terminalia australis</i> Cambess.	<i>Coptotriche parvisacculata</i> Diškus & Stonis (Stonis et al. 2019c)
<b>Apocynaceae:</b>	
<i>Forsteronia myriantha</i> Donn. Sm.	<i>Coptotriche forsteroniae</i> Stonis & Diškus, 2008
<b>Asteraceae:</b>	
<i>Astroecupatorium inulifolium</i> (Kunth) R. M. King & H. Rob.	<i>Astrotischeria trilobata</i> Diškus & Stonis (Stonis et al. 2018a)
<i>Baccharis emarginata</i> (Ruiz & Pav.) Pers.	<i>Astrotischeria bacchariphaga</i> Diškus & Stonis (Stonis et al. 2019c)
<i>B. latifolia</i> (Ruiz & Pav.) Pers.	<i>Astrotischeria bacchariphaga</i> Diškus & Stonis (Stonis et al. 2019c)
<i>B. spicata</i> (Lam.) Baill.	<i>Astrotischeria atlantica</i> sp. nov. (new record)
<i>Elephantopus mollis</i> Kunth	<i>Paratischeria guarani</i> sp. nov. (new record)
<i>Eupatorium</i> sp.	<i>Astrotischeria truncata</i> Diškus & Stonis (Stonis et al. 2019c)
<i>Lasianthea fruticosa</i> (L.) K. M. Becker	<i>Astrotischeria</i> spp. (Stonis et al. 2020a)
<i>Montanoa atriplicifolia</i> (Pers.) Sch. Bip.	<i>Astrotischeria casila</i> Diškus & Stonis (Stonis et al. 2018a)
<i>M. hibiscifolia</i> Benth.	<i>Paratischeria mesoamericana</i> Diškus & Stonis (new record)
<i>Otopappus verbesinoides</i> Benth.	<i>Paratischeria</i> sp. (Stonis et al. 2020a)
<i>Podanthus ovatifolius</i> Lag.	<i>Astrotischeria chilei</i> Puplesis & Diškus (Puplesis and Diškus 2003)
<i>Rhyssolepis incana</i> (Pers.) H. Rob. & A. J. Moore	<i>Astrotischeria plagifera</i> (Meyrick) (Stonis et al. 2018a)
<i>Scalesia affinis</i> Hook. f.	<i>Astrotischeria alcedoensis</i> Landry (Landry and Roque-Albelo 2004)
<i>S. baurii</i> B.L. Rob. & Greenm.	<i>Astrotischeria scalesiaella</i> Landry (Landry and Roque-Albelo 2004)
<i>S. pedunculata</i> Hook. f.	<i>Astrotischeria scalesiaella</i> Landry (Landry and Roque-Albelo 2004)
<i>Synedrella nodiflora</i> (L.) Gaertn.	<i>Astrotischeria selvica</i> Diškus, Carvalho-Filho & Stonis (Stonis et al. 2018a)
<i>Sphagneticola trilobata</i> (L.) Pruski	<i>Astrotischeria selvica</i> Diškus, Carvalho-Filho & Stonis (Stonis et al. 2018a)
<i>Tessaria integrifolia</i> Ruiz & Pav.	<i>Astrotischeria koehleri</i> (Bourquin 1962)
<i>Tilesia baccata</i> (L.) Pruski	<i>Astrotischeria selvica</i> Diškus, Carvalho-Filho & Stonis (Stonis et al. 2018a)
<i>Wedelia calycina</i> Rich.	<i>Astrotischeria colombiana</i> Stonis & Vargas (Stonis et al. 2019b)
<b>Urticaceae:</b>	
<i>Phenax hirtus</i> (Sw.) Wedd.	<i>Paratischeria ferruginea</i> Diškus & Stonis (Stonis et al. 2017)

invasive in Europe (Verloove et al. 2017). We expect that this species also occurs in other South American countries, and mainly in grasslands and roadsides.

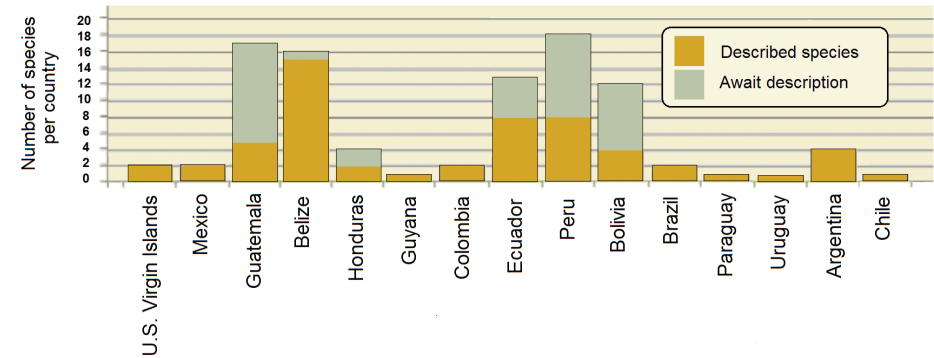
*Paratischeria guarani* sp. nov. is currently known only from a single locality in Paraguay, Departamento de Itapúa, Hohenau and feeds on *Elephantopus mollis* Kunth, Asteraceae. *E. mollis*, or “elephant’s foot”, is an herbaceous perennial plant with compound flower heads, native to the American tropics and subtropics (Dematteis 2014). It is an invasive weed and it has been widely introduced elsewhere (e.g., Africa, Asia, Australia, and the Pacific) (CABI 2020). In the Americas, we expect this tischeriid species may occur from Mexico and the Caribbean to Argentina (Fig. 140), in high rainfall areas with fertile tropical conditions, especially in open areas, pastures, plantations, forest edges, roadsides, and disturbed or marshy areas.

*Paratischeria mesoamericana* sp. nov. is currently known only from a single locality in Guatemala, Antigua Guatemala, San Juan del Obispo, and feeds on

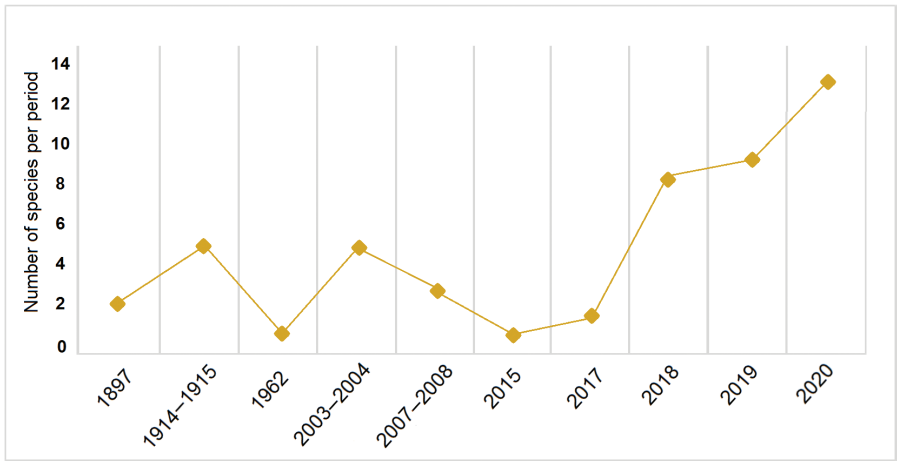


**Figures 138–141.** Predicted host-specific Tischeriidae distribution from host plant distribution. **138** *Astrotischeria jociui* sp. nov. **139** *A. atlantica* sp. nov. **140** *Paratischeria guarani* sp. nov. **141** *P. suprafasciata* sp. nov.

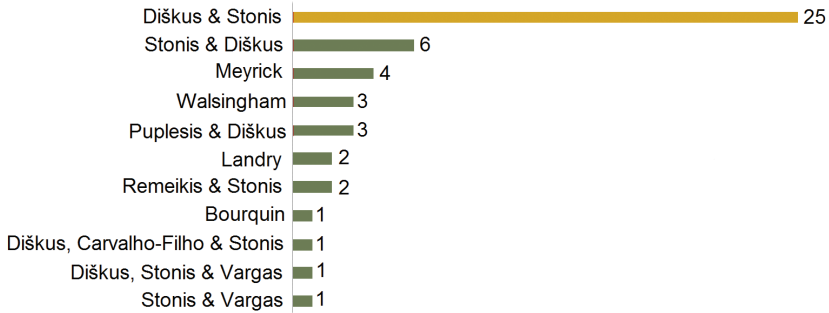
*Montanoa hibiscifolia* Benth., Asteraceae. *M. hibiscifolia*, known in Guatemala as “cajete”, “cana rancho”, “quil”, “toquillo”, “vara de jaula”, “xixil” (Tropicos 2020), is a southern North American and Central American shrub with 3–5-lobed leaves and



142



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**Figures 142–144.** Overview on the Neotropical Tischeriidae fauna and history of the description of species. **142** currently described diversity of Tischeriidae per country (Note that some species occur in more than one country, therefore, there is some overlap so the total in the graph does not agree with the total 49 species known from the Neotropics) **143** description history of the Tischeriidae from the Neotropics **144** authorship of all currently known Tischeriidae species of the fauna of the Neotropics.

prominent petiolar auricles (Funk 1982). We expect this tischerioid species to also occur in Costa Rica, Nicaragua, Belize, and north to Chiapas in Mexico, in pine-oak forests, on hillsides and along streams, lakes and roads from 350 to 2500 m.

*Paratischeria suprafasciata* sp. nov. is currently known only from a single locality, Puerto Iguazú, in northeastern Argentina, and feeds on *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl., Sapindaceae. *A. edulis*, the “cocú” or “chal chal”, is a South American shrub or little tree with persistent, 3-foliate leaves and edible, red fruits, extending from Guiana to Argentina (Ferrucci 2004) (Fig. 141). We expect this tischerioid species to occur in the tropical, subtropical, and riverine forests of Guianas, Brazil, Paraguay, Uruguay, and north to central Argentina.

## Summary on species description of the Neotropical Tischeriidae

The study of the Tischeriidae fauna in the Neotropics began in the late nineteenth to early twentieth centuries, but only during the last decade the inventory and especially collecting of the Neotropical Tischeriidae has become more purposeful and active (Fig. 143). The overall impression is that the Neotropical fauna is an isolated entity: there is no overlap at the species level between the fauna of the Neotropics and that of the rest of world, including the adjacent Nearctic region. The total number of Tischeriidae of the Neotropics now numbers 49 described species including the seven new species described in this paper and six new species by Stonis et al. 2020a. Additionally, some other new species have already been recognized, dissected, and are under preparation for publication by us (see Fig. 142). The number of described Tischeriidae species by country is unequal, mostly due to different research effort (Fig. 142). Some species occur in more than one country, therefore, there is some overlap, and the total (57) does not agree with the total of 49 species known from the Neotropics.

In total, the world fauna of Tischeriidae now numbers 158 described species, but only 153 species are named. Five South African species were documented and published but were left unnamed because of lack of males (Puplesis and Diškus 2003, Stonis et al. 2019a). Thus, the Neotropical fauna forms one third of the currently known global fauna. The history of species description is given in Fig. 143, the authorship in Fig. 144. In total, eight researchers were involved in species descriptions from the Neotropics, some of them described at least one or two species of Tischeriidae, others are responsible for the bulk, Notably Arūnas Diškus who, in the last two decades, is responsible for the discovery and descriptions (all with co-authors) of 36 species.

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