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Research Article

# Discovery of five new species of *Allacta* from Yunnan and Hainan, China (Blattodea, Pseudophyllodromiidae)

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## Abstract

We examined new *Allacta* materials from Yunnan and Hainan Province, China, and discovered new species using both morphological and molecular species delimitation (ABGD) methods. Five new species are described: *A. bifolium* Li & Wang, **sp. nov.**, *A. hemiptera* Li & Wang, **sp. nov.**, *A. lunulara* Li & Wang, **sp. nov.**, *A. redacta* Li & Wang, **sp. nov.**, and *A. unicaudata* Li & Wang, **sp. nov.** All five species are placed under the *hamifera* species group. An updated key and checklist of *Allacta* species from China are provided.

**Key words:** ABGD, checklist, cockroach, cryptic species, DNA barcodes, female genitalia, identification key

## Introduction

The genus *Allacta* Saussure & Zehntner, 1895 belongs to Pseudophyllodromiidae, with 47 known species mainly distributed in the Oriental and Australasian regions (Beccaloni 2014; He et al. 2019; Prabakaran et al. 2019; Senraj et al. 2021). Species of this genus are found inhabiting tree trunk surfaces at night or under the barks in the daytime (He et al. 2019). They are distinguished from other Pseudophyllodromiidae by the tarsal pulvillus only present on the fourth tarsomere. Recently, Prabakaran et al. (2019) and Senraj et al. (2021) described four new *Allacta* species from India, all with a solidly dark pronotal disk, broadly V-shaped or keel-like male interstylar margin, and all belonging to the *hamifera* species group (Roth 1993b).

Eight species were recorded from China according to He et al. (2019). However, the specimen depository of *Allacta hainanensis* (Liu et al. 2017) was not assigned (see Liu et al. 2017). Therefore, this species is invalid according to the International Code of Zoological Nomenclature (see Article 16.4.2) (ICZN 1999).

DNA barcoding has been widely used in cockroach identification in recent years, but is considered more reliable when used in combination with morphological evidence (Evangelista et al. 2013; Che et al. 2017; Yang et al. 2019; He et al. 2021). Although male genital morphology is traditionally used in cockroaches, female genitalia characters have also been shown to be useful in the identification of cockroaches, such as genera *Cryptocercus* and *Anaplecta* (Bai et al. 2018; Zhu et al. 2022).

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In this study, newly collected *Allacta* materials from Yunnan and Hainan Provinces were examined, and they were found morphologically different from the known species. Based on morphological characters as well as the ABGD approach, five new species were confirmed, including the establishment of *Allacta hemiptera* Li & Wang, sp. nov. for the *nomen nudum Temnopteryx hainanensis* Liu et al., 2017.

## Materials and methods

### Morphological examination

Twenty-six studied specimens of *Allacta* were collected from Yunnan, Hainan and Xizang Provinces and were deposited in College of Plant Protection, Southwest University, Chongqing, China (**SWU**) and Shanghai Entomology Museum, Shanghai, China (**SEM**). Morphological terminology used in this paper follows Roth (2003), McKittrick (1964) and Li et al. (2018). Vein abbreviations in the figures are as follows:

| | |
|---|---|
| **CuA** | cubitus anterior; |
| **CuP** | cubitus posterior; |
| **M** | media; |
| **R** | radius; |
| **RA** | radius anterior; |
| **RP** | radius posterior; |
| **ScP** | subcosta posterio; |
| **V** | vannal; |
| **Pcu** | postcubitus. |

All materials are preserved in absolute ethanol and stored at -20 °C. The genitalia were handled based on a standard procedure in which terminal segments of the abdomen were cut off, heated in tap-water and rinsed with sterile water to remove trace amounts of NaOH, and then immersed in glycerol for further photography, dissection and preservation. Photos were taken with Leica DFC camera through a Leica M205A stereomicroscope; dissection and observation were performed under a Motic K400 stereomicroscope. All photos and images were edited with Adobe Photoshop CC 2019.

### DNA sequencing

Total DNA was extracted from hindleg tissues by the Hipure Tissue DNA Mini Kit (Magen Biotech, Guangzhou), and the remaining body parts were stored in absolute ethanol as voucher specimens. Primers for PCR amplification were LCO1490 (5’-GGTCAACAAATCATAAGATATTGG-3’) and HCO2198 (5’-TAAACTTCAGGGTGACCAAAAAATCA-3’) (Folmer et al. 1994). The PCR reactions were carried out in a 25 µL volume. The amplification conditions were: initial denaturation at 98 °C for 2 min, followed by 35 cycles for 15 s at 98 °C, 10 s at 49 °C, and 1 min at 72 °C, with a final extension of 5 min at 72 °C. All DNA purification and sequencing were carried out by Tsingke Biotech Co., Ltd. (Beijing, China) using the aforementioned primers.

### Sequence processing and phylogenetic analyses

A total of 30 *COI* sequences were analyzed, including 18 newly obtained sequences from this study; eight sequences representing eight *Allacta* species downloaded from GenBank; and four sequences represent the outgroup from four genera (*Margattea* Shelford, 1911, *Sorineuchora* Caudell, 1927, *Balta* Tepper, 1893 and *Shelfordina* Hebard, 1929) of Pseudophyllodromiidae (Table 1). Sequences were assembled and aligned using Geneious Prime 2023.1.2 (Kearse et al. 2012) and MEGA 7.0 (Kumar et al. 2007), respectively. Intraspecific and interspecific genetic divergences were computed using MEGA 7.0 based on the Kimura 2-parameter (K2P) distance model (Kimura 1980). A Maximum likelihood (ML) tree was constructed in PhyloSuite v.1.2.2 (Zhang et al. 2020), using IQ-TREE v.2.2.0 (Minh et al. 2020) with 1000 standard bootstrap replicates. The GTR+F+I+G4 model was selected by ModelFinder (Kalyaanamoorthy et al. 2017) according to the corrected Akaike Information Criterion (AICc). For ABGD (Puillandre et al. 2012), we used the Jukes-Cantor (JC69) model with a relative gap width X = 1.0, and the rest of parameters set to default (website: https://bioinfo.mnhn.fr/abi/public/abgd/).

## Results

ML analysis clustered females together with morphologically similar males. We identified 11 morphospecies of *Allacta* on the basis of morphological characters, mainly body color, pronotum pattern, head features, legs, wing venation and male genitalia (Fig. 1A), of which, four new morphological species were identified (four branches with red, yellow, green and blue highlights in Fig. 1). All *Allacta* species were divided into 12 molecular operational taxonomic units (MOTUs) by ABGD analysis as indicated by the pink bar (Fig. 1B). Taxonomic results were identical between morphological delimitation and ABGD except the branch highlighted with blue color, which is a single morphospecies but divided into two MOTUs by ABGD.

### Taxonomy

#### *Allacta* Saussure & Zehntner, 1895

**Diagnosis.** The characteristics of the external structure and male genitalia were given in full in Roth (1993b) and He et al. (2019). The following are supplements or adjustments. Tegmina and wings usually fully developed, sometimes reduced (*A. bifolium* Li & Wang, sp. nov. and *A. redacta* Li & Wang, sp. nov.). Subgenital plate usually with two styli, a few with one stylus (*A. unicaudata* Li & Wang, sp. nov.).

**Remarks.** Species of *Allacta* from China were listed by He et al. (2019); three belong to the *hamifera* species group (*A. alba*, *A. bimaculata* and *A. bruna*) and the remaining four belong to the *polygrapha* species group (*A. ornata*, *A. robusta*, *A. transversa* and *A. xizangensis*) (Roth 1993b; Wang et al. 2014; He et al. 2019). The five new species are placed in the *hamifera* species group by the male interstylar margin being broadly V-shaped (Roth 1993b).

**Table 1.** Samples used in this study.

| Species | Voucher ID | GenBank accession number | Collection information |
|---|---|---|---|
| **ingroup** | | | |
| *A. bimaculata* | | OQ736904 | Menglun, Yunnan, China |
| | 5002287 | PP133869 | Menglun, Yunnan, China |
| | 5002288 | PP133870 | Menglun, Yunnan, China |
| | 5002329, F | PP133873 | Menglun, Yunnan, China |
| | 5002286 | PP133874 | Menglun, Yunnan, China |
| *A. transversa* | | OQ736996 | Wuzhishan, Hainan, China |
| | 5002314, F | PP133872 | Jianfengling, Hainan, China |
| *A. bruna* | | OQ736905 | Puer, Yunnan, China |
| | 5002343, F | PP133875 | Jianfengling, Hainan, China |
| | 5002342, F | PP133876 | Jianfengling, Hainan, China |
| *A. xizangensis* | | OQ736995 | Linzhi, Xizang, China |
| | 5002302, F | PP133871 | Linzhi, Xizang, China |
| *A. robusta* | | OQ736903 | Limushan, Hainan, China |
| | 5002282, F | PP133867 | Puer, Yunnan, China |
| | 5002308, F | PP133868 | Puer, Yunnan, China |
| *A. ornata* | | KY349665 | |
| *A. australiensis* | | MG882127 | |
| *A. redacta* sp. nov. | 5002334 | PP133862 | Honghe, Yunnan, China |
| *A. unicaudata* sp. nov. | 5002289, F | PP133863 | Honghe, Yunnan, China |
| | 5002291, F | PP133866 | Honghe, Yunnan, China |
| | 5002290 | PP133865 | Honghe, Yunnan, China |
| *A. lunulara* sp. nov. | 5015272, F | PP133864 | Chuxiong, Yunnan, China |
| *A. bifolium* sp. nov. | 5002309 | PP133860 | Baoshan, Yunnan, China |
| *A. hemiptera* sp. nov. | 5002310 | PP133861 | Baoshan, Yunnan, China |
| | | OQ736902 | Jianfengling, Hainan, China |
| | 5013913 | PP133877 | Jianfengling, Hainan, China |
| **outgroup** | | | |
| *Margattea concava* | | MW970256 | |
| *Balta vilis* | | KT279743.1 | |
| *Sorineuchora nigra* | | KY349516 | |
| *Shelfordina volubilis* | | KY349562 | |

Note: “F” after voucher number means female sample, without F is male sample.

## Checklist of *Allacta* species from China

### *polygrapha* species group:

*Allacta alba* He, Zheng, Qiu, Che & Wang, 2019: 6. China (Zhejiang).
*Allacta bimaculata* Bey-Bienko, 1969: 858. China (Yunnan, Guangxi).
*Allacta bruna* He, Zheng, Qiu, Che & Wang, 2019: 4. China (Hainan).
*Allacta xizangensis* Wang, Gui, Che & Wang, 2014: 449. China (Xizang).

***hamifera*** **species group:**

*Allacta ornata* Bey-Bienko, 1969: 859. China (Yunnan, Hainan).
*Allacta robusta* Bey-Bienko, 1969: 860. China (Yunnan).
*Allacta transversa* Bey-Bienko, 1969: 859. China (Hainan); Vietnam.
*Allacta bifolium* Li & Wang, sp. nov. China (Yunnan).
*Allacta lunulara* Li & Wang, sp. nov. China (Yunnan).
*Allacta redacta* Li & Wang, sp. nov. China (Yunnan).
*Allacta unicaudata* Li & Wang, sp. nov. China (Yunnan).
*Allacta hemiptera* Li & Wang, sp. nov. China (Hainan).

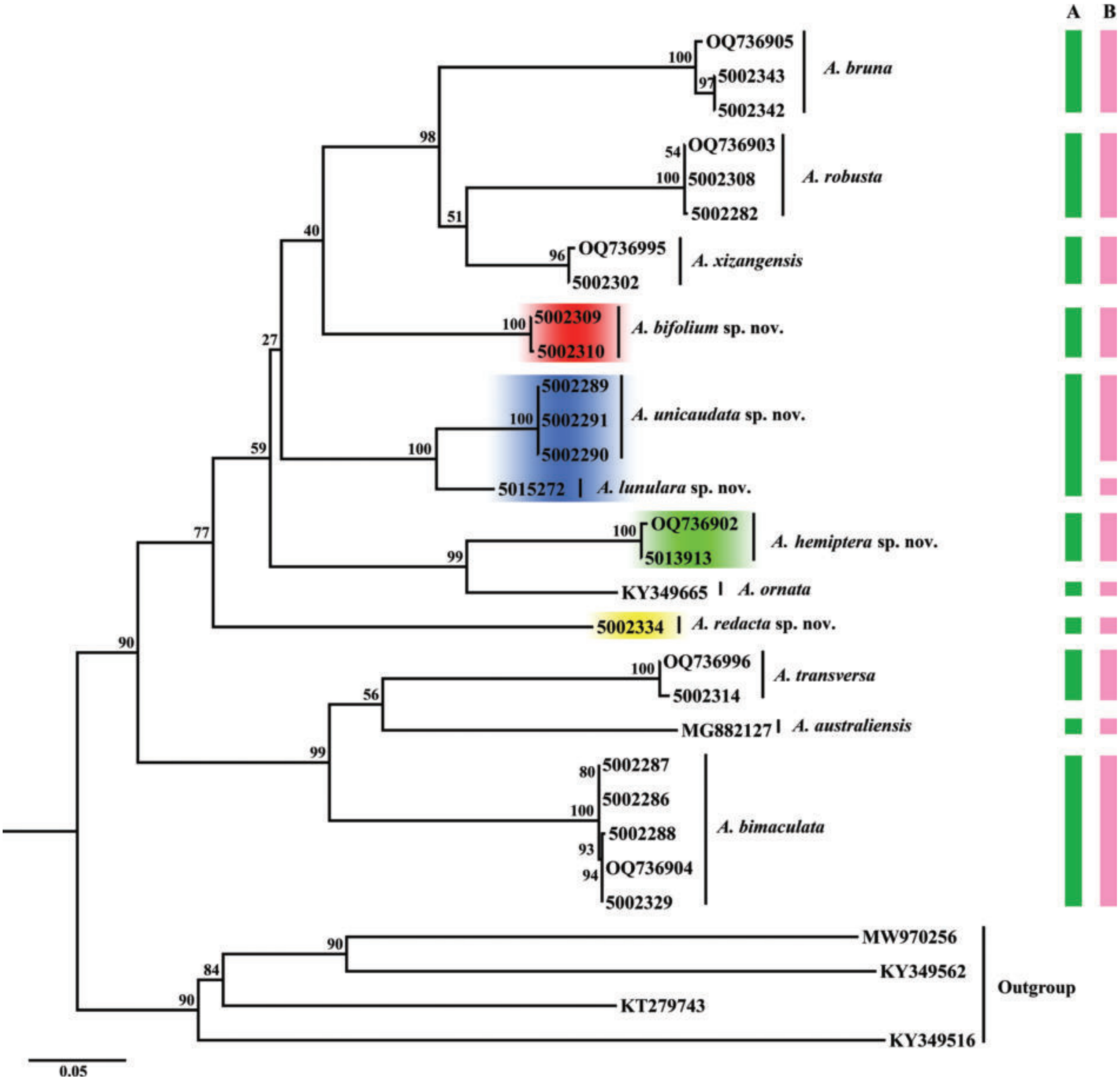

**Figure 1.** Maximum likelihood (ML) tree based on *COI* sequence. Branch node labels are support values. Colored bars indicate different species delimitation by different methods **A** morphology (green) **B** ABGD results (pink). The colored clades (red, yellow, green and blue highlights) on the tree correspond to four new morphological species.

## Key to species of *Allacta* from China

1 Male interstylar margin broadly V-shaped .................... **2** (***hamifera*-group**)

– Male interstylar margin without a keel-like ridge....... **9** (***polygrapha*-group**)

2 Tegmina and hind wings reduced, not reaching end of abdomen ............**3**

– Tegmina and hind wings fully developed, both extending beyond end of abdomen .......................................................................................**5**

3 hind wings absent ...............................................***A. bifolium* sp. nov.**

– hind wings present ......................................................................**4**

4 Body broad, disc of pronotum dark brown with a yellowish vertical stripe in the middle ..................................................... ***A. hemiptera* sp. nov.**

– Body narrow, disc of pronotum dark brown without vertical stripe ............ ...........................................................................***A. redacta* sp. nov.**

5 Head with two dark brown longitudinal stripes reaching from vertex to frons between the antennal sockets, and subgenital plate with dissimilar styli ..................................................***A. robusta* Bey-Bienko, 1969**

– Head with one dark brown longitudinal stripe reaching from vertex to clypeus or not, and subgenital plate with similar styli ...................................**6**

6 Pronotal disk with an inverted triangular yellowish spot in the middle .....**7**

– Pronotal disk without an inverted triangular yellowish spot in the middle..... **8**

7 Face with one vertical wide dark brown stripe..... ***A. ornata* Bey-Bienko, 1969**

– Face with three narrow horizontal dark brown stripes................................ ........................................................***A. transversa* Bey-Bienko, 1969**

8 Female genitalia with third valves asymmetrical and slender rod-shaped .... ........................................................................***A. unicaudata* sp. nov.**

– Female genitalia with third valves symmetrical and broad crescent-shaped ....................................................................***A. lunulara* sp. nov.**

9 Subgenital plate symmetrical...***A. bruna* He, Zheng, Qiu, Che & Wang, 2019**

– Subgenital plate asymmetrical ...................................................................**10**

10 Pronotal disc brown without maculae ...... ***A. bimaculata* Bey-Bienko, 1969**

– Pronotal disc with maculae .......................................................................**11**

11 Pronotal disc with trapezoidal symmetrical white maculae........................ .................................................. ***A. alba* He, Zheng, Qiu, Che & Wang, 2019**

– Pronotal disc without large trapezoidal shaped white maculae posteriorly.... ................................................. ***A. xizangensis* Wang, Gui, Che & Wang, 2014**

### *Allacta bifolium* Li & Wang, sp. nov.

https://zoobank.org/1175CE1D-9C23-4CC9-9EE9-28A2677B9FD3
Fig. 2A–M

**Type material (All in SWU).** ***Holotype*:** China • male; Yunnan Prov., Baoshan City, Baihualing; 1253 m; 24 Aug., 2015; Xin-Ran Li, Zhi-Wei Qiu leg. ***Paratypes*:** China • 3 males; same data as holotype; 1 male, Yuxi City, Xinping County, Mount Ailao, 1933 m, 12 May, 2016, Lu Qiu, Zhi-Wei Qiu leg.

**Diagnosis.** This species can be easily distinguished from its congeners by the small leaf-shaped tegmina, the absence of hind wings as well as the right side of the right stylus with a long, finger-like protrusion.

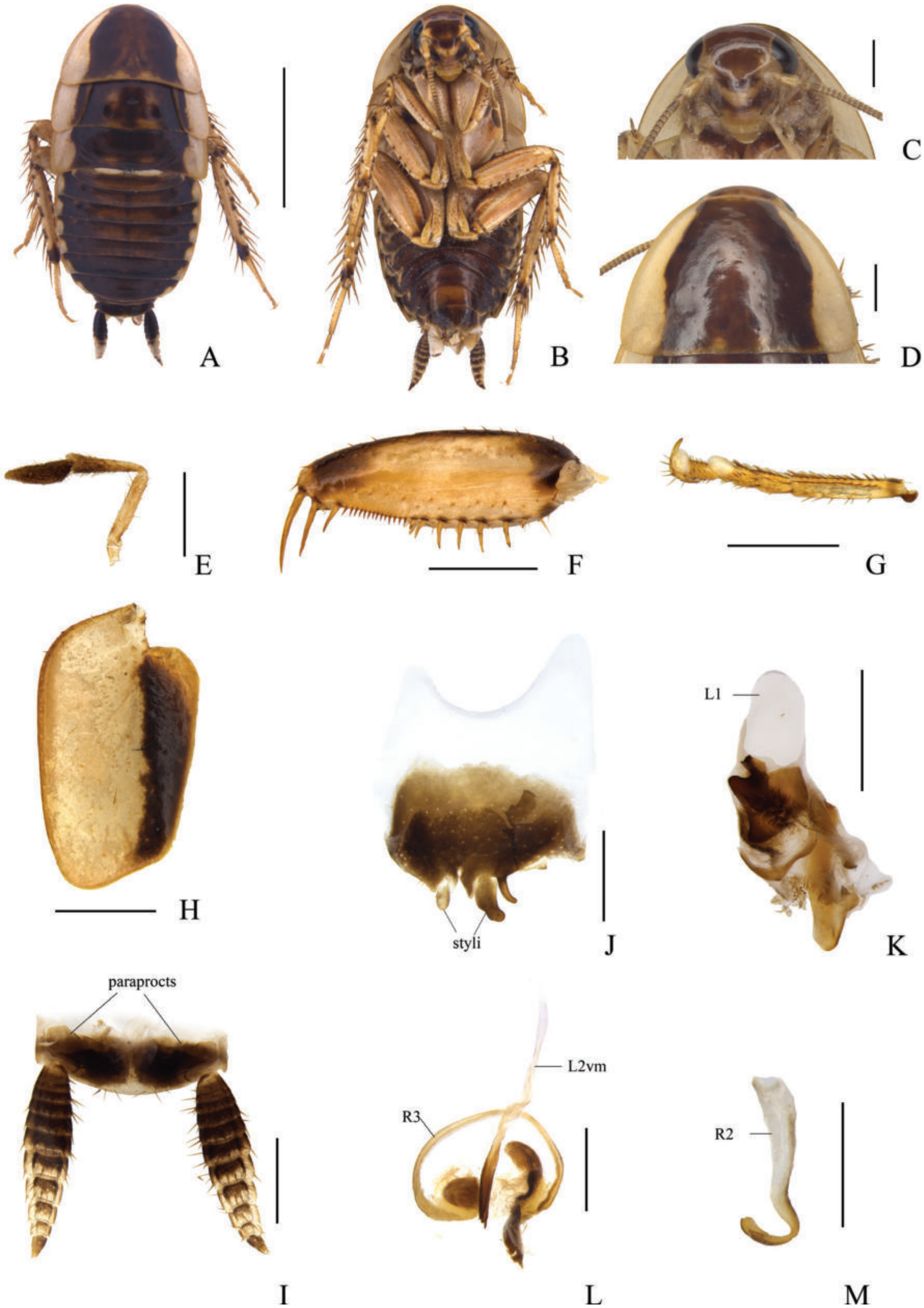

**Figure 2.** *Allacta bifolium* sp. nov., male holotype **A** dorsal view **B** ventral view **C** head, ventral view **D** pronotum, dorsal view **E** maxillary palpi, ventral view **F** front femur, ventral view **G** tarsus and tarsal claws of front leg **H** tegmen, dorsal view **I** supra-anal plate and paraprocts, ventral view **J** subgenital plate, dorsal view **K** left phallomere, dorsal view **L** median phallomere, dorsal view **M** hook-like phallomere, dorsal view. Scale bars: 5 mm (**A, B**); 1 mm (**C–M**).

**Measurements (mm).** Male, pronotum length × width: 3.1–3.2 × 4.9–5.2, tegmina length: 1.9–2.3, overall length: 11.2–12.5.

**Description. Male.** Body dark brown (Fig. 2A, B). Face brown with a yellowish-brown transverse crescent band below antennal sockets (Fig. 2C). Lateral portions of thorax yellowish brown, including pronotum, mesonotum and metanotum as well as most of the tegmina (Fig. 2A). Tibiae yellowish brown with base dark brown. Cerci dorsally with basal half blackish brown, terminal parts yellowish brown; each segment ventrally with basal half dark brown and apical half light brown.

Vertex with interocular space greater than the distance between antennal sockets. The third, and fourth maxillary palpi of approximately the same length, slightly longer than the fifth (Fig. 2E). Pronotum subparabolic with hind margin nearly straight. Tegmina greatly reduced (Fig. 2H), slightly surpass mesonotum, without veins. Hind wings absent. Anteroventral margin of front femur Type $B_3$ (Fig. 2F). Pulvillus only present on the fourth tarsomere (Fig. 2G). Tarsal claws symmetrical and unspecialized, arolia present.

***Male abdomen and genitalia*.** Abdominal terga unspecialized. Supra-anal plate short, symmetrical, and hind margin arc-shaped. Paraprocts simple and plate-like (Fig. 2I). Subgenital plate asymmetrical with two styli arising in two concavities of hind margin. The right stylus longer than the left; the right cylindrical with a finger-like projection on right side; the left stylus nearly elliptical (Fig. 2J). The interstylar margin broadly V-shaped. Left phallomere complex (Fig. 2F). Median phallomere (L2vm) stem slender rod-like, slightly curved, apex blunt round with several small spines, base sharp with a large spine subsidiary sclerite; median phallomere subsidiary sclerite (R3) C-shaped clavate (Fig. 2L). Hooked phallomere (R2) on the right of subgenital plate, with pre-apical incision (Fig. 2M).

**Etymology.** The Latin words *bi*- means pair, double, and *folium* means leaf, referring to the tegmina being degenerated into small leaf-like structures and hind wings absent.

**Distribution.** China (Yunnan).

### *Allacta redacta* Li & Wang, sp. nov.

https://zoobank.org/43882093-F05A-47B2-8072-E08C323B0FEB
Fig. 3A–M

**Type material.** ***Holotype*:** China • male (SWU); Yunnan Prov., Pingbian County, Mount Dawei; 1496 m; 15 May, 2016; Lu Qiu, Zhi-Wei Qiu leg.

**Diagnosis.** This species can be easily distinguished from its congeners by the wings being reduced and the pronotal disk with a brownish mushroom-shape marking.

**Measurements (mm).** Male, pronotum length × width: 3.3 × 4.5, tegmina length: 4.5, overall length: 13.5.

**Description. Male.** Body medium-sized, yellowish brown (Fig. 3A, B). Face yellowish brown with a large brown crescent band; antennae brownish yellow, darkening apically; the fifth maxillary palpus brown, the rest brownish yellow (Fig. 3C). Pronotum dark brown, lateral borders and posterolateral corners of pronotum pale yellowish brown (Fig. 3D). Tegmina yellowish brown. Abdomen

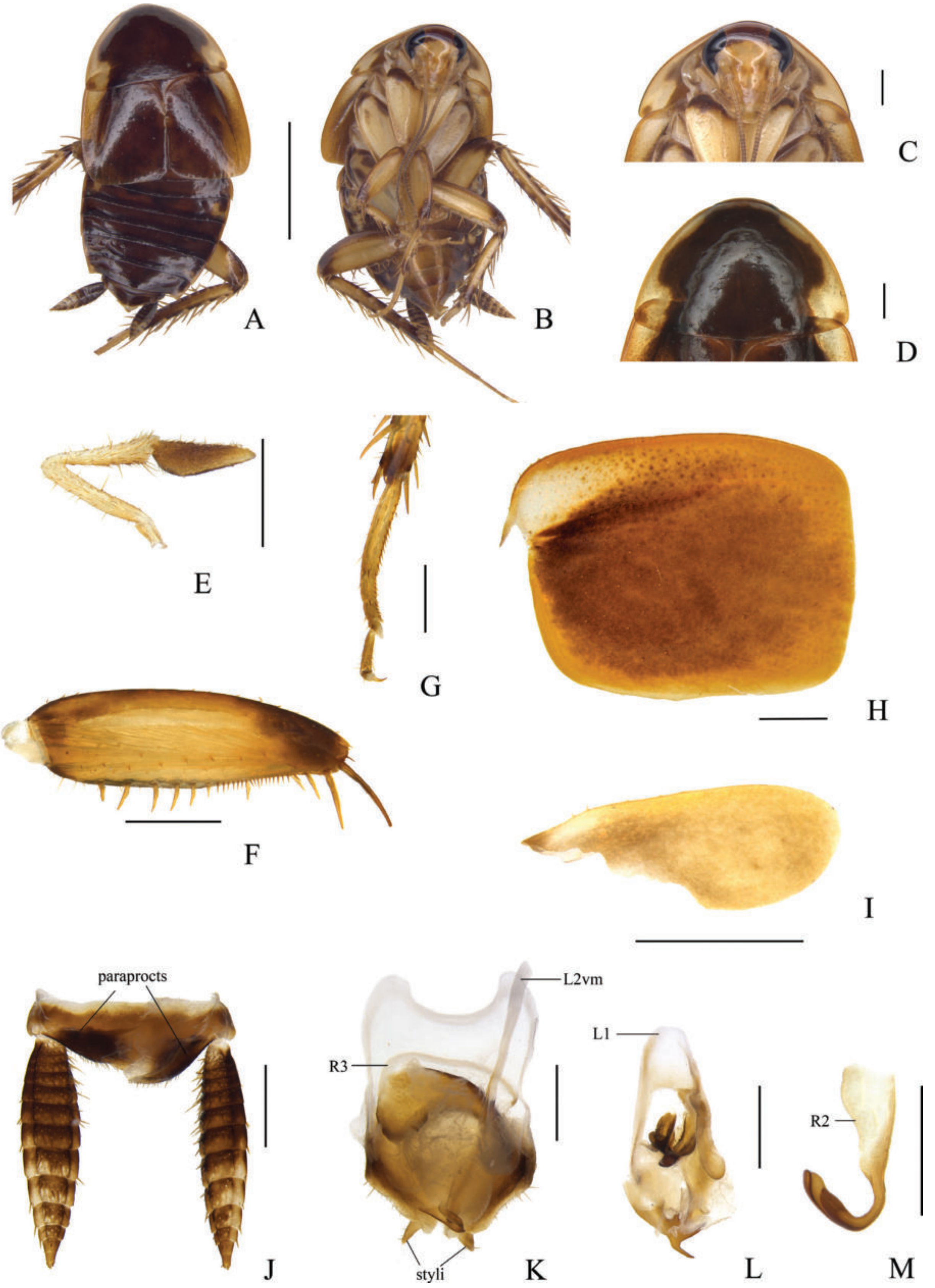

**Figure 3.** *Allacta redacta* sp. nov., male holotype **A** dorsal view **B** ventral view **C** head, ventral view **D** pronotum, dorsal view **E** maxillary palpi, ventral view **F** front femur, ventral view **G** tarsus and tarsal claws of front leg **H** tegmen, dorsal view **I** hind wing, dorsal view **J** supra-anal plate and paraprocts, ventral view **K** subgenital plate and median phallomere, dorsal view **L** left phallomere, dorsal view **M** hook-like phallomere, dorsal view. Scale bars: 5 mm (**A, B**); 1 mm (**C–M**).

terga reddish brown, lateral border light brown; sterna brownish yellow. Subgenital plate with posterior half brown (Fig. 3K). Cerci black in basal half of dorsal surface, and yellowish brown ventrally. Legs brownish yellow, coxae darker, tibiae yellowish with spines attachment area brown (Fig. 3J).

Vertex with interocular space greater than distance between antennal sockets. Pronotum subparabolic with hind margins nearly straight (Fig. 3D). The third and fourth maxillary palpi of approximately same length, slightly longer than the fifth (Fig. 3E). Tegmina and hind wings reduced, tegmina reach anterior edge of the second abdominal tergite; hind wings reach nearly two-thirds length of metanotum, width approximately one-tenth of tegmina (Fig. 3H, I). Anteroventral margin of front femur Type $B_3$ (Fig. 3F). Pulvillus only present on the fourth tarsomere (Fig. 3G). Tarsal claws symmetrical and unspecialized, arolia present.

***Male abdomen and genitalia*.** Abdominal terga unspecialized. Supra-anal plate short, nearly triangular, symmetrical, with hind margin blunt round. Paraprocts simple and plate-like, with scattered setae on distal margin (Fig. 3J). Subgenital plate slightly asymmetrical, styli nearly elliptical, arising from the posterior margin concavities, right stylus slightly larger than the left, interstylar margin with broadly V-shaped notch (Fig. 3K). Left phallomere complex (Fig. 3L). Median phallomere (L2vm) stem slender, rod-like, apex blunt round with several small spines, with fine spines and bifurcation at three-quarters from base; median phallomere subsidiary sclerite (R3) C-shaped (Fig. 3K). Hooked phallomere (R2) on the right of subgenital plate, with V-shaped incision (Fig. 3M).

**Etymology.** The specific name *redacta* derived from Latin, refers to both the tegmina and hind wings being reduced, which do not reach half the length of the normal wings of its congeners.

**Distribution.** China (Yunnan).

### *Allacta unicaudata* Li & Wang, sp. nov.

https://zoobank.org/6DFBFA71-EF72-470D-A851-F135D668408D
Fig. 4A–Q

**Type material (All in SWU).** ***Holotype*:** China • male; Yunnan Prov., Pingbian County, Mount Dawei; 1496 m; 15 May, 2016; Lu Qiu, Zhi-Wei Qiu leg. ***Paratypes*:** China • 1 male and 1 female, same data as holotype.

**Diagnosis.** This species can be easily distinguished from all congeners by the absence of the left stylus in males, except for *Allacta lunulara* sp. nov., of which males are unknown (see below for females). This species shares a similar appearance with *A. lunulara* sp. nov., but it can be differentiated from the latter mainly by the following characters of the female genitalia: 1) third valves asymmetrical and slender rod-shaped, while symmetrical and broad crescent-shaped in *A. lunulara*; 2) posterior half of basivalvula narrower than the basal half, while basivalvula oval-shaped in *A. lunulara*; 3) spermatheca plate rounded with a sharp protrusion in the middle of the spermatheca plate, while front margin of spermatheca plate truncated in *A. lunulara*; and 4) laterosternal shelf asymmetrical, narrow, long and slightly curved, while symmetrical, broad and triangular in *A. lunulara*.

**Measurements (mm).** Male, pronotum length × width: 3.7–4.0 × 5.5–5.9, tegmina length: 10.9–12.6, overall length: 14.9–16.0; female, pronotum

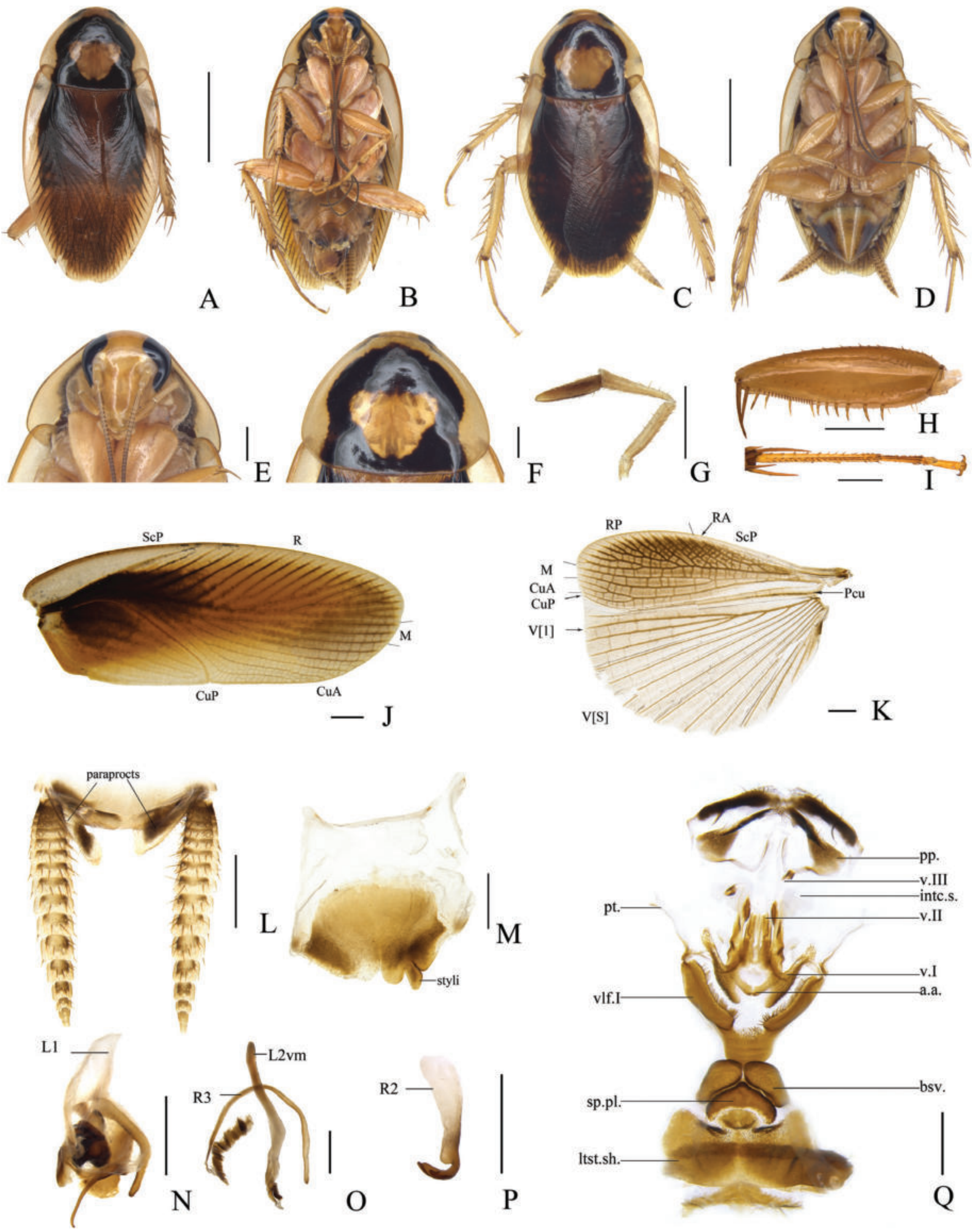

**Figure 4.** *Allacta unicaudata* sp. nov., male holotype **A** dorsal view **B** ventral view **C** paratype (female), dorsal view **D** paratype (female), ventral view **E** head, ventral view **F** pronotum, dorsal view **G** maxillary palpi, ventral view **H** front femur, ventral view **I** tarsus and tarsal claws of front leg **J** tegmen, dorsal view **K** hind wing, dorsal view **L** supra-anal plate and paraprocts, ventral view **M** subgenital plate, dorsal view **N** left phallomere, dorsal view **O** median phallomere, dorsal view **P** hook-like phallomere, dorsal view **Q** female subgenital plate, dorsal view. Scale bars: 5 mm (**A–D**); 1 mm (**E–Q**). Abbreviations: **a.a.** anterior arch, **bsv.** basivalvula, **intc.s.** intercalary sclerite, **ltst.sh.** laterosternal shelf, **pp.** paraprocts, **pt.** paratergites, **sp.pl.** spermathecal plate, **vlf.I** first valvifer, **v.I** first valves, **v.II** second valves, **v.III** third valves. For vein abbreviations see Material and methods.

length × width: 3.7–4.4 × 4.6–5.7, tegmina length: 9.2–11.4, overall length: 11.5–14.7.

**Description. Male.** Body yellowish brown (Fig. 4A–D). Head yellow with ocelli white, frons with a yellowish-brown longitudinal stripe (Fig. 4E). The third and fourth maxillary palpi dark yellow, and the fifth maxillary palpus brown (Fig. 4G). Antennae yellowish brown, darkening apically. Lateral borders and front margin of pronotum translucent yellowish, a dark yellow inverted triangular pattern in the middle (Fig. 4F). Tegmina yellowish orange, clearly uneven in color with radial field, mediocubital field, and anal field darkening basally. Hind wings pale brown (Fig. 4J, K). Legs yellowish brown. Subgenital plate with posterior half grayish yellow (Fig. 4M). Cerci yellowish brown, with basal segment darker (Fig. 4L).

Vertex with interocular space narrower than distance between antennal sockets. The third and fourth maxillary palpi slightly longer than the fifth (Fig. 4G). Pronotum subparabolic with hind margins truncated (Fig. 4F). Tegmina and hind wings fully developed, both extending beyond the end of abdomen. Tegmina slender, with M and CuA longitudinal, CuA with four branches (Fig. 4J). M of hind wings with two branches, CuA curved with three complete branches (Fig. 4K). Anteroventral margin of front femur Type $B_3$ (Fig. 4H). Pulvillus only present on the fourth tarsomere. Tarsal claws symmetrical and unspecialized, arolium present.

***Male abdomen and genitalia*.** Abdominal terga unspecialized. Supra-anal plate short, symmetrical, with hind margin slightly concave. Paraprocts simple and plate-like (Fig. 4L). Subgenital plate asymmetrical with a V-shaped notch at the interstylar margin, without left stylus, right stylus cylindrical arising in a concavity of the hind margin near right posterolateral corner (Fig. 4M). Left phallomere complex (Fig. 4N). Median phallomere (L2vm) stem slender, rod-like, slightly curved, apex bluntly round with a small spine; median phallomere subsidiary sclerite (R3) C-shaped, apex sharp with a brush-like structure (Fig. 4O). Hooked phallomere (R2) on the right of subgenital plate, with pre-apical incision (Fig. 4P).

***Female genitalia*.** Supra-anal plate nearly symmetrical. Paraprocts broad. Intercalary sclerite irregular plate-shaped and translucent. First valves robust, with inward protrusions. Second valves small. Third valves asymmetrical, slender rod-shaped, and the left branch obviously curved outward. The anterior margin of anterior arch slightly sclerotized. First valvifer long and narrow plate-like with setae on the inside. Basivalvula spindle-shaped, wide in the middle and tapers at both ends. Laterosternal shelf asymmetrical, narrow, long and slightly curved. Front margin of spermathecal plate rounded with a sharp protrusion in the middle. The spermatheca lobe forked, the end of one spermatheca branch enlarged, and the other long and tubular (Fig. 4R, S).

**Remarks.** This species resembles *A. alba*, but it can be differentiated from the latter by the following characters: 1) pronotal disc with an inverted triangular yellowish spot, while with subtrapezoidal symmetrical white markings in *A. alba*; 2) tegmina and hind wings slightly extending beyond the end of the abdomen, while extending far beyond the end of the abdomen in *A. alba*; and 3) subgenital plate without left stylus, while with two styli in *A. alba*. This species is placed in the *hamifera* species group by having the male interstylar margin broadly V-shaped.

**Etymology.** The Latin words *uni*- meaning one, single, and *caudata* meaning tailed, referring to subgenital plate with only one stylus.

**Distribution.** China (Yunnan).

### ***Allacta lunulara*** Li & Wang, sp. nov.

https://zoobank.org/B362287A-A0F7-4723-9E99-1EE39F9CE78A
Fig. 5A–L

**Type material (All in SWU).** ***Holotype*:** China • female; Yunnan Prov., Chuxiong City, Mount Zixi; 2239 m; 31 Jul., 2022; Lin Guo, Wei Han leg. ***Paratype*:** China • 1 female, same data as holotype.

**Diagnosis.** This species resembles *A. unicaudata*, but it can be differentiated from *A. unicaudata* mainly by the symmetrical and crescent-shaped third valves.

**Measurements (mm).** Female, pronotum length × width: 3.3–3.4 × 4.8–5.2, tegmina length: 8.5–9.0, overall length: 11.6–12.2.

**Description. Female.** Body yellowish brown (Fig. 5A, B). Head yellow with ocelli white; stripe between the eyes dark brown. Maxillary palpi light brown. Antennae yellowish brown (Fig. 5C). Lateral borders and front margin of pronotum translucent yellowish; an inverted triangular yellowish spot in the middle (Fig. 5D). Tegmina yellowish brown, and hind wings light brown (Fig. 5H, I). Legs yellowish brown.

Vertex with interocular space narrower than distance between antennal sockets (Fig. 5C). The third and fourth maxillary palpi of approximately same length, slightly longer than the fifth (Fig. 5E). Pronotum subparabolic with hind margins truncated (Fig. 5D). Tegmina and hind wings fully developed, both extending beyond the end of abdomen. Tegmina slender, with M and CuA longitudinal, CuA with four branches. M of hind wings with three branches, CuA curved with three complete branches (Fig. 5H, I). Anteroventral margin of front femur Type $B_3$ (Fig. 5F). Pulvilli only present on the fourth tarsomere. Tarsal claws symmetrical and unspecialized, arolium present.

***Female genitalia*.** Supra-anal plate nearly symmetrical. Paraprocts broad, not extending to the posterior margin of supra-anal plate. Intercalary sclerite irregular plate-shaped and translucent. First valves robust, with inward protrusions. Second valves small. Third valves symmetrical and broad crescent-shaped. The anterior margin of anterior arch slightly sclerotized. First valvifer long and narrow plate-like with setae on the inside. Basivalvula oval-shaped. Laterosternal shelf symmetrical, broad and triangle. Front margin of spermathecal plate truncated. The spermatheca lobe forked, the end of one spermatheca branch enlarged, and the other long and tubular (Fig. 5K, L).

**Remarks.** This species was found to be a cryptic species, very similar to *A. unicaudata* Li & Wang, sp. nov. but it can be differentiated from *A. unicaudata* by the female genitalia characters aforementioned. In this study, after comparing the female genitalia in five *Allacta* species, it is confirmed that the variation in female genitalia can be applied to identify the species of *Allacta*. The *COI* divergence between them (6.6%) is significantly larger than the usual intraspecies distance in *Allacta* (Suppl. material 1). This species is placed in the *hamifera* species group by having a dark pronotum.

**Etymology.** The specific epithet is derived from the Latin word *lunulara* which means moon-like or relating to a crescent shape, referring to its crescent-shaped third valves.

**Distribution.** China (Yunnan).

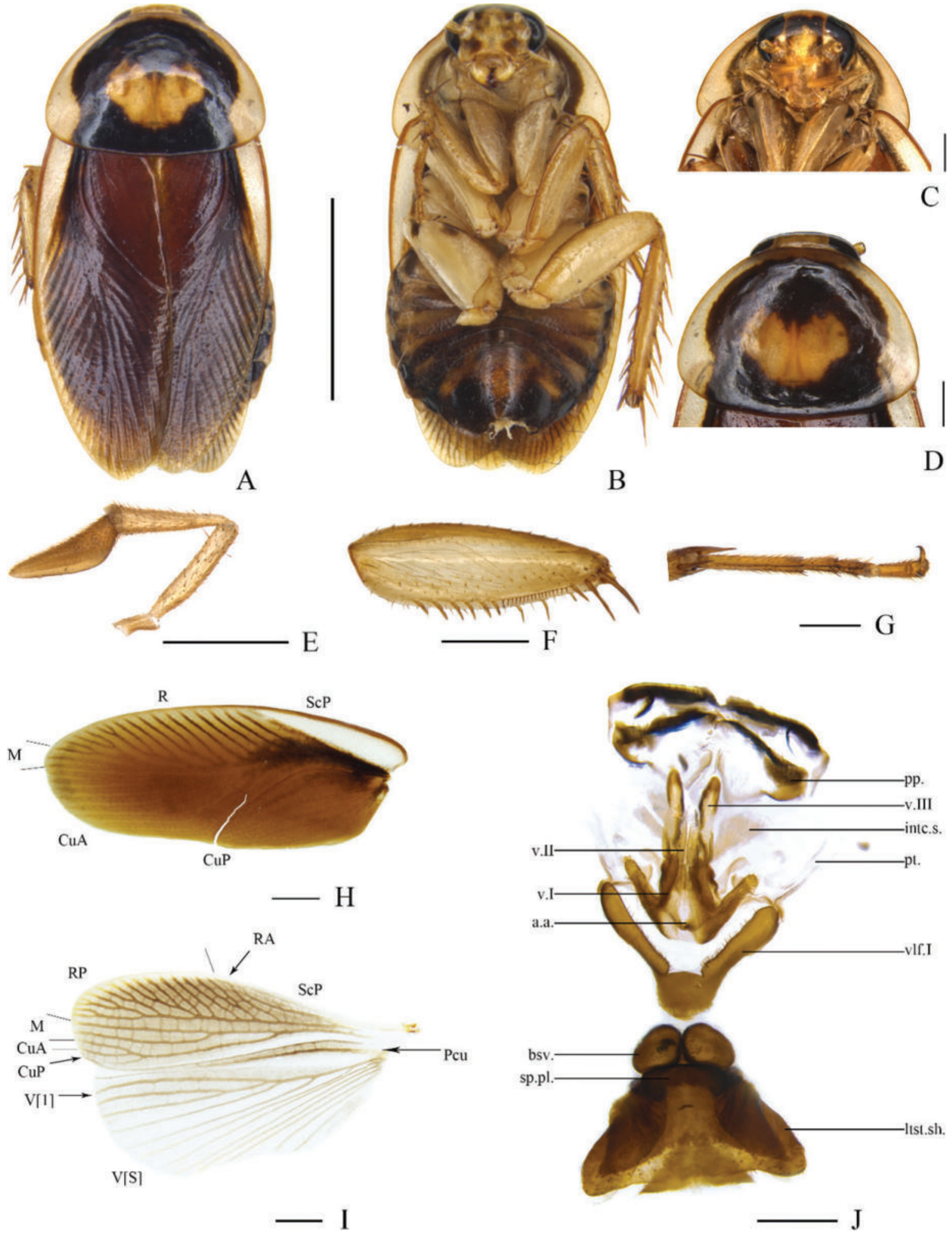

**Figure 5.** *Allacta lunulara* sp. nov., female holotype **A** dorsal view **B** ventral view **C** head, ventral view **D** pronotum, dorsal view **E** maxillary palpi, ventral view **F** front femur, ventral view **G** tarsus and tarsal claws of front leg **H** tegmen, dorsal view **I** hind wing, dorsal view **J** subgenital plate, dorsal view **K** supra-anal plate, dorsal view **L** supra-anal plate, ventral view. Scale bars: 5 mm (**A, B**); 1 mm (**C–L**). Abbreviations: **a.a.** anterior arch, **bsv.** basivalvula,**intc.s.** intercalary sclerite, **ltst.sh.** laterosternal shelf, **pp.** paraprocts, **pt.** paratergites, **sp.pl.** spermathecal plate, **vlf.I** first valvifer, **v.I** first valves, **v.II** second valves, **v.III** third valves. For vein abbreviations see Materials and methods.

### ***Allacta hemiptera*** **Li & Wang, sp. nov.**

https://zoobank.org/3F418EF5-5850-420B-AFCE-CE43A91514FF
Fig. 6A–O

*Temnopteryx hainanensis* Liu et al., 2017: 179 (*nomen nudum*); Qin and Liu 2019: 175.
*Allacta hainanensis*: He et al. 2019: 8.

**Type material.** ***Holotype*:** China • male (SWU); Hainan Prov., Ledong County, Mount Jianfeng; 997 m; 16 Apr., 2015; Lu Qiu leg. ***Paratypes*:** China • 1 male (SEM); Hainan Prov., Changjiang County, Mount Bawang; 1495 m; 22 Sep., 2011; Xian-Wei Liu leg • 1 male (SWU); Hainan Prov., Ledong County, Mount Jianfeng; 1050 m; 6 Jul., 2007; Wei-Wei Zhang leg • 1 female (SWU); Hainan Prov., Ledong County, Mount Jianfeng; 997 m; 16 Apr., 2015; Lu Qiu leg • 3 males & 5 females (SWU); Hainan Prov., Qiongzhong County, Limushan Stone Forest; 585 m; 12 Jul., 2023; Wen-Bo Deng leg • 3 females (SWU); Hainan Prov., Qiongzhong County, Quling Valley; 662 m; 11 Jul., 2023; Yi-Shu Wang leg.

**Diagnosis.** This species resembles *A. redacta*, but it can be differentiated from *A. redacta* mainly by the pronotal disk with a nib-shaped yellowish spot.

**Measurements (mm).** Male, pronotum length × width: 4.3–4.6 × 6.9–7.4, tegmina length: 5.5–5.7, overall length: 17.0–17.2; female, pronotum length × width: 4.0–4.4 × 6.5–7.4, tegmina length: 5.3–5.8, overall length: 16.9–17.2.

**Description. Male.** Body dark brown (Fig. 6A, B). Face brown with dark brown stipples and spots in the middle (Fig. 6D). Antennae brown. The fifth maxillary palpi brown, the rest yellowish brown. Lateral borders and front margin of pronotum translucent yellowish; a nib-shaped yellowish spot in the middle (Fig. 6C). Tegmina brown, lateral borders translucent (Fig. 6I). Legs yellowish brown. Cerci yellowish brown, with basal dark brown (Fig. 6L).

Vertex with interocular space obviously narrower than distance between antennal sockets (Fig. 6D). The third and fourth maxillary palpi of approximately same length, slightly longer than the fifth (Fig. 6E). Pronotum nearly triangle with front margins blunt round and hind margins truncated (Fig. 6C). Tegmina and hind wings reduced. Tegmina nearly quadrilateral, veins not obvious. Hind wings small, thin and transparent, about half the length of tegmina (Fig. 6I, J). Anteroventral margin of front femur Type $B_3$ (Fig. 6F). Pulvilli only present on the fourth tarsomere. Tarsal claws symmetrical and unspecialized, arolium present (Fig. 6G).

***Male abdomen and genitalia*.** Abdominal terga unspecialized. Supra-anal plate short, nearly triangular, symmetrical, with incision at the middle of hind margin. Paraprocts simple and plate-like, with scattered setae on distal margin (Fig. 6L). Subgenital plate symmetrical, lateral margins round and styli nearly cylindrical, arising from the posterior margin concavities, right stylus slightly larger than the left, interstylar margin with W-shaped notch (Fig. 6K). Left phallomere complex (Fig. 6M). Median phallomere (L2vm) stem slender, rod-like, apex sharp, with a crack at quarter from base; median phallomere subsidiary sclerite (R3) C-shaped rod-like (Fig. 6N). Hooked phallomere (R2) on the right of subgenital plate, with V-shaped incision (Fig. 6O).

***Female genitalia*.** Supra-anal plate nearly symmetrical. Paraprocts broad, not extending to the posterior margin of supra-anal plate. Intercalary sclerite irreg-

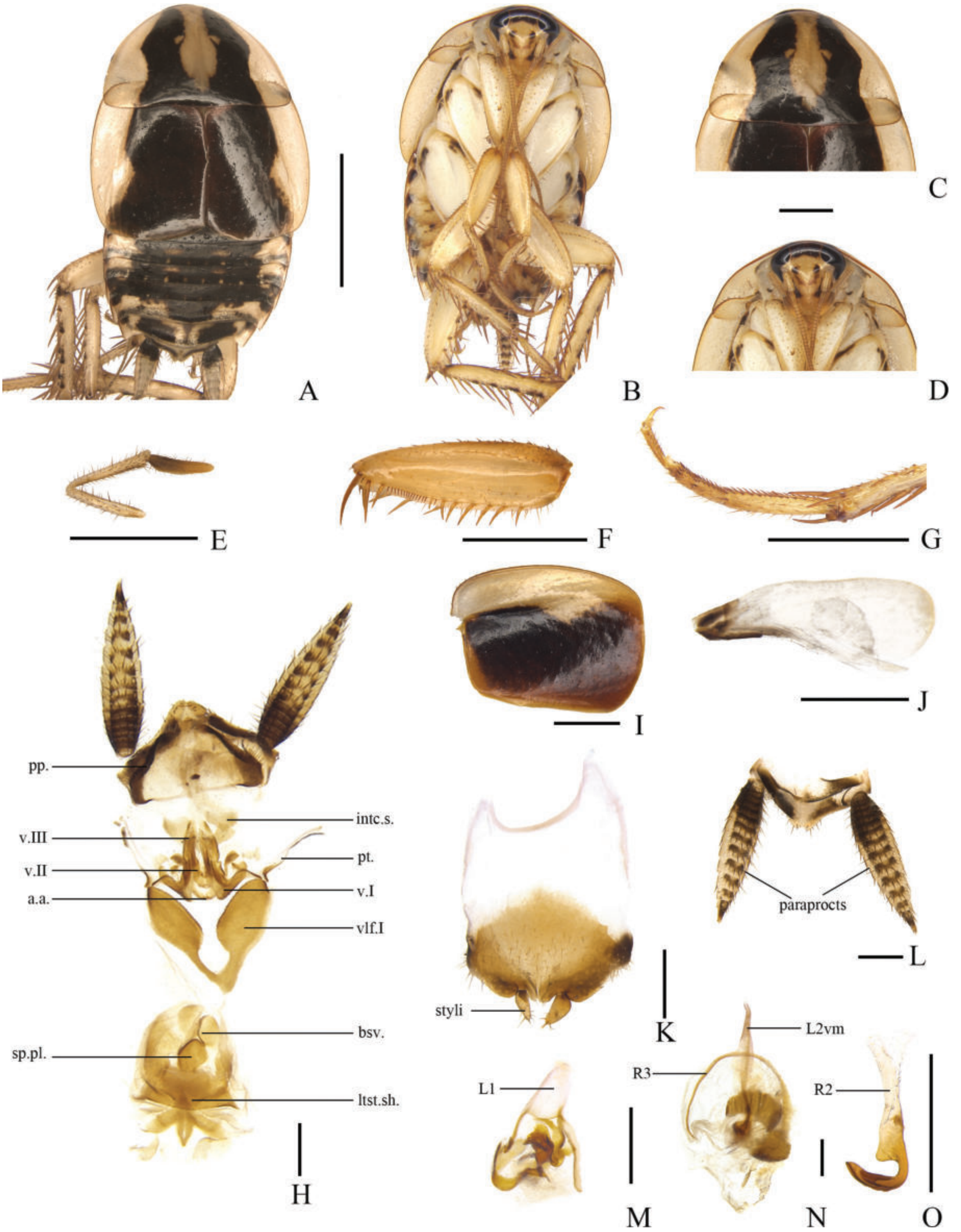

**Figure 6.** *Allacta hemiptera* sp. nov., male holotype **A** dorsal view **B** ventral view **C** pronotum, dorsal view **D** head, ventral view **E** maxillary palpi, ventral view **F** front femur, ventral view **G** tarsus and tarsal claws of front leg **H** female subgenital plate, dorsal view **I** tegmen, dorsal view **J** hind wing, dorsal view **K** subgenital plate, dorsal view **L** supra-anal plate and paraprocts, ventral view **M** left phallomere, dorsal view **N** median phallomere, dorsal view **O** hook-like phallomere, dorsal view. Scale bars: 5 mm (**A, B**); 2 mm (**C–I**); 1 mm (**J–O**). Abbreviations: **a.a.** anterior arch, **bsv.** basivalvula, **intc.s.** intercalary sclerite, **ltst.sh.** laterosternal shelf, **pp.** paraprocts, **pt.** paratergites, **sp.pl.** spermathecal plate, **vlf.I** first valvifer, **v.I** first valves, **v.II** second valves, **v.III** third valves.

ular plate-shaped and translucent. First valves robust, with inward protrusions. Second valves small. Third valves symmetrical and broad rod-shaped. The anterior margin of anterior arch slightly sclerotized. First valvifer irregular swollen and oval with short setae on the inside. Basivalvula oval-shaped. Laterosternal shelf symmetrical, broad and trapezoid. Front margin of spermathecal plate truncated. The spermatheca lobe forked, the end of one spermatheca branch enlarged, and the other long and tubular (Fig. 6H).

**Remarks.** According to the International Code of Zoological Nomenclature (Article 16.4.2) (ICZN 1999), *Temnopteryx hainanensis* Liu et al., 2017 is invalid. He et al. (2019) did not realize that and moved *Temnopteryx hainanensis* to the genus *Allacta*. We here describe it as a new species based on the new material and the type specimens of *Temnopteryx hainanensis* Liu et al., 2017.

**Etymology.** The Latin terms *hemi*- means half, *ptera* means wing, and *hemiptera* means that the tegmina is half the normal wing length.

**Distribution.** China (Hainan).

## Discussion

External characteristics and male genitalia have been traditionally used to define species of *Allacta* (Roth 1993b; Wang et al. 2014; He et al. 2019), but identifying species relied too much on male characteristics. For example, the male genitalia of *A. lunulara* Li & Wang, sp. nov. was not available and therefore could not be used to determine whether it was a new species in this study. As such, we tried to look for morphological divergence in female morphology. We compared the female genitalia of four known species and *A. hemiptera* sp. nov., and found that there were significant differences mainly in valvifer, first valvifer, basivalvula and laterosternal shelf (Figs 6, 7), indicating that female genitalia could be used for identification in *Allacta*.

The clade highlighted in blue (Fig. 1) was divided into two MOTUs. We carefully compared the female external genitalia of these two MOTUs and found evidence that they differed in the third valves, basivalvula, spermatheca plate and laterosternal shelf. According to the material sampled here, the maximum intraspecific genetic distances of *Allacta* for *COI* was 1.1%, but the minimum divergence of these two clades reaches 6.6% (Suppl. material 1). Female genitalia differences combined with this larger genetic distance indicated that specimen 5015272 was not *A. unicaudata* Li & Wang, sp. nov. Therefore, we proposed that it is a new species, *A. lunulara* Li & Wang, sp. nov.

In future research, morphology specific to females should be taken into greater consideration, as it played a key role in the discovery of new species in this study. Sometimes female genitalia can even be used to discover cryptic species, for example, Zhu et al. (2022) distinguished three new cryptic species from *Anaplecta omei* through differences in female genitalia.

In this study, the absence of one stylus in the family Pseudophyllodromiidae was observed for the first time (*A. unicaudata* Li & Wang, sp. nov.), but this is not a unique case in Blattodea (Kumar and Prinis 1978; Roth 1989, 1993a), for example, *Blattella parilis* Walker, 1868, *Symplocodes euryloba* Zheng et al., 2015 and *Symplocodes ridleyi* Shelford, 1913 in Blattellidae; *Pycnoscelus indicus* Fabricius, 1775 and *Pycnoscelus nigra* Brunner von Wattenwyl, 1865 in Blaberidae. However, the causes and mechanisms for this phenomenon remains to be discovered.

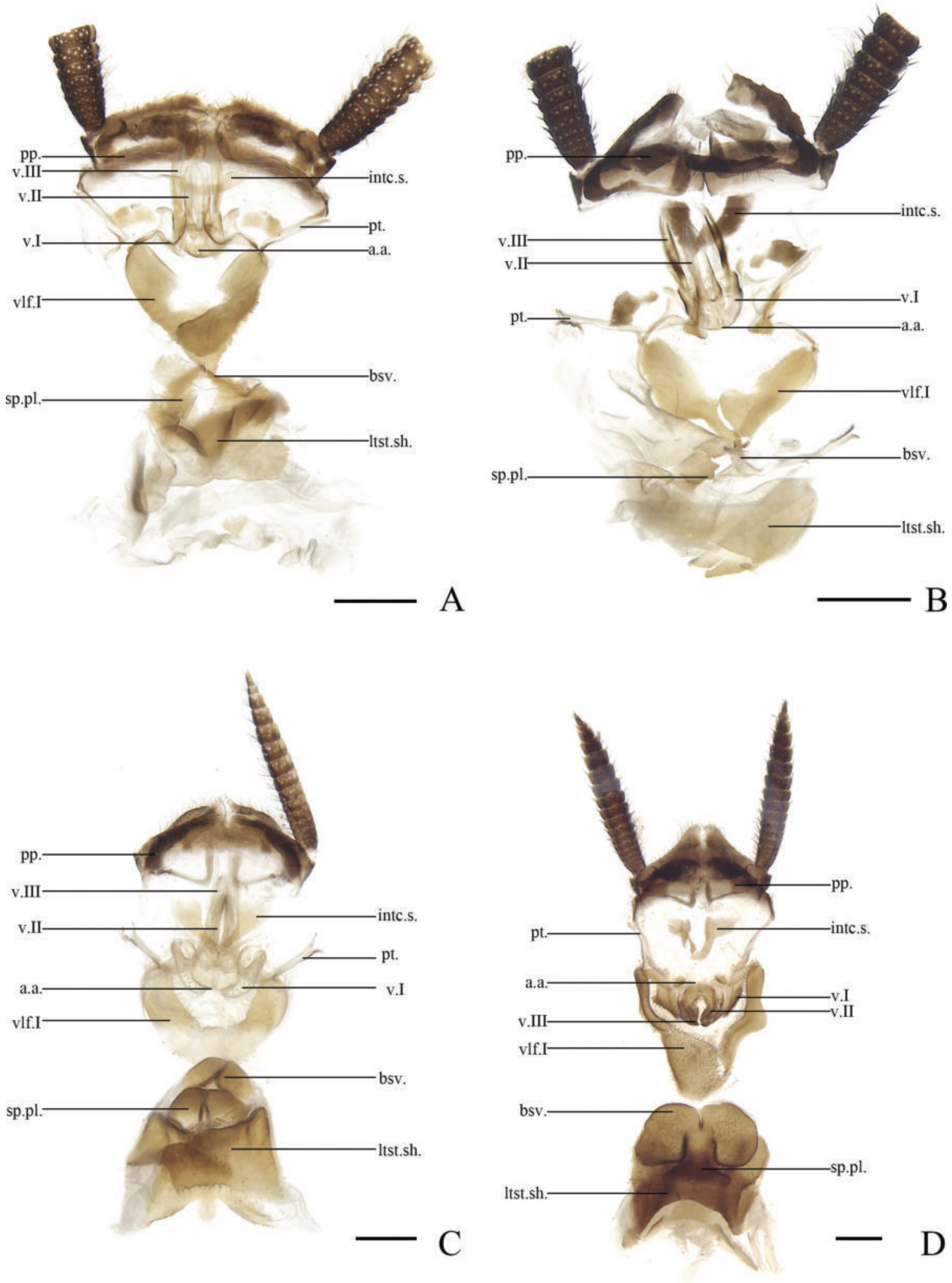

**Figure 7. A** *Allacta transversa* Bey-Bienko, 1969. Female **B** *Allacta bimaculata* Bey-Bienko, 1969. Female **C** *Allacta robusta* Bey-Bienko, 1969. Female **D** *Allacta bruna* He, Zheng, Qiu, Che & Wang, 2019. Female **A–D** supra-anal plate, dorsal view. Scale bars: 1 mm. Abbreviations: **a.a.** anterior arch, **bsv.** basivalvula, **intc.s.** intercalary sclerite, **ltst.sh.** laterosternal shelf, **pp.** paraprocts, **pt.** paratergites, **sp.pl.** spermathecal plate, **vlf.I** first valvifer, **v.I** first valves, **v.II** second valves, **v.III** third valves.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Bianlun Li: Data curation (equal); methodology (lead); visualization (equal); writing – original draft (lead); writing – review and editing (equal). Penghui Hu: Data curation (equal); visualization (supporting); Lin Guo: Data curation (equal); visualization (supporting); writing – review and editing (supporting). Yanli Che: Funding acquisition (equal); project administration (equal); supervision (equal); writing – review and editing (equal). Zongqing Wang: Funding acquisition (equal); methodology (supporting); project administration (equal); supervision (equal); writing – review and editing (equal).

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### Interspecific and intraspecific genetic distances of *Allacta*

Authors: Bian-Lun Li, Peng-Hui Hu, Lin Guo, Yan-Li Che, Zong-Qing Wang

Data type: xls

Link: https://doi.org/10.3897/zookeys.1191.113043.suppl1

ZooKeys 1191: 23–33 (2024)
DOI: 10.3897/zookeys.1191.110217

Research Article

# New species in the genera *Eumacrocyrtus* Schultze, 1923 and *Enoplocyrtus* Yoshitake, 2017 from Luzon Island, Philippines (Coleoptera, Curculionidae, Entiminae, Pachyrhynchini)

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## Abstract

We describe and illustrate two new species from two previously monotypic genera *Eumacrocyrtus* Schultze, 1923 and *Enoplocyrtus* Yoshitake, 2017 from Luzon Island, Philippines: *Eumacrocyrtus robertfoxi* **sp. nov.**, and *Enoplocyrtus angelalcalai* **sp. nov.** *Eumacrocyrtus robertfoxi* **sp. nov.** serves as a new record for Luzon Island for *Eumacrocyrtus* which was only previously represented by *E. canlaonensis* Schultze, 1923 from Negros Island whereas *Enoplocyrtus angelalcalai* **sp. nov.** serves as an additional record of *Enoplocyrtus* in Mountain Province in Luzon Island. The discovery of these two new species from the Zoological Collections of the Philippine National Museum, collected in 1947 and 1985, respectively, highlights the value of natural history collections for the present and future generations of researchers.

**Key words:** Angel Alcala, endemic, flightless, new record, Robert Bradford Fox, taxonomy, weevils

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## Introduction

The tribe Pachyrhynchini is represented by 18 known genera distributed throughout Papua New Guinea, Australia, Fiji, Reunion, Moluccas, Borneo, island fringes of Taiwan and Japan, and the Philippines, the latter serving as its center of diversity. Luzon Island in the Philippines is the center of diversity for the tribe Pachyrhynchini in the country, represented by 12 genera, of which seven are endemic to the island: *Macrocyrtus* Heller, 1912, *Enoplocyrtus* Yoshitake, 2017, *Trichomacrocyrtus* Yoshitake, 2018, *Pseudapocyrtus* Heller, 1912, *Nothapocyrtus* Heller, 1912, *Exnothapocyrtus* Schultze, 1924 and *Eupachyrrhynchus* Heller, 1912, while five genera, *Pachyrhynchus* Germar, 1824, *Metapocyrtus* Heller, 1912, *Apocyrtus* Erichson, 1834, *Proapocyrtus* Schultze, 1918 and *Homalocyrtus* Heller, 1912, are shared with other islands. Luzon also has the highest concentration of described Pachyrhynchini species, accounting for more than 260 out of the more than 600 known species. Despite this, new genera and species are still discovered in many underexplored localities (Yoshitake 2017, 2018).

Among the 18 genera of Pachyrhynchini in the Philippines, two are monotypic: *Eumacrocyrtus* and *Enoplocyrtus*. *Eumacrocyrtus* is previously known only from a single species, *Eumacrocyrtus canlaonensis* Schultze, 1923 from the Canlaon Volcano in Negros Occidental, Negros Island (Schultze 1924). It is closely related to the genus *Macrocyrtus* Heller, 1912, a Luzon endemic genus (von Dalla Torre et al. 1931). However, Schultze separated it from *Macrocyrtus* based on the "scape of antenna reaching beyond posterior margin of eye, prothorax with distinct and sharply defined anterior and posterior submarginal groove and a dimple like depression dorsolaterally, elytra dorsally flattened with apical fourth extending beyond abdomen forming a mammilla-shaped projection in both sexes" (Schultze 1924, p. 372). *Enoplocyrtus* is a newly described genus known only from a single species, *Enoplocyrtus marusan* Yoshitake, 2017 from Mt. Polis and Barlig, Mountain Province. It is also related to *Macrocyrtus*, but Yoshitake distinguished it for having a subtriangular depression on the apical margin of the antennal scrobe, wide, flattened, and keeled fore tibia, and granulated hind tibia along internal margins (Yoshitake 2017).

In 1947, Dr Robert Bradford Fox, head of the Philippine National Museum's anthropology division and a biological specimen collector, collected several beetles in the Province of Zambales that he deposited at the Philippine Zoological Collections. This collection under the National Museum of Natural History, formally inaugurated and established in 2018, houses hundreds of undetermined weevil specimens including the specimen collected by Dr Fox. Upon examination by the first author, this specimen was determined to be new to science, together with another undetermined specimen collected in 1985. The discovery of these new species in the Zoological Collections reiterates the importance of keeping natural history collections in their best condition for present and future generations of researchers. The two new species are named in honor of Dr Robert Bradford Fox (†) and National Scientist Dr Angel Chua Alcala (†) for their groundbreaking and unparalleled contribution to advancing our knowledge of pre-Hispanic history, biodiversity and conservation in the Philippines. This paper describes and illustrates the new species of *Eumacrocyrtus* from Zambales and *Enoplocyrtus* from Bontoc, Mountain Province, bearing the names of these two doyens of Philippine science.

## Material and methods

Morphological characters were observed under Leica, Luxeo 4D, and Nikon SMZ745T stereomicroscopes. The treatment of the genitals follows Yoshitake (2011). Images of the habitus were taken using Canon EOS 6D digital camera equipped with a Canon MP-E 65-mm macro lens. Images were stacked and processed using a licensed version of Helicon Focus v.6.7.0; light and contrast were adjusted in Photoshop CS6 Portable software. Label data are indicated verbatim.

Abbreviations and symbols mentioned are abbreviated as follows:

| | |
|---|---|
| **/** | different lines; |
| **//** | different labels; |
| **LB** | body length, from the apical margin of pronotum to the apex of elytra; |
| **LR** | length of rostrum; |
| **LP** | pronotal length, from the base to apex along the midline; |

| | |
|---|---|
| **LE** | elytral length, from the level of the basal margins to the apex of elytra; |
| **WR** | maximum width across the rostrum; |
| **WP** | maximum width across the pronotum; |
| **WE** | maximum width across the elytra. |

Comparative materials, including types and specimens used in the study, are deposited in the Philippine National Museum of Natural History (**PNM)**, Manila, Philippines.

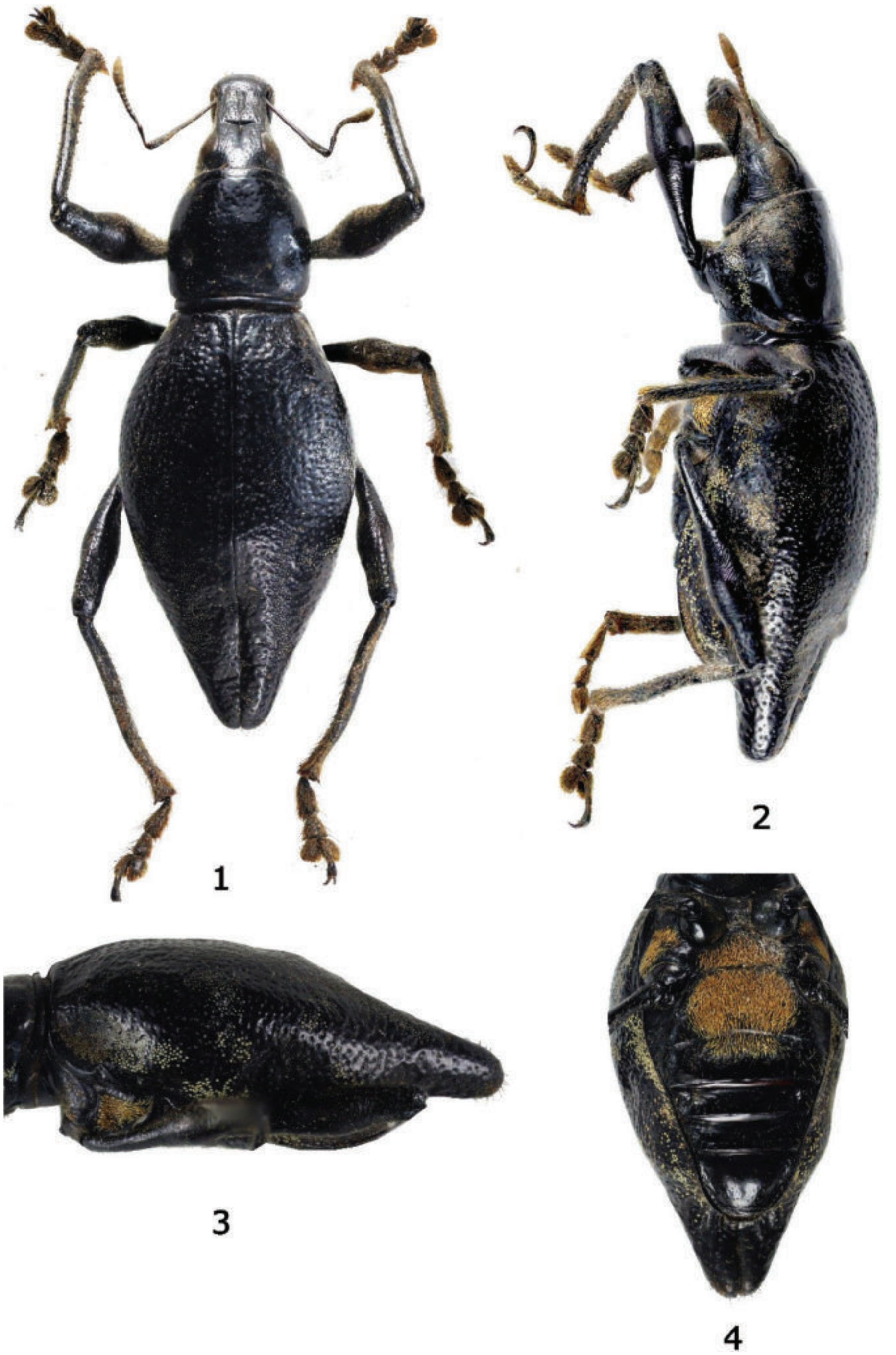
## Taxonomy

***Eumacrocyrtus robertfoxi*** **Cabras, sp. nov.**
https://zoobank.org/A9927681-7082-4484-A6A7-DA5F14EA7C68
Figs 1–4, 7–9

**Type material.** ***Holotype*** (Figs 1, 2), female: "Philippines- Luzon Island, Zambales, Villar / October, 1947/ leg. R.B. Fox (typed on white card) // HOLOTYPE female / *Eumacrocyrtus robertfoxi* sp. nov. / CABRAS, 2024 (typed on red card)" (PNM 15217).

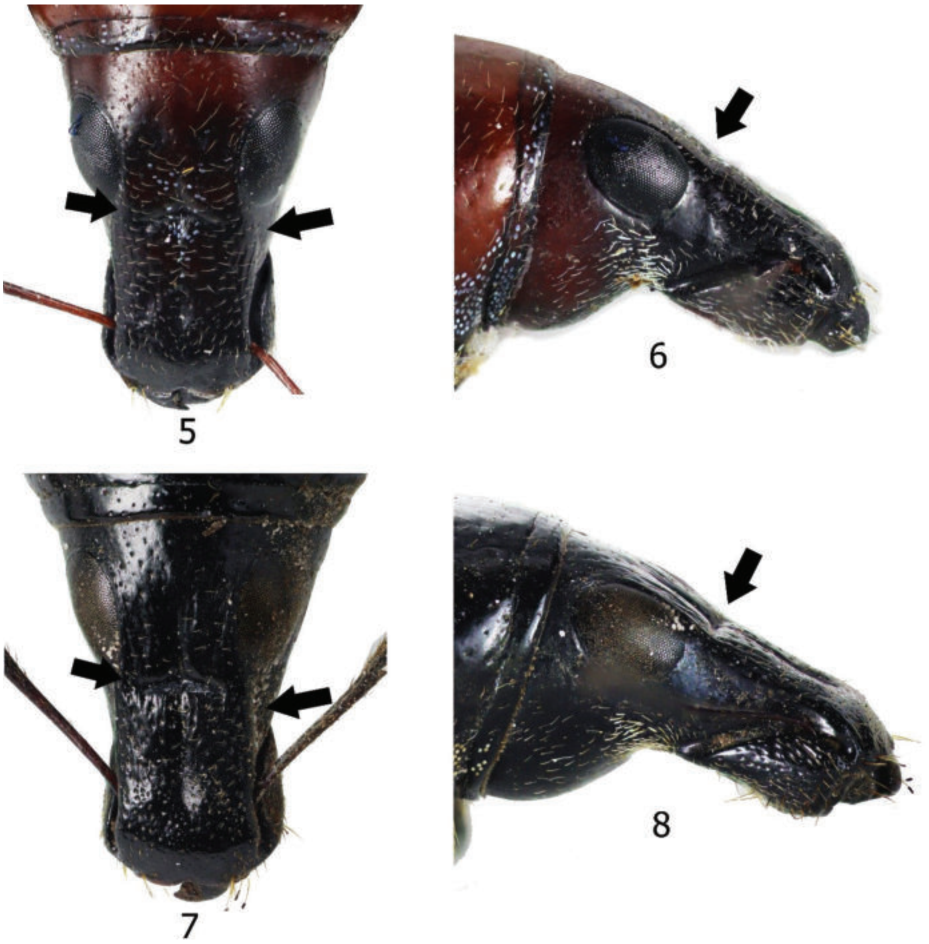
**Description.** ***Dimensions*****:** LB: 13.5 mm. LR: 2.5 mm. WR: 1.2 mm. LP: 3.3 mm. WP: 3.8 mm. LE: 10.0 mm. WE: 6.0 mm. *N* = 1. Integument black. Body surface matte, rostrum, head, legs, and underside moderately lustrous. ***Head*** dorsal surface moderately rugose and irregularly punctured with few sparse appressed setae; lateroventral side below eye with sparse appressed setae; forehead between eyes flat with distinct midline groove reaching frons; eyes medium-sized, feebly convex, and weakly prominent on lateral outline of head. ***Rostrum*** dorsal surface moderately rugose on basal half with coarse punctures up to anterior two-thirds and finely punctate on apical third, and with sparse minute appressed setae; twice as long as wide (LR/WR:2.5 mm/1.2 mm); with distinct transverse and deep basal groove but not reaching lateral margin, dorsum with a distinct and narrowly shallow midline groove reaching basal half; dorsal contour flat until anterior two-thirds then gradually declining towards apex; lateral sides with subtruncate margin, wide from base then gradually constricted towards middle, and gradually widened towards apex. Antennal scape longer than funicle, scape reaching posterior margin of eye, sparsely covered with subappressed pubescence, and funicle with suberect brownish setae. Funicular segment I slightly longer than II, four times longer as wide, funicular segment II approximately three times longer as wide, segments III–V as long as wide, slightly shorter and narrower than VI and VII, segments VI as long as wide, slightly longer and wider than III–V and VII slightly wider than long, wider and longer than VI; club lanceolate.

***Prothorax*** cylindrical, wider at base than apex, wider than long (LP/WP:3.3/3.8 mm), finely punctate and mostly glabrous with very few sparse setae, widest near base, weakly convex on dorsal surface, dorsal contour highest point at middle; with two dimple like depression on each side of disc. ***Elytra*** ovate, moderately longer than wide (LE/ WE:10.0/6.0 mm), three times as long and twice as wide as prothorax (WE/ WP: 6.0/3.8 mm, LE/LP: 10.0/3.3 mm), coarsely and irregularly punctate, with sparse minute pale-yellow to off-white appressed round scales on dorsum and dense yellow-ochre round scales on lateral sides, dorsum weakly convex, lateral sides near base and apex with



**Figures 1–4.** *Eumacrocyrtus robertfoxi* sp. nov., female holotype **1** dorsal habitus **2** lateral habitus **3** elytra, lateral view **4** meso-metasternum and abdominal sternites.

round depressions, dorsal contour highest at middle, lateral contour gradually widening from basal margin towards middle then gently constricted towards apex and forming a mammilla-shaped apex, widest at middle, apex with brown erect setae. ***Legs*** with moderately clavate femora. Femora black covered with brown appressed setae. Fore tibiae covered with subappressed brown setae, inner edge moderately serrate with short denticles, and long brown suberect setae. Fore and mid tibiae bear a mucro at apex. Mid and hind tibiae covered with appressed brown setae, inner edge with brown dense suberect setae and

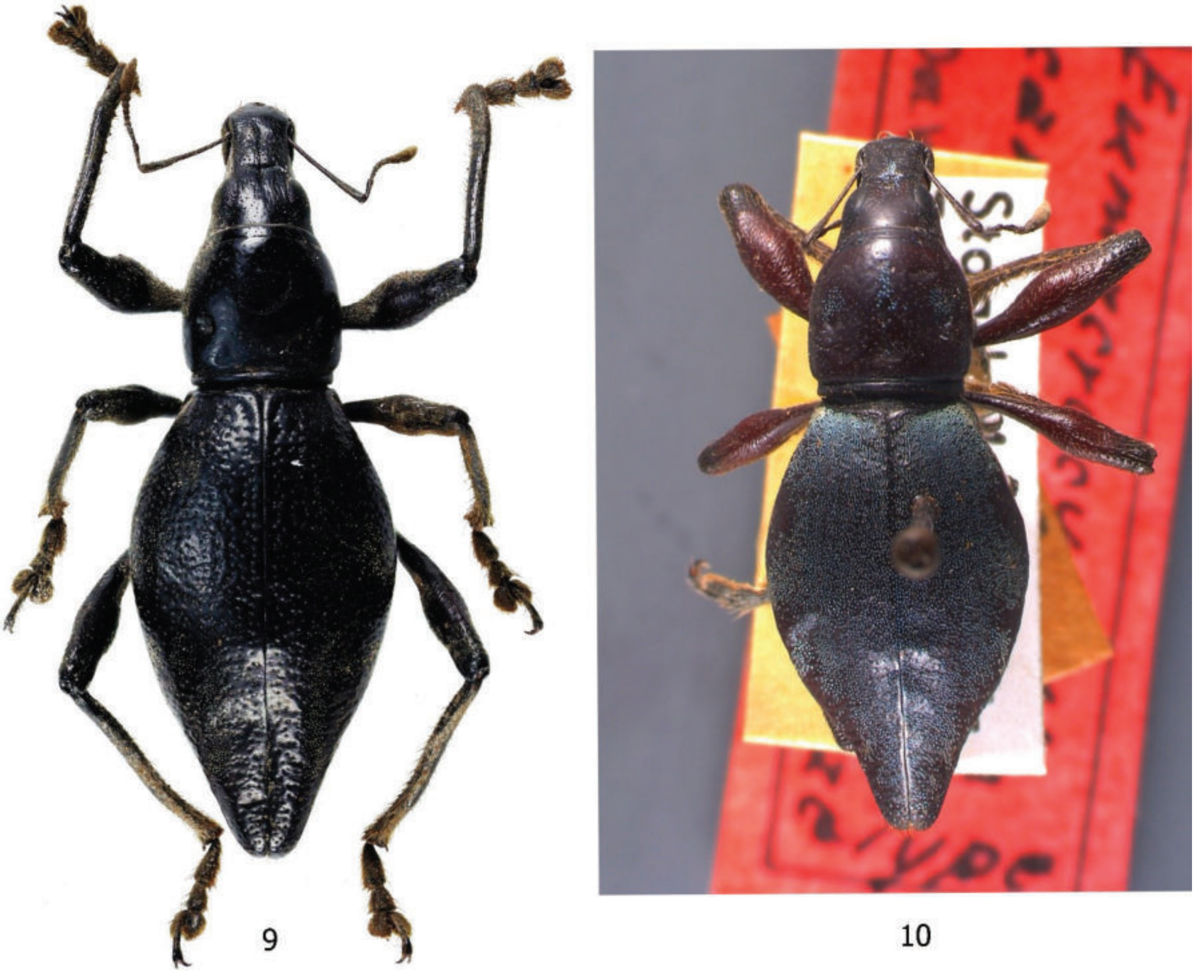


**Figures 5–8.** Head of *Eumacrocyrtus* spp. **5, 6** *Eumacrocyrtus canlaonensis* Schultze, 1923 **5** dorsal view **6** lateral view **7, 8** *Eumacrocyrtus robertfoxi* sp. nov. **7** dorsal view **8** lateral view.

few denticles along inner edge towards the apex. Tarsomeres pubescent. Fore coxae with sparse appressed golden yellow round, ovate and piliform scales towards anterior side, and sparse suberect metallic piliform scales towards posterior side. Mid and hind coxa with sparse appressed yellowish piliform scales. Mesoventrite with sparse appressed golden yellow piliform scales on disc and dense golden yellow piliform scales on distal ends. Metaventrite moderately depressed, especially at anterior margin, densely beset with golden yellow piliform scales on disc and thin ovate and piliform scales on distal ends. Ventrite I weakly depressed on disc, densely beset with golden yellow piliform scales on disc. Ventrite II weakly depressed and beset with golden yellow piliform scale on anterior half of disc. Ventrite III to V with fine sparse brown setae.

**Male.** Unknown.

**Diagnosis.** The new species is different from the only known species *Eumacrocyrtus canlaonensis* Schultze, 1923 (Fig. 10) based on the following morphological differences: a) rostrum longer and more slender with a more angled dorsolateral edge near the base compared to *E. canlaonensis* with almost rounded edge (Figs 5–8), b) head with distinct and deep median furrow, and weak rugae, c) outline of head and rostrum discontinuous with a more distinct transverse basal groove reaching near the lateral margin (Figs 5–8), d) integuments matte



**Figures 9, 10.** Type specimens **9** *Eumacrocyrtus robertfoxi* sp. nov. **10** *Eumacrocyrtus canlaonensis* Schultze, 1923.

black, e) elytra longer with coarser punctures, and rounded basal and post-median depression on lateral sides, and f) more slender and longer mammilla-shaped apex of elytra. In addition, the new species is found on Luzon Island outside the known range of *E. canlaonensis* which is only known from Negros Island (Fig. 21).

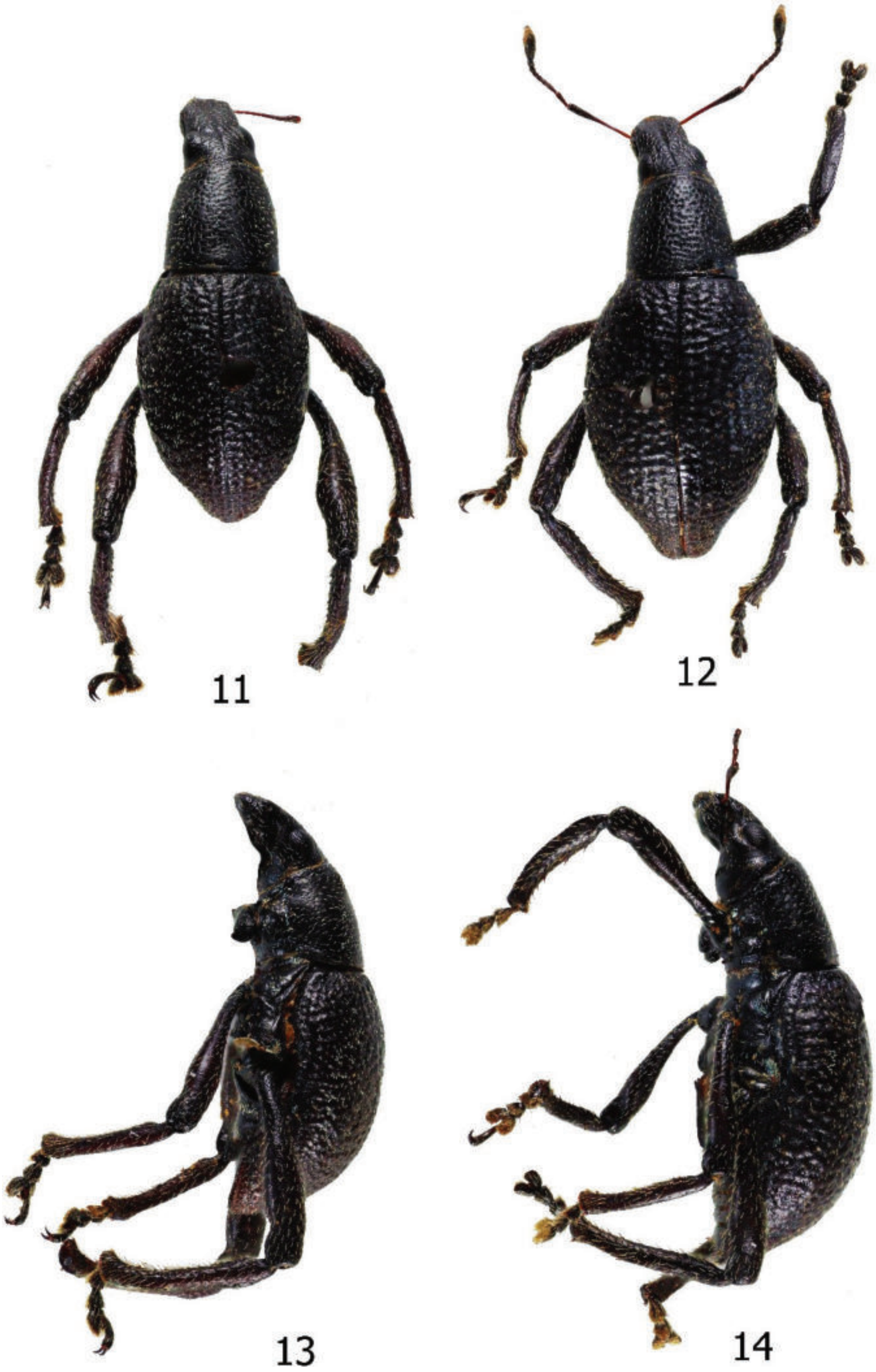
**Etymology.** The species epithet "*robertfoxi*" is dedicated to Robert Bradford Fox (1918–1985), who collected the type material in Zambales for his groundbreaking and unparalleled discoveries in anthropology, which significantly advanced our current knowledge of the pre-Hispanic era from the Philippines.

**Distribution.** *Eumacrocyrtus robertfoxi* sp. nov. is known only by the type specimen from Zambales, Luzon Island.

### ***Enoplocyrtus angelalcalai*** **Cabras, sp. nov.**

https://zoobank.org/D305F11A-D77C-4BB4-A2B3-E629F52C3971
Figs 11–20

**Type materials.** ***Holotype*** (Figs 11, 13), male: "Philippines- Luzon Island, Mountain Province, Bontoc, Palapal / July, 1985/ leg. Samarita (typed on white card) // HOLOTYPE male / *Enoplocyrtus angelalcalai* sp. nov./ CABRAS, 2024 (typed on red card)"(PNM 15218). ***Paratypes*** 1 ♀: same data as the holotype (PNM 15219).



**Figures 11–14.** *Enoplocyrtus angelalcalai* sp. nov. **11** male holotype, dorsal habitus **12** female paratype, dorsal habitus **13** male, lateral habitus **14** female, lateral habitus.

**Description.** ***Dimensions*:** LB: 8.4 mm. LR: 1.1 mm. WR: 1.1 mm. LP: 2.5 mm. WP: 2.5 mm. LE: 5.8 mm. WE: 4.0 mm. *N* = 1. Integument dark brown. Body surface, rostrum, head, legs matte, and underside weakly lustrous. ***Head*** dorsal surface weakly punctate and each puncture with subappressed white piliform scales; lateral side with weak rugae and sides below eye with sparse appressed bluish piliform scales; forehead between eyes flat with distinct but faint midline groove; eyes medium-sized, feebly convex, and moderately prominent on lateral outline of head. ***Rostrum*** dorsal surface weakly rugose up to anterior two-thirds with appressed white piliform scales; apical third finely punctate with fine sparse setae; as long as wide (LR/WR:1.1 mm/1.1 mm); transverse groove at base absent; with midline groove distinct until middle and progressively fainter and indistinct towards apex; dorsal contour flat, slightly curved towards apex but without apical bulge; lateral sides at upper margin of antennal scrobe with subtriangular depression. Antennal scape slightly longer than funicle, scape reaching beyond the posterior margin of eye, with few sparse subappressed pubescence, and funicle with suberect brownish setae. Funicular segment I nearly four times as long as wide, slightly longer than II, funicular segment II nearly three times as long as wide, longer than segments III–V, segments III–V as long as wide, shorter and narrower than VI, segment VI as long as wide, longer and wider than segments III–V, segment VII as long as wide, wider and longer than segments VI; club lanceolate. ***Prothorax*** subcylindrical, significantly wider at posterior margin then narrowed towards anterior margin, as long as wide (LP/WP:2.5/2.5 mm), coarsely punctate and rugose with sparse appressed white piliform scales and lanceolate pale turquoise and pale blue scales, widest at base, dorsal contour flat. ***Elytra*** pyriform (LE/ WE:5.8/4.0 mm), moderately longer than wide; moderately longer and wider than prothorax (WE/ WP: 4.0/2.5 mm, LE/LP: 5.8/2.5 mm); elytral surface coarse and with granulately rugose intervals, sparsely covered with minute white appressed piliform scales and pale turquoise and pale blue lanceolate scales, dorsum weakly convex, lateral contour widest before middle. ***Legs*.** Mid and hind femora dark brown covered with white subappressed piliform scales. Mid tibiae covered with white subappressed piliform scales on outer edge and suberect brown setae along inner edge. Hind tibiae covered with subappressed white piliform scales on outer edge and suberect brown setae along inner edge; inner edge and part of outer edge coarsely granulated. Mid and hind tibiae mucronate. Tarsomeres pubescent. Coxae with sparse appressed pale blue and white piliform scales. Mesoventrite with sparse appressed pale blue lanceolate scales and white setae. Metaventrite and ventrite I weakly depressed on disc, mostly glabrous except distal ends with appressed pale blue and pale-yellow lanceolate scales and white piliform scales. Ventrite II with sparse pale blue and yellow lanceolate scales and white setae. Ventrite III to V with fine sparse brown setae.

**Female** (PNM 15219). Dimensions: LB: 8.0 mm: LR: 1.1 mm: WR:1.1 mm.LP: 2.5 mm. WP: 2.5 mm. LE: 5.8 mm. WE: 4.1 mm. *N* = 1. Habitus, as shown in Figs 12, 14. Females differ from males in the following: a) fore tibiae flat; b) pronotum narrower with more flat dorsal contour; c) elytra moderately wider, and slightly longer; d) ventrite I flat. Otherwise, it is similar to the male.

**Diagnosis.** The new species is easily distinguished from the only known species, *Enoplocyrtus marusan* Yoshitake, 2017, based on the following morphological characteristics: a) coarsely punctate and rugose pronotum, b) elytral surface coarse and with granulately rugose intervals, c) integument dark brown, d) pronotum and elytra sparsely covered with appressed white piliform scales and pale turquoise and pale blue lanceolate scales, and e) differently shaped aedeagus (Figs 15, 16).

**Etymology.** The name "*angelalcalai*" is dedicated to National Scientist Angel Chua Alcala (1929–2023, Dumaguete, Negros Oriental, Philippines) for his contributions to advancing the Philippines' herpetological and marine research

**Figures 15–20.** Male and female genitalia of *Enoplocyrtus angelalcalai* sp. nov. **15** median lobe in dorsal view **16** idem in lateral view **17** sternite IX in dorsal view **18** sternite VIII in ventral view **19** ovipositor in dorsal view **20** spermatheca.

and conservation. Additionally for inspiring the authors to work on biodiversity research and conservation in the Philippines.

**Distribution.** *Enoplocyrtus angelalcalai* sp. nov. is known only from the type locality in Palapag, Bontoc, Mountain Province (Fig. 21).

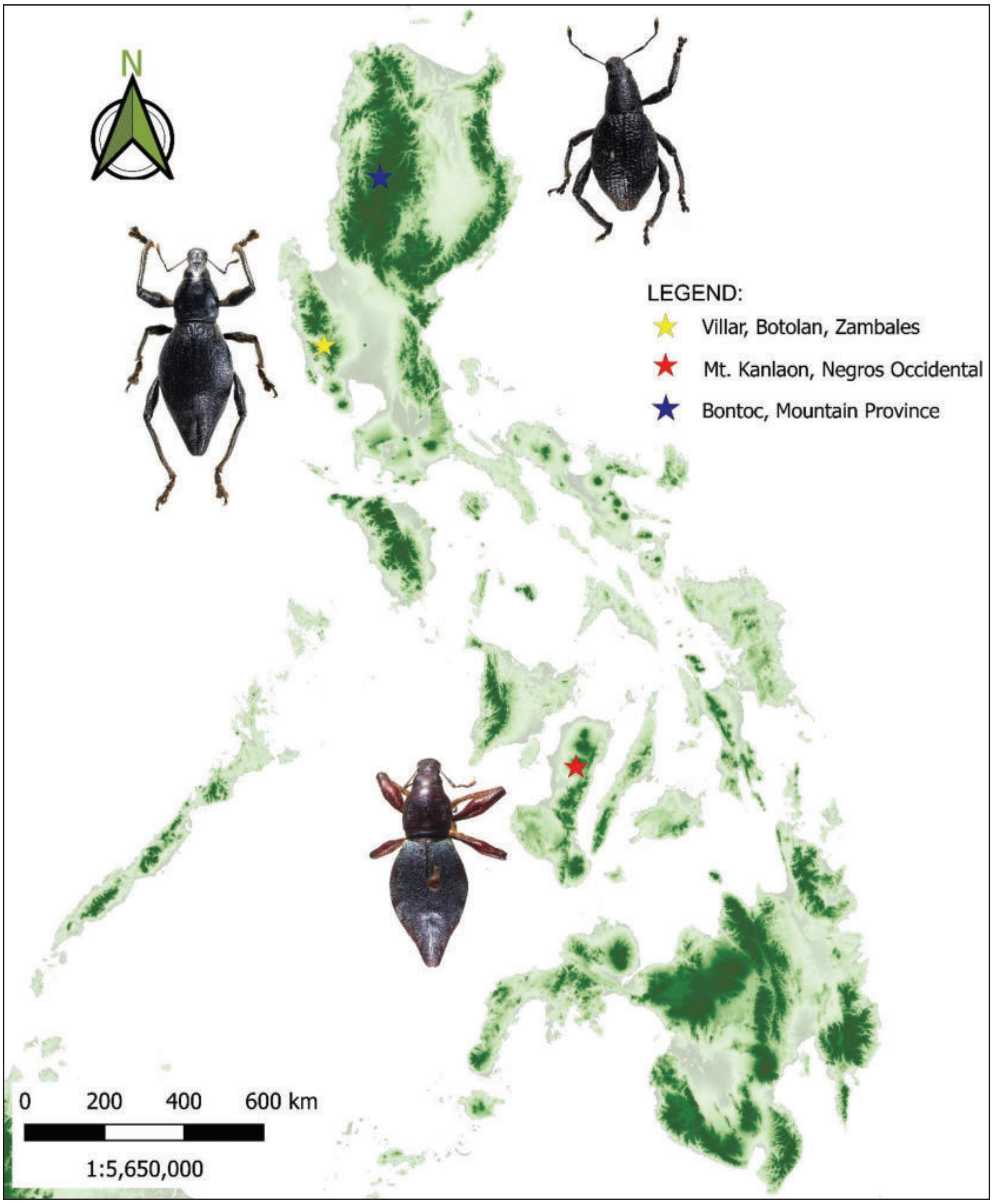


**Figure 21.** Distribution of *E. robertfoxi* sp. nov. (yellow), *E. canlaonensis* Schultze, 1923 (red) and *Enoplocyrtus angelalcalai* sp. nov. (blue) in the Philippines.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

All authors have contributed equally.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# Taxonomic revision of the *Nitocra affinis* Gurney, 1927 species complex (Harpacticoida, Ameiridae) with descriptions of four new species and re-evaluation of its subspecies

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## Abstract

Due to the recent increasing importance of microcharacters in copepod taxonomy, it has become evident that many species lacking detailed descriptions actually constitute to a species complex. In this study, *Nitocra affinis* is redescribed based on lectotype material from Lake Timsah (Egypt) which facilitated a thorough detailed comparison with specimens of *N. affinis* recorded from distantly related localities. The results unequivocally revealed that the specimens of *N. affinis* examined in this study belong to a different species. As a result, four new species, *Nitocra sonmezi* **sp. nov.** and *Nitocra serdarsaki* **sp. nov.** from the Turkish coast, *Nitocra alperi* **sp. nov.** from the Indian Ocean, and *Nitocra loweae* **sp. nov.** from Brighton, England are herein described as new to science. On the other hand, all subspecies of *N. affinis*, namely *N. affinis rijekana* Petkovski, 1954, *N. affinis californica* Lang, 1965, *N. affinis stygia*, Por. 1968, and *N. affinis colombiensis* Fuentes-Reinés & Suárez-Morales, 2014 are elevated to species rank. An updated key the species of the *affinis* group is also provided.

**Key words:** Copepoda, marine habitat, meiofauna, microcharacters, new species, taxonomy

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## Introduction

The family Ameiridae Boeck, 1865 is ranked third in terms of number of taxa in the Harpacticoida, after Miraciidae Dana, 1846 and Canthocamptidae Sars, 1906, comprising 47 genera and up to 300 species (Corgosinho et al. 2020). Boeck (1865) originally established both *Ameira* Boeck, 1865 and *Nitocra* Boeck, 1865 with limited descriptions. The genus *Nitocra* is represented by 81 valid species and subspecies (Karanovic et al. 2015; Huys 2021; Fuentes-Reinés et al. 2022). The taxonomy of the genus *Nitocra*, similar to numerous other genera within the family, has posed challenges due to the lack of detailed species descriptions and taxonomic information

(Karanovic and Pesce 2002). Initially designated as *"Nitokra"* by Boeck (1865), the nomenclature was later amended to *"Nitocra"* (Giesbrecht 1881), a spelling upheld until Bowman (1988) highlighted its erroneous usage. This viewpoint was endorsed by Wells (2007), referencing ICZN (1999: § 33.3.1), which advocates for prevailing name usage, thereby asserting the adoption of *"Nitocra"*.

*Nitocra affinis* was originally described by Gurney (1927) from Ismailia and Port Tawfiq (Egypt), collected during the Cambridge Expedition to the Suez Canal (1924), who described both sexes based on an undisclosed number of specimens. The distributional range of *N. affinis* has expanded with the description of several subspecies from different ecological environments: *N. affinis rijekana* Petkovski, 1954 was described from the North Adriatic, *N. affinis stygia* Por, 1968 was described from the Red Sea, *N. affinis californica* Lang, 1965 was described from California, and *N. affinis colombiensis* Fuentes-Reinés & Suárez-Morales, 2014 was described from a coastal lagoon in Colombia (Petkovski 1954; Lang 1965; Por 1968; Fuentes-Reinés and Suárez-Morales 2014).

Considering the distributional range of the species, including its subspecies, the wide morphological variations observed among the populations, and the diversity in their ecological habitats, postulations arise that more than one species (i.e., a species complex) may exist under the name of *N. affinis*, and hence needing an urgent revision. Here, *N. affinis* is partially redescribed based on the only incomplete female specimen collected and deposited at the collection of the NHMUK by R. Gurney himself, and proposed here as lectotype (see below), and several populations previously identified as *N. affinis* from a wide range of habitats and geographic localities were re-examined in detail to morphologically delineate the specific range.

## Material and methods

Specimens were dissected in glycerin and mounted on slides. All drawings were made using an Olympus BX-51 differential interference contrast microscope with the aid of a camera lucida. Figures were prepared with Adobe Photoshop CC using with a Wacom Intuos Pro Graphical tablet. Huys et al. (1996) was followed for the terminology used in the text.

### Abbreviations used in the text

| | |
|---|---|
| **A1** | antennule |
| **A2** | antenna |
| **Ae** | aesthetasc |
| **Exp** | exopod |
| **Enp** | endopod |
| **Exp or enp-1, 2, 3** | proximal, middle and distal segments of ramus |
| **P1–P6** | legs 1–6 |
| **NHMUK** | Natural History Museum United Kingdom |
| **TCRC** | Turkish Copepod Research Collection |
| **TÜBİTAK** | The Scientific and Technological Research Council of Türkiye |

## Results

### Order Harpacticoida Sars, 1903

### Family Ameiridae Boeck, 1865

**Updated diagnosis.** Body semi-cylindrical or cylindrical with prosome composed of cephalothorax with completely fused first pedigerous somite, and three free pedigerous somites with smooth hyaline frills. Urosome five-segmented, comprising the fifth pedigerous somite, genital double-somite and three free abdominal somites. Rostrum small, triangular and defined at base or not. Anal operculum apically with row of robust spinules or smooth. Caudal ramus with seven setae. Antennule five to eight-segmented in female, nine or ten-segmented and geniculate in male, first segment not unusually elongate. Antenna with coxa, allobasis or basis, one-segmented endopod, and one or two-segmented exopod. P1–P4 with one to three-segmented exopod and endopod. The inner spine of basis of P1 hook-like in male. P5 with baseoendopod and separate exopod.

### Genus *Nitocra* Boeck, 1865

**Diagnosis.** Body semi-cylindrical. Rostrum small, triangular and defined at base. Anal operculum apically with row of robust spinules. Caudal rami short, and with seven setae. Antennule eight-segmented in female, nine- or ten-segmented and haplocer in male. Antenna with coxa, allobasis, one-segmented endopod, and one-segmented exopod. Partial suture line between basis and first endopodal segment near base of exopod indicates ancestral segmentation. Exopod one-segmented with three setae. Mandible with coxal gnathobase with coarse teeth ventrally, one unipinnate seta dorsally; palp two-segmented, comprising basis and one-segmented endopod. Maxillular endopod represented by minute but distinct segment with two setae. Exopod absent. Maxilla with two endites on the syncoxa. Maxilliped subchelate; syncoxa with subapical seta; endopod represented by strong claw accompanied at base by a minute naked seta. P1–P4 with three-segmented exopod and three-segmented endopod. Inner spine of basis of P1 hook-like in male. P1 exp-2 with one inner seta, P1 exp-3 with four or five setae. P2–P4 exp-1 without inner setae, exp-2 with one inner seta. P2–P4 without sexual dimorphism. P5 with baseoendopod and separate exopod. Male P6 asymmetrical. Sexual dimorphism in the antennule, the inner spine of P1 basis, the inner distal seta of P3 exp-3, P5 and P6 and urosomal segmentation.

**Type species.** *Nitocra typica* Boeck, 1865 (type species by indication).

**Valid species and subspecies.** *N. affinis* Gurney, 1927; *N. arctolongus* Shen & Tai, 1973; *N. australis* Soyer, 1975; *N. balli* Rouch, 1972; *N. balnearia* Por, 1964; *N. bdellurae* (Lidell, 1912); *N. bisetosa* Mielke, 1993; *N. blochi* Soyer, 1974; *N. californica* Lang, 1965; *N. cari* Petkovski, 1954; *N. chelifer* Wilson, 1932; *N. colombiensis* Fuentes-Reinés & Suárez-Morales, 2014; *N. delaruei* Soyer, 1974; *N. divaricata caspica* Behning, 1936; *N. divaricata divaricata* Chappuis, 1923; *N. dubia* Sars, 1927; *N. elegans* (Scott, 1905); *N. elongata* Marcus, 1968;

*N. esbe* Karanovic, Eberhard, Cooper & Guzik, 2014; *N. evergladensis* Bruno & Reid, 2002; *N. fallaciosa baltica* Lang, 1965; *N. fallaciosa fallaciosa* Klie, 1937; *N. fragilis fragilis* Sars, 1905; *N. fragilis paulistana* Jakobi, 1956; *N. galapagoensis* Mielke, 1997; *N. gracilimana* Giesbrecht, 1902; *N. hamata* Bodin, 1970; *N. hibernica bulgarica* (Apostolov, 1976); *N. hibernica hibernica* (Brady, 1880); *N. humphreysi* Karanovic & Pesce, 2002; *N. hyperidis* Jakobi, 1956; *N. incerta* (Richard, 1893); *N. intermedia* Pesce, 1983; *N. karanovici* Chullasorn, Kangtia & Klangsin, 2014; *N. kastjanensis* Kornev & Chertoprud, 2008; *N. koreana* Chang, 2007; *N. lacustris azorica* Kunz, 1983; *N. lacustris colombianus* Reid, 1988; *N. lacustris lacustris* (Schmankevitsch, 1895); *N. lacustris pacifica* Yeatman, 1983; *N. lacustris richardi* Karanovic, Eberhard, Cooper & Guzik, 2014; *N. lacustris sinoi* Marcus & Por, 1961; *N. laingensis* Fiers, 1986; *N. langi* Karanovic, Eberhard, Cooper & Guzik, 2014; *N. malaica* Kiefer, 1929; *N. mediterranea jakubisiaki* Karanovic, Eberhard, Cooper & Guzik, 2014; *N. mediterranea mediterranea* Brian, 1928; *N. medusae* Humes, 1953; *N. minor minor* Willey, 1930; *N. mozambica* Huys, 2021; *N. parafragilis* Roe, 1958; *N. phlegraea* Brehm, 1909; *N. phreatica* Bozic, 1964; *N. pietschmanni* Chappuis, 1934; *N. platypus bakeri* Chappuis, 1930; *N. platypus platypus* Daday, 1906; *N. pontica* Jakubisiak, 1938; *N. pori* Karanovic, Eberhard, Cooper & Guzik, 2014; *N. psammophila* Noodt, 1952; *N. pseudospinipes* Yeatman, 1983; *N. puebloviejensis* Fuentes-Reinés, Suárez-Morales & Silva-Briano, 2022; *N. pusilla* Sars, 1911; *N. quadriseta* Wells & Rao, 1987; *N. reducta fluviatilis* Galhano, 1968; *N. reducta reducta* (Schäfer, 1936); *N. reunionensis* Bozic, 1969; *N. rijekana* Petkovski, 1954; *N. sewelli husmanni* Kunz, 1976; *N. sewelli sewelli* Gurney, 1927; *N. sphaeromata* Bowman, 1988; *N. spinipes armata* Lang, 1965; *N. spinipes orientalis* Sewell, 1924; *N. spinipes spinipes* Boeck, 1865; *N. stygia* Por, 1968; *N. taylori* Gómez, Carrasco & Morales-Serna, 2012; *N. typica adriatica* Petkovski, 1954; *N. typica typica* Boeck, 1865; *N. uenoi* Miura, 1962; *N. vietnamensis* Tran & Chang, 2012; *N. woltereckі* Brehm, 1909; *N. yeelirrie* Karanovic, Eberhard, Cooper & Guzik, 2014.

### ***Nitocra affinis* Gurney, 1927**

Figs 1, 2

**Unverified records.** Bermuda (Willey 1930), Italia (Chappuis 1938), Sweden (Lang 1935), England (Gurney 1932), Federated States of Micronesia (Vervoort 1964).

**Type material. *Lectotype*:** Egypt • 1 ♀; Ismailia. Mounted on one slide. Damaged. Abdomen lost. Gurney, R leg.; NHMUK reg. no. 1928.4.2.107.

Gurney (1927) recorded *N. affinis* from both Ismailia and Port Tawfiq and described both sexes based on an undisclosed number of specimens. Since a holotype was not designated by Gurney (1927) all specimens collected from both localities are collectively regarded as the type series. The incomplete female specimen collected and identified by R. Gurney (incorrectly labelled as a cotype) and deposited in the NHMUK under reg. no. 1928.4.2.107 is the only surviving syntype and is here designated as the lectotype of *N. affinis*. The place of origin of the latter is Lake Timsah, Ismailia which becomes the type locality of *N. affinis* according to ICZN Art. 76.2.

**Redescription (based on the original description and examination of the lectotype).** Prosome slightly tapering proximally with several sensilla as figured

(Fig. 1A, B). First urosomite (P5-bearing somite) with lateral spinule row extending to the dorsal edge of the somite. Abdomen missing.

Antennule (Fig. 1C) eight-segmented and joined to the cephalothorax with small triangular pseudosegment (arrowed in Fig. 1C); first segment with spinules at the ventrolateral margin and with a tube pore near the inner dorsal margin, and with row of slender spinules on ventral surface. Long, slender aesthetasc on fourth segment fused basally with adjacent large seta. Two lateral setae on seventh segment and four lateral setae on eighth segment biarticulate at base. Setal formula 1-[1, plumose], 2-[8 +1 plumose], 3-[8], 4-[3 +1 ae], 5-[2], 6-[3], 7-[4], 8-[5 + acrothek)]. Maximum length/maximum width ratio of antennular segments as 1:1.2:1.3:1.8:1.2:1.8:1.3:2.8.

Rostrum (Fig. 1D). Small with two dorsal sensilla near the base of apical rostral projection, which is ~ half of the rostral length, with an opening (pore) distally.

Antenna (Fig. 1E). Coxa small, unornamented. Basis and proximal endopodal segment fused forming allobasis (ancestral segmentation between basis and first endopodal segment visible near base of exopod) with a spinule row near the base of exopod. Exopod one-segmented, with two unipinnate spines and one slender naked seta; endopod lost.

Mandible (Fig. 1F). Gnathobase with coarse teeth ventrally, dorsal unipinnate seta could not be observed due to natural position of structure. Uniramous palp two-segmented comprising basis and one-segmented endopod. Basis armed with a bipinnate spine. Endopod with one plumose lateral seta, and four naked setae (two of them basally fused).

Maxillule not observed. Note: this appendage was impossible to be reliably observed in detail because its position underneath the maxilla. But the structure and setation of the maxillule agrees with the that of *N. loweae* sp. nov. On the other hand, the lectotype material was too fragile and the mouth parts were too small; therefore, the only specimen was not dissected. The maxillule had better be redescribed based on newly collected materials, preferably from newly collected topotype.

Maxilla (Fig. 1G) with two well-developed endites on the syncoxa with a robust row of spinules on outer margin; distal endite with a strong unipinnate seta and two naked setae; proximal endite small, with two naked setae. Allobasis transformed into claw, with one naked seta at base. Endopod a reduced segment with one seta. The maxilla should be redescribed based on newly collected topotypes.

Maxilliped (Fig. 1H) subchelate. Syncoxa unornamented with one subapical plumose seta. Basis ~ 2.4 × as long as maximum width, with row of spinules along inner margin and three small spinules on outer distal corner. Endopod represented by strong claw accompanied at base by a minute naked seta.

Swimming legs (Fig. 2A–D); P1–P4 with three-segmented exopods and endopods (Fig. 2A–D). Intercoxal sclerite rectangular and smooth. Praecoxa wide and with a row of spinules on outer margin (P1–P4).

P1 (Fig. 2A). Coxa rectangular, outer distal margin ornamented with fine setules; anterior surface with a row of spinules. Basis with spinule row at the base of strong pinnate inner spine; with spinule row along distal margin. Inner margin of basis with robust spinules. Exp-1,2 with outer pinnate spine. Exp-2 with an inner plumose seta. Exp-3 with two geniculate apical setae and three outer pinnate spines. Enp-1 longer than exopod, 5 × as long as maximum width and ornamented with row of fine spinules on the middle of the segment along inner

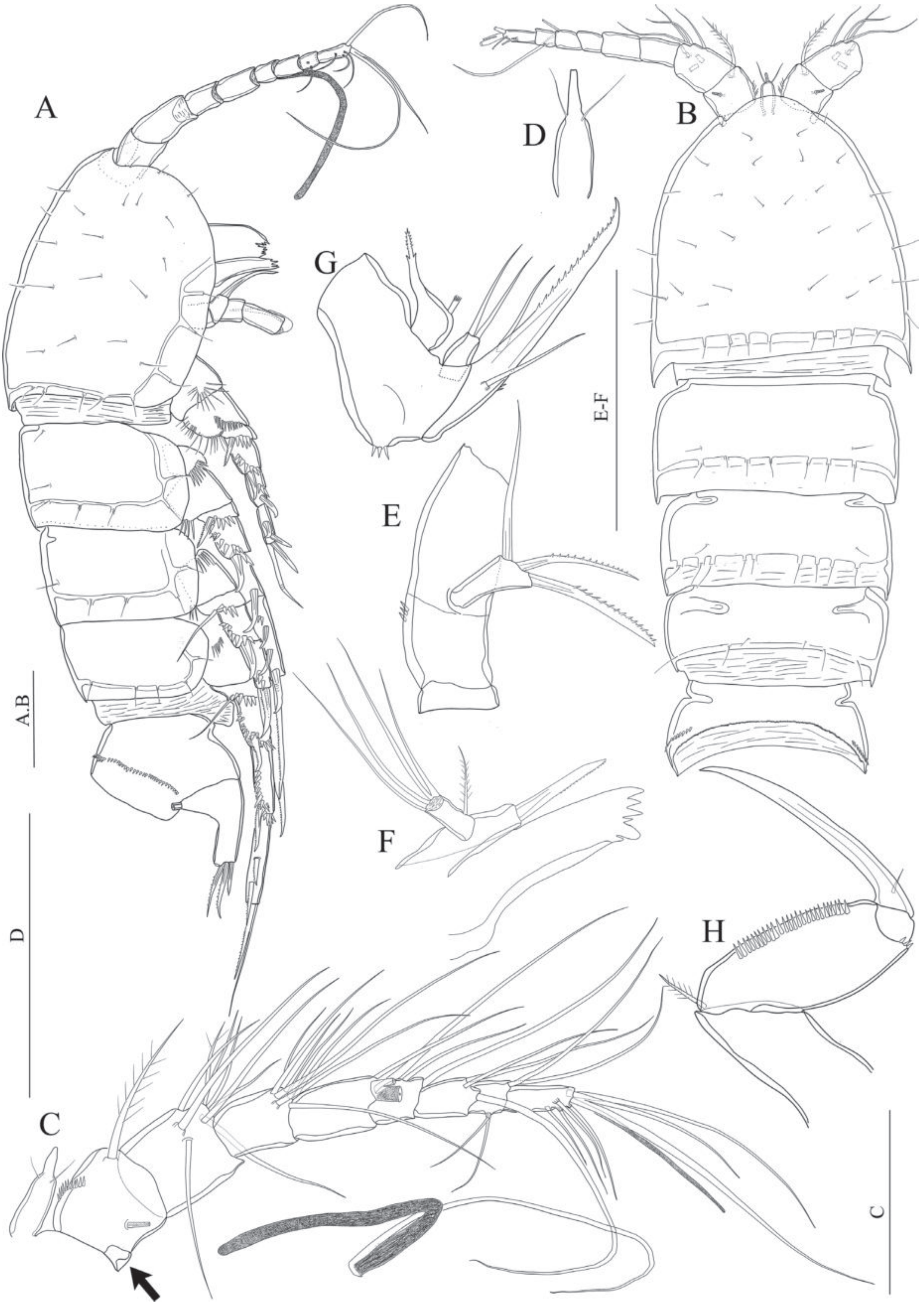

**Figure 1.** *Nitocra affinis* female lectotype **A** habitus, lateral **B** habitus, dorsal **C** antennule (arrow pointing pseudosegment) **D** rostrum **E** antennary coxa, allobasis, and exopod **F** mandible **G** maxilla **H** maxilliped. Scale bars: 50 µm.

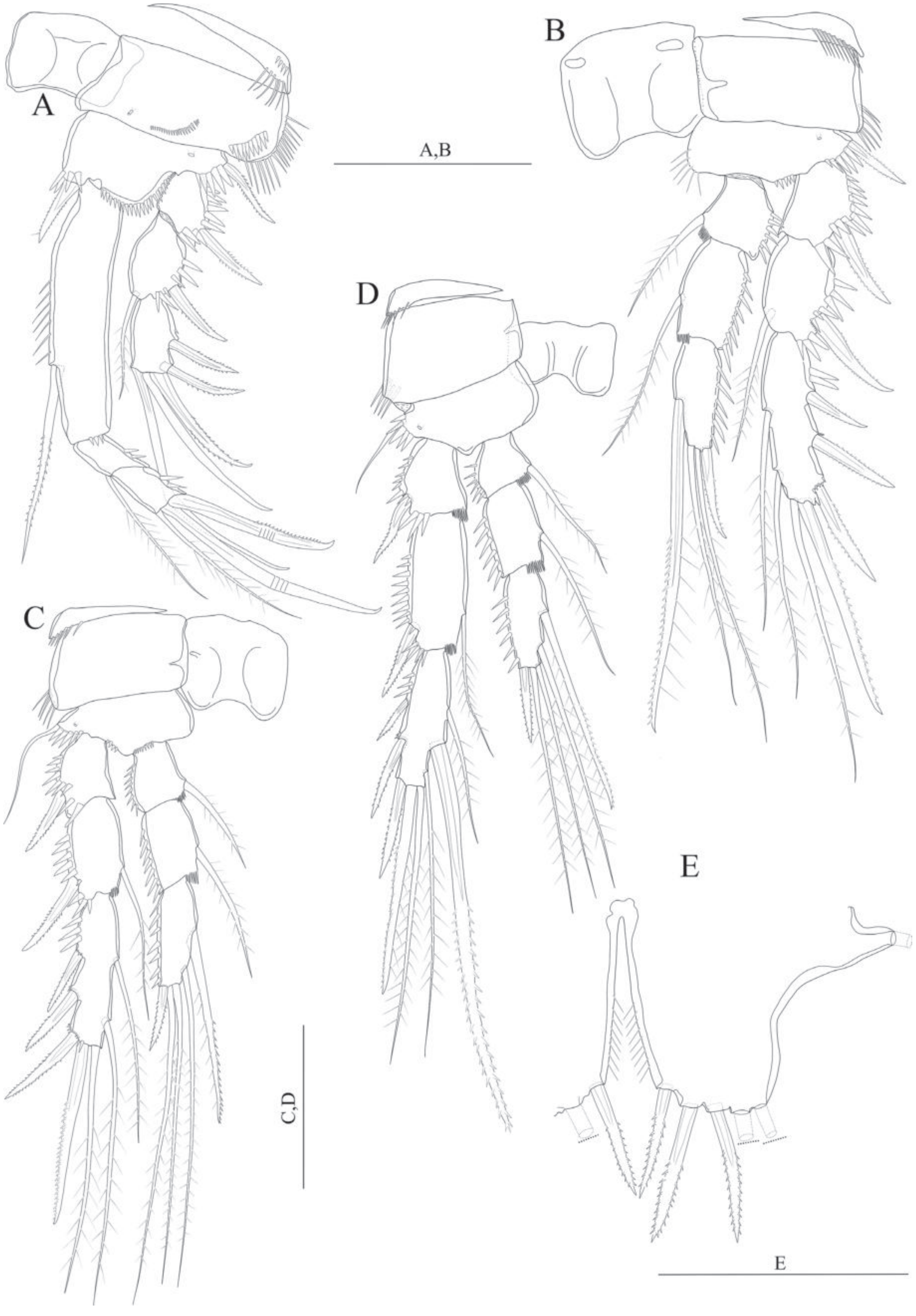

**Figure 2.** *Nitocra affinis* female lectotype **A** P1, anterior **B** P2, anterior **C** P3, anterior **D** P4, anterior **E** P5, anterior. Scale bars: 50 µm.

margin, with three spinules on distal margin and with a bipinnate spine originating from the distal half of the segment; enp-2 with a plumose seta on inner corner and with spinules on outer margin; enp-3 with one plumose seta and two geniculate setae distally and with few spinules on outer margin.

P2–P4 (Fig. 2B–D). Coxa rectangular, outer distal margin naked. Inner margin of basis naked (P3, P4) or ornamented with fine setules (P2). Exp-1 without inner seta; (P2–P4) and inner distal margin of exp-1,2 with small spinules (P3, P4). Exp-1,2 with robust spinules and pinnate spine (P2–P4) on outer margin; exp-2 with an inner plumose seta (P2–P4); P2 and P3 exp-3 with seven elements; two inner plumose setae, two apical setae (the outermost being spiniform and unipinnate, the innermost slender and plumose) and three pinnate outer spines. P4 exp-3 with eight elements; two slender inner plumose setae, one well-developed inner pinnate seta, two apical setae, (the outermost being spiniform and unipinnate, the innermost slender and plumose) and three pinnate outer spines. Enp-1, 2 ornamented with robust spinules on outer margin, with small spinules on inner distal margin, and with a plumose inner seta (P2–P4); P2 enp-3 with four elements; one proximal inner unipinnate seta, two distal plumose setae and one distal outer spine; P3 and P4 enp-3 with five elements; one proximal inner unipinnate seta, one inner subdistal seta, two distal plumose setae and one distal outer spine.

P5 damaged, exopod lost (Fig. 2E). Distal half of inner margin of baseoendopod with setules; endopodal lobe with five setae (two broken off, but these two missing setae depicted in the original description (see Gurney 1927: fig. 154 D, E) Armature formula of the swimming legs as follows:

| P1<br>Exp/ Enp | P2<br>Exp/ Enp | P3<br>Exp/ Enp | P4<br>Exp/ Enp |
|---|---|---|---|
| 0.1.023 / 1.1.111 | 0.1.223 / 1.1.121 | 0.1.223 / 1.1.221 | 0.1.323/1.1.221 |

### ***Nitocra loweae*** **sp. nov.**

https://zoobank.org/4DA4374E-752C-4EFC-8891-C0B25C11256C

Figs 3–8

**Type material.** ***Holotype***: England • 1 ♀ (dissected on 7 slides) (NHMUK reg. no. 2023.0000); paratype: 1 ♂ (ethanol-preserved) (NHMUK reg. no. 2023.0000); additional paratypes; 2 ♀♀ (ethanol-preserved) (NHMUK reg. no. 2023.0000-0000). Brighton, 50°48.46'N, 00°04.85'W; washings of *Polysiphonia fucoides* algae collected at 1.5 m depth. Leg. David Ventham, 13.10.1993 (material originally registered as *N. affinis* under NHMUK reg. no. 2015.1108) (see Ventham 2011).

**Description (adult female holotype).** Body semi-cylindrical (Fig. 3A, B), total body length measured from the tip of the rostrum to posterior end of the caudal rami 560–571 µm (average = 564.6, *n* = 3; holotype length = 571 µm). Sensilla and pore ornamentation as figured (Fig. 3A, B). Prosome composed of cephalothorax with completely fused first pedigerous somite, and three free pedigerous somites with smooth hyaline frills. Urosome five-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites. Fifth pedigerous somite wider than other urosomites, with six sensilla and a lateral spinule row slightly extending dorsally. Genital double-somite (Figs 3A, B, 4B) squarish, internal suture line (remnant of segmental fusion) strongly sclerotised, visible dorsolaterally at midlength of somite, ornamented with spinules as figured. Second and third abdominal somites with sensilla and spinules as figured (Figs 3A, B, 4B). Genital field positioned near anterior margin of genital double-somite (Fig. 4B); paired gonopores opening via common midventral slit covered by genital operculum derived from fused vestigial sixth legs. P6 with one plumose seta and one naked seta (Fig. 4B). Copulatory pore large (Fig. 4B), leading via chitinised copulatory duct with supporting chitinised rod. Anal somite (Figs 3A, C; 4B) with a lateral row of spinules medially; ventrally with medial row of spinules (Fig. 4B); anal operculum apically with row of twelve robust spinules (Fig. 3C). Caudal rami (Fig. 3C) with robust spinules near inner margin running dorso-ventrally, and a middorsal pore; with a posterior row of strong spinules ventrally; with seven setae (Fig. 3C): seta I minute; seta II slightly displaced dorsally; setae IV and V well-developed and pinnate (Fig, 3D); seta VI located near inner distal margin and naked; seta VII proximally tri-articulate.

Antennule (Fig. 5A) eight-segmented. Setal formula 1-[1, plumose], 2-[7 +2 plumose], 3-[7+1 plumose], 4-[3+1 ae], 5-[2], 6-[3], 7-[4], 8-[5+acrothek)]. Maximum length/maximum width ratio of antennular segments 1:1:1.4:1.2:1.2:2:1.5:2.8.

Rostrum (Fig. 5A) small, triangular, without clear demarcation between the distal and the proximal part of rostrum (cf. Fig. 1C of *N. affinis*) with tube pore distally and with two dorsal sensilla (Fig. 5A).

Antenna (Fig. 5B) comprising coxa, allobasis, one-segmented endopod and one-segmented exopod.. Coxa very short and unornamented. Allobasis cylindrical, ~ 2.7 × as long as maximum width, ornamented proximally with three spinule rows. Free endopodal segment with proximal part narrower than distal part, ~ 2.5 × as long as its maximum width, ornamented with surface frill subdistally, and with longitudinal row of spinules along inner margin, with another spinule row near the base of two lateral unipinnate spines flanking thin naked seta; apical armature consisting of five geniculate setae, one of them fused basally to additional unipinnate non-geniculate seta. Exopod with narrow proximal half and somewhat wider distal part, ~ 2.5 × as long as its maximum width, unornamented, armed with two curved, strong unipinnate apical setae and one spinulose subdistal seta, the latter longest.

Mandible (Fig. 5C). Coxal gnathobase with coarse teeth ventrally and with one unipinnate seta dorsally. Palp uniramous, two-segmented, comprising basis and one-segmented endopod. Basis with lateral spinule row midway and one curved robust unipinnate apical spine. Endopod with one short plumose lateral seta, five naked apical setae (three of them basally fused).

Maxillule (Fig. 5D). Praecoxa large with few spinules. Praecoxal arthrite rectangular; with two setae on anterior surface, lateral spinule row and distal armature consisting of four spines (two of which with apical combs) and one unipinnate seta. Coxal endite shorter than praecoxal arthrite, with long distally curved spine and three slender naked setae. Basis rectangular, with five slender naked setae on distal margin. Endopod represented by minute but distinct segment, unornamented and armed with two plumose apical setae. Exopod absent.

Maxilla (Fig. 5E). Syncoxa with spinule row and two well-developed (coxal) endites; proximal endite somewhat bulbous, expanded distally and armed with two plumose setae; distal endite cylindrical with two naked apical setae of equal in length. Allobasis transformed into claw-like pinnate endite; with a pinnate seta at base and with few spinules along convex margin near the base of endopod. Endopod represented by two slender naked setae equal in length.

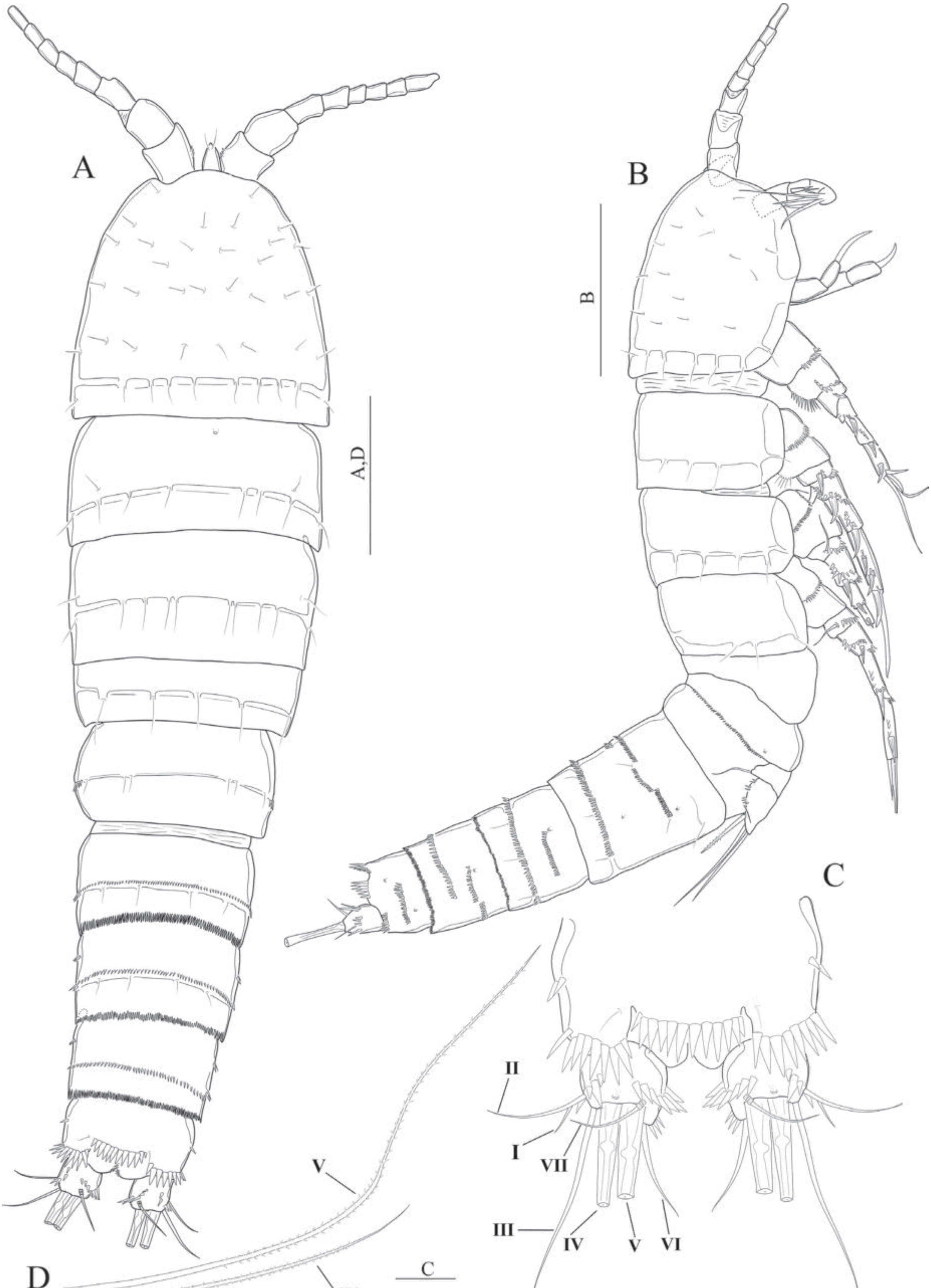

**Figure 3.** *Nitocra loweae* sp. nov. female holotype **A** habitus, dorsal **B** habitus, lateral **C** anal somite, dorsal **D** furcal setae IV and V. Scale bars: 100 μm (**A, D**); 50 μm (**B**); 12 μm (**C**).

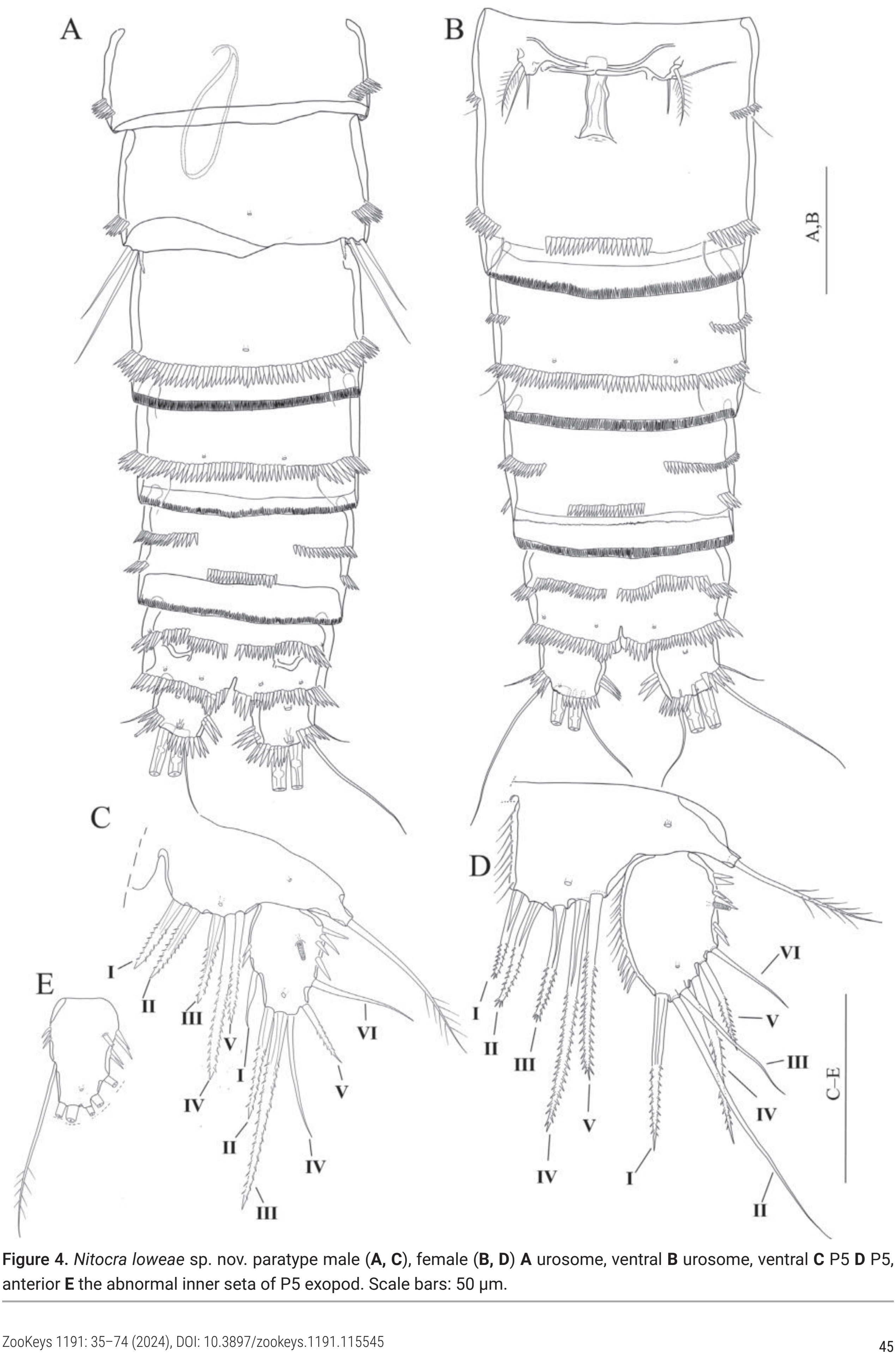

**Figure 4.** *Nitocra loweae* sp. nov. paratype male (**A, C**), female (**B, D**) **A** urosome, ventral **B** urosome, ventral **C** P5 **D** P5, anterior **E** the abnormal inner seta of P5 exopod. Scale bars: 50 µm.

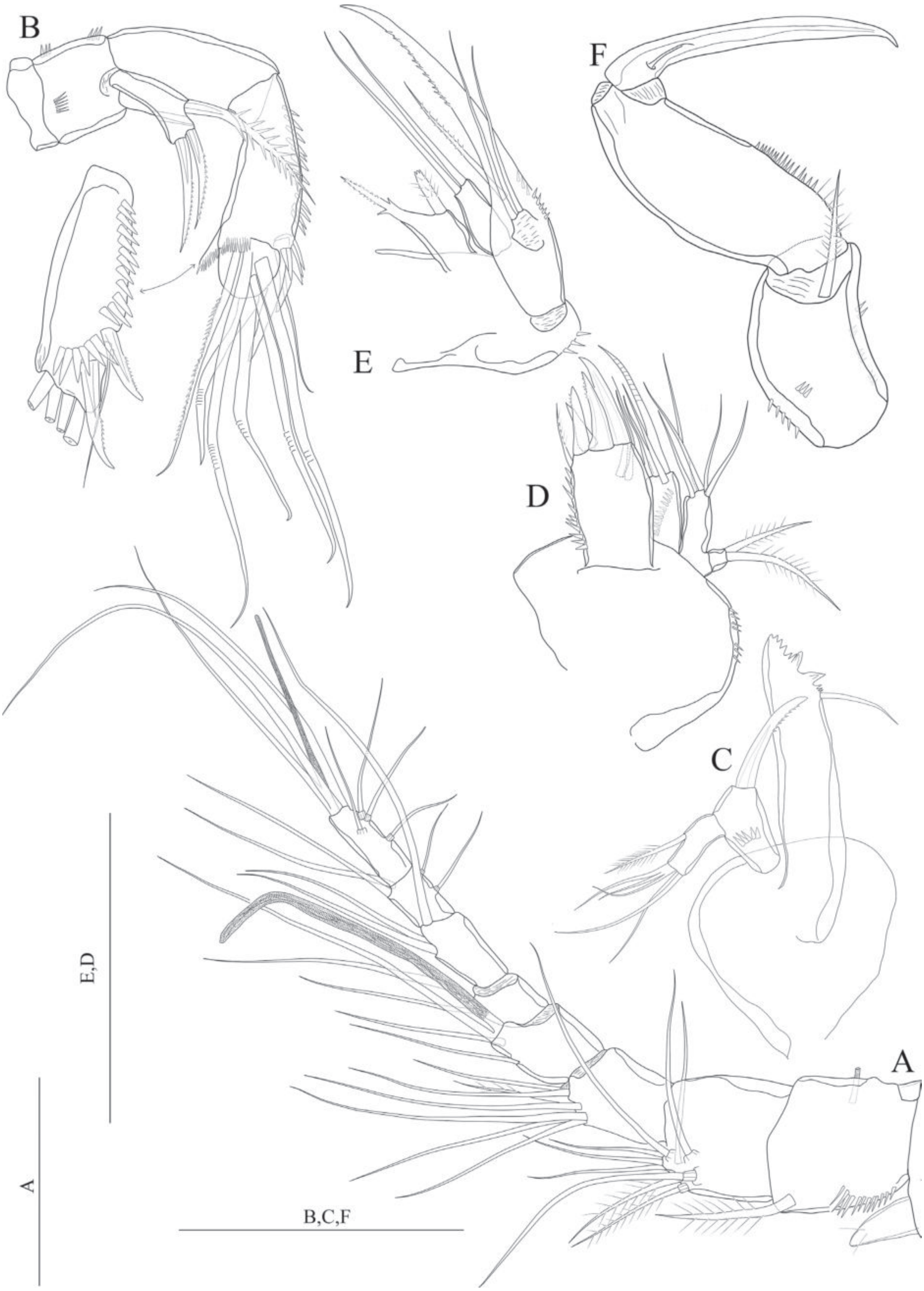

**Figure 5.** *Nitocra loweae* sp. nov. female holotype **A** antennule **B** antenna, with insert showing free endopodal lobe from another view **C** mandible **D** maxillule **E** maxilla **F** maxilliped. Scale bars: 50 μm.

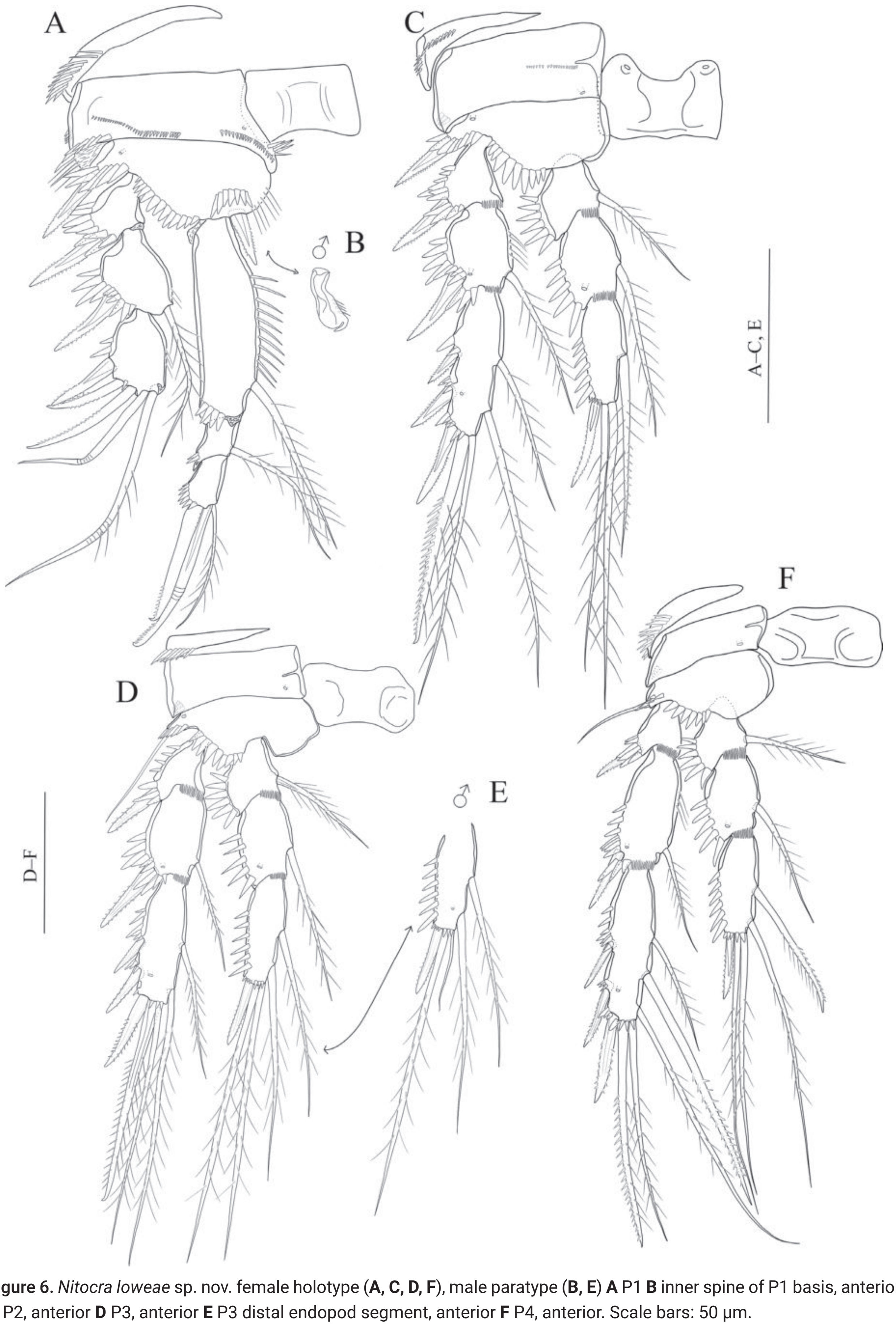

**Figure 6.** *Nitocra loweae* sp. nov. female holotype (**A, C, D, F**), male paratype (**B, E**) **A** P1 **B** inner spine of P1 basis, anterior **C** P2, anterior **D** P3, anterior **E** P3 distal endopod segment, anterior **F** P4, anterior. Scale bars: 50 µm.

**Figure 7.** *Nitocra loweae* sp. nov. male paratype **A** habitus, dorsal **B** habitus, lateral **C** anal somite and caudal rami, dorsal. Scale bars: 250 µm (**A, B**); 50 µm(**C**).

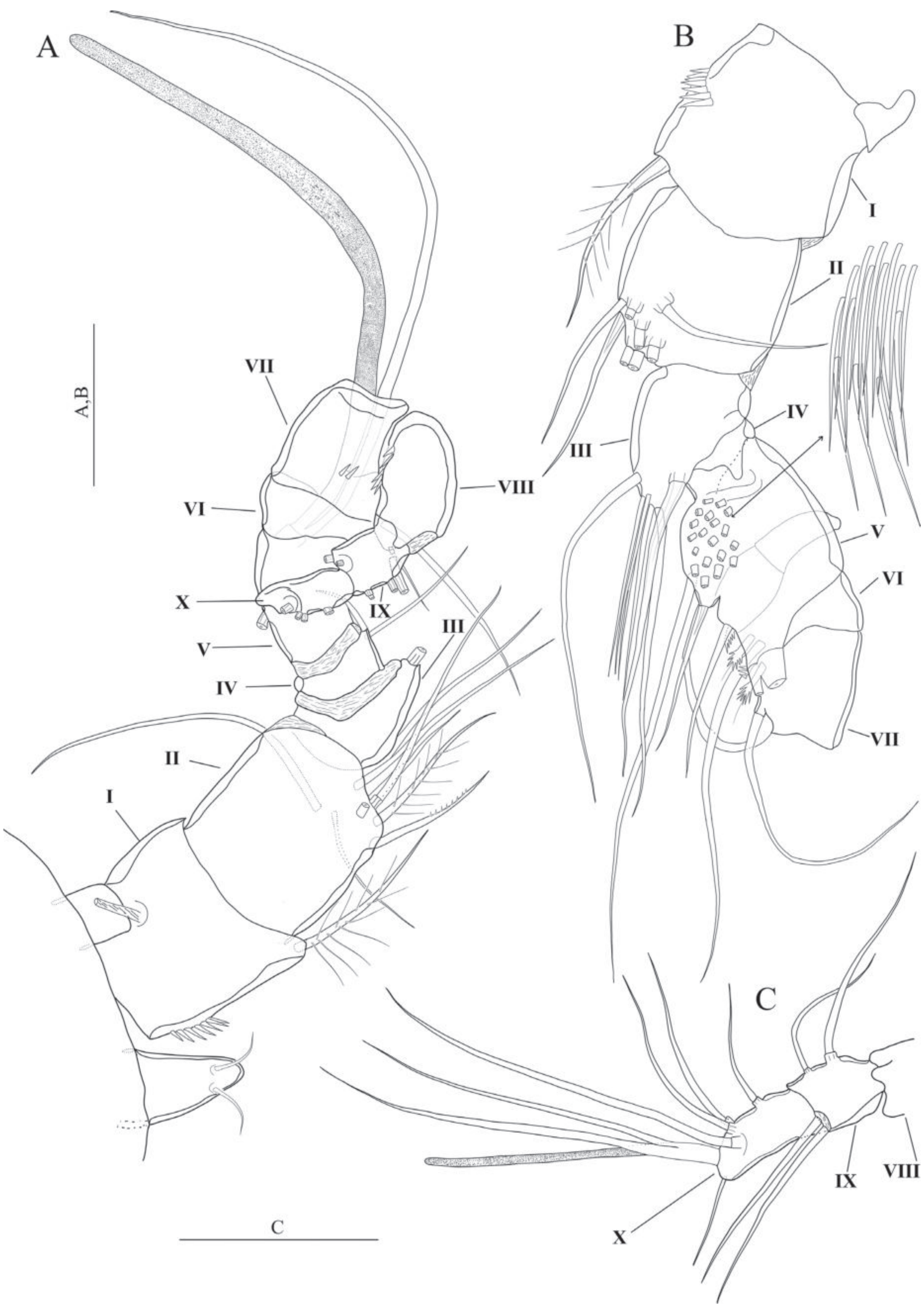

**Figure 8.** *Nitocra loweae* sp. nov. male paratype **A** antennule dorsal **B** antennule 1–7 segments, ventral **C** antennule 8–10 segments, ventral. Scale bars: 25 µm.

Maxilliped (Fig. 5F) subchelate. Syncoxa with one plumose subapical seta and with spinule rows on posterior surface. Basis ~ 2.6 × as long as maximum width with row of spinules along inner margin and with row of spinules on outer distal corner. Endopod represented by strong claw accompanied at base by minute naked seta.

P1–P4 (Fig. 6A, C, D, F) exopod and endopod three-segmented. Intercoxal sclerite squarish and unornamented. Praecoxa triangular, outer margin with row of spinules. Exp-1 without inner seta. P1, P2 and P4 exp-2 with few, P3 exp-2 without few spinules along inner margin.

P1 (Fig. 6A). Coxa with anterior row of spinules as figured and few spinules along inner margin. Basis with fine setules along inner margin, and with spinule row near the base of short pinnate inner spine located at the base of endopod. Outer basal bipinnate spine located close to the exopod, overlaid by a row of strong spinules. Exp-1 smallest segment, carrying row of strong spinules on outer margin and subapically one bipinnate outer spine. Exp-2 also with an outer row of strong spinules, a bipinnate outer spine, and a long plumose seta on inner margin. Exp-3 with fine setules near inner distal margin, with one geniculate semi-plumose apical seta, one geniculate naked distal seta and three pinnate outer spines. Enp-1 longer than exopod, ~ 3 × as long as maximum width, and ~ 2 × as long as enp-1, 2 combined; inner margin with long longitudinal spinules; distal margin with four robust spinules, and a long plumose seta on inner subdistal margin; enp-2, 3 squarish and equal in length; enp-2 with a long, plumose seta on inner margin, and with two spinules on outer distal margin; enp-3 with one plumose inner seta, one apical unipinnate distal geniculate seta, and one apical unipinnate outer seta, outer margin with a row of spinules.

P2–P4 (Fig. 6C, D, F). Coxa with row of posterior spinules near outer margin and with an anterior pore near inner distal corner. Basis triangular, ornamented with spinule row along distal margin between the base of exopod and endopod, with anterior spinules on outer corner near the base of outer seta/spine. Exp-1, 2 with anterior spinules near the base of outer spine extending to the outer margin of the segment. Exp-1, 2 and enp-1, 2 with hyaline frills along inner distal margin. All endopodal segments covered with robust spinules along outer margin. Exp-2, 3 and enp-2 with a pore on anterior surface. P2–P4 exp-2 with one plumose seta; P2, P3 exp-3 with seven, P4 exp-3 with eight elements.

P5 (Fig. 4D). Baseoendopod with five spinulose setae (slightly fringed at tip) along distal margin and with setules along inner margin, with two anterior pores (one near the base of outer basal seta and the other one near the distal margin; outer basal seta plumose. Exopod with one anterior pore distally, with setules along inner margin and with robust spinules along distal margin, with six setae (setae I–VI, numbered from inner to outer margin respectively), setae I, IV, and V pinnate; setae II, III, and VI naked; seta II is the longest; outer margin of exopodal lobe with one tube pore, and with double spinules group.

Armature formula of the swimming legs:

| P1<br>Exp/ Enp | P2<br>Exp/ Enp | P3<br>Exp/ Enp | P4<br>Exp/ Enp |
|---|---|---|---|
| 0.1.023 / 1.1.111 | 0.1.223 / 1.1.121 | 0.1.223 / 1.1.221 | 0.1.323/1.1.221 |

**Male.** Body sensilla and surface pores as figured (Fig. 7A, B). Anal operculum with sensilla and spinules as figured (Fig. 7C). Sexual dimorphism in antennule (Fig. 8A–C), inner spine of P1 basis (Fig. 6B), inner distal seta of P3 exp-3 (Fig. 6E), P5 (Fig. 4C, D), and P6 (Fig. 4A). The innermost seta of P5 is abnormal in paratype (Fig. 4E).

Antennule (Fig. 8A–C), ten-segmented, setal formula; 1- [1, plumose], 2- [1 plumose+ 1 unipinnate+ 8], 3-[7], 4-[2], 5-[19 setiform elements+ 4 multipinnate spine+3+1+ae], 6- [2], 7- [3], 8-[2], 9-[5], 10- [5 +acrothek)].

Inner spine of basis of P1 hook-like (Fig. 6B).

Inner distal seta of P3 exp-3 (Fig. 6E) slender and shorter than in female.

P5 (Fig. 4C) baseoendopod armed with five spinulose setae (four of them equal in length, the second inner seta longest and 1.5 × as long as the other setae) and with two pores on anterior surface; exopod with six setae (outer margin with one naked seta (seta VI) and one spinulose seta (seta V), apical margin with one naked (seta IV) and two spinulose setae (setae II and III), inner margin with one long plumose seta (seta I) (abnormal seta of one leg arrowed in Fig. 4C; the same seta of the other leg normal), with four strong spinules along outer proximal margin and with two or three spinules along inner proximal margin.

P6 (Fig. 4A) asymmetrical, only one leg functional; each leg with two naked outer setae and short inner plumose robust seta.

**Etymology.** The specific name is given in honour of Dr Miranda Lowe for her contribution to copepod taxonomy as a curator of the Crustacea collection of The Natural History Museum of London. It is a noun in the genitive case.

### ***Nitocra sonmezi* sp. nov.**

https://zoobank.org/8D69B94B-57EF-44DC-B356-FF245B506028
Figs 9–11

**Type material.** ***Holotype*:** Türkiye • 1 ♀ (dissected on 9 slides) (reg. no. TCRC-2007/10). Hatay Province Arsuz (Mağaracık); 36°14.008'N, 35°50.220'E; 24/11/2007 collected from interstitial habitat; leg. Drs Serdar Sönmez, Alp Alper, Serdar Sak, Süphan Karaytuğ (this specimen was previously deposited in the collection of Biology Department of Mersin University and was labelled as *N. affinis* as a result of the faunistic project from Mediterranean Sea, under the project number TÜBİTAK TBAG-106T590).

**Description (adult female holotype).** Body (Fig. 9A) semicylindrical; total body length measured from tip of the rostrum to posterior end of the caudal rami 400 µm (*n* = 1). Surface sensilla and pores as figured (Fig. 9A, B). Urosomites with finely serrated hyaline frills, and with complex spinule rows as figured (Fig. 9A–C). Genital double-somite (Fig. 9A, C) viewed as squarish in dorsal and ventral view, rectangular in lateral view (Fig. 9B), with lateral suture line; with two continuous spinule rows dorsally extending laterally as figured. Anal somite (Fig. 9A, C) with two pores located ventrolaterally and medially, anal operculum with fifteen robust spinules. Caudal rami (Fig. 9A, C) short and squarish; with fine setules near the base of seta VII, with row of spinules dorsally near the base of seta II; few spinules present around inner distal margin; with seven setae: seta I minute; seta II slightly displaced dorsally; setae IV and V well-developed and pinnate; seta VI located near inner distal margin and naked; seta VII tri-articulate at base.

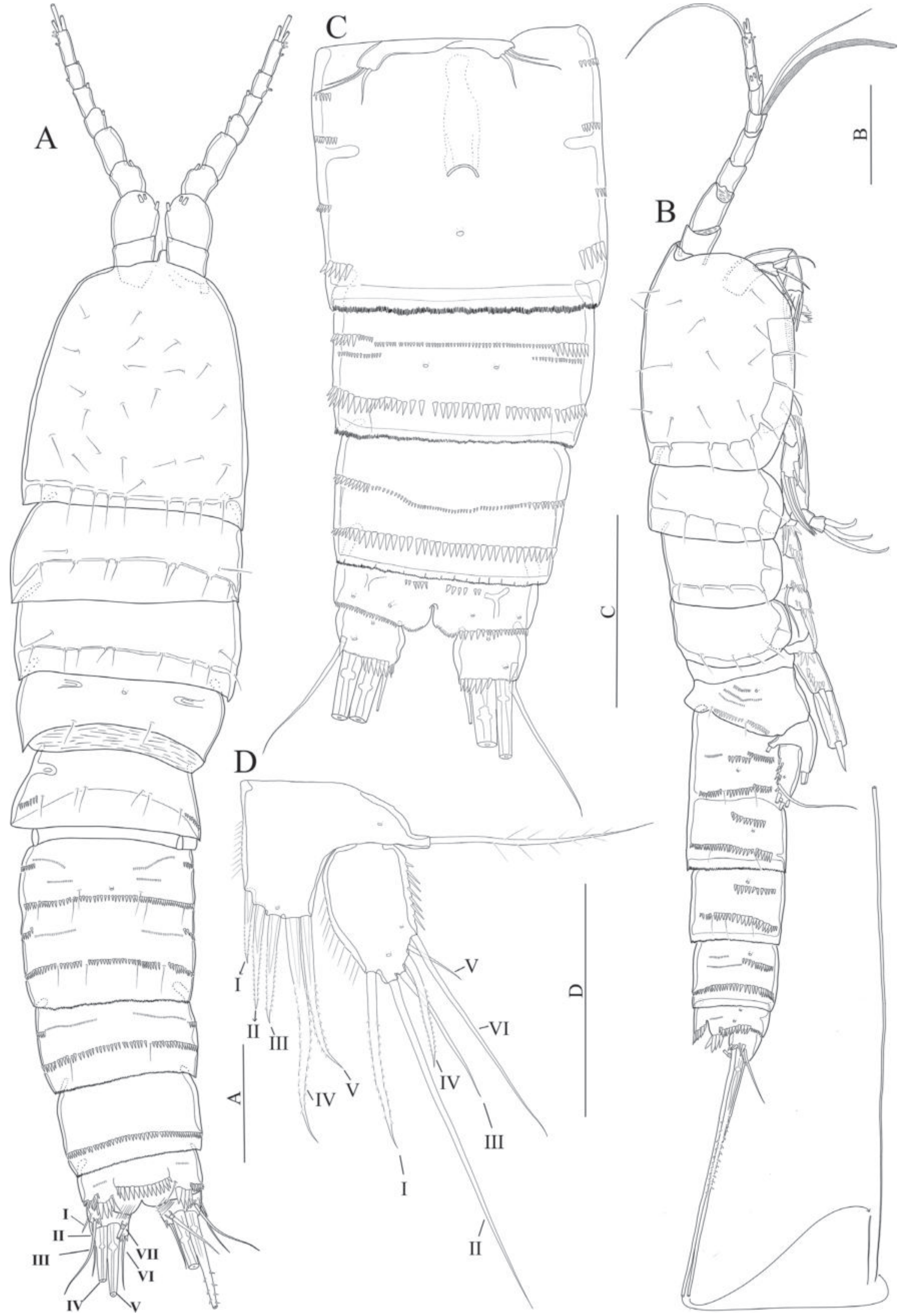

**Figure 9.** *Nitocra sonmezi* sp. nov. female holotype **A** habitus, dorsal **B** habitus, lateral **C** urosome, ventral (P5-bearing somite omitted) **D** P5, anterior. Scale bars: 50 µm.

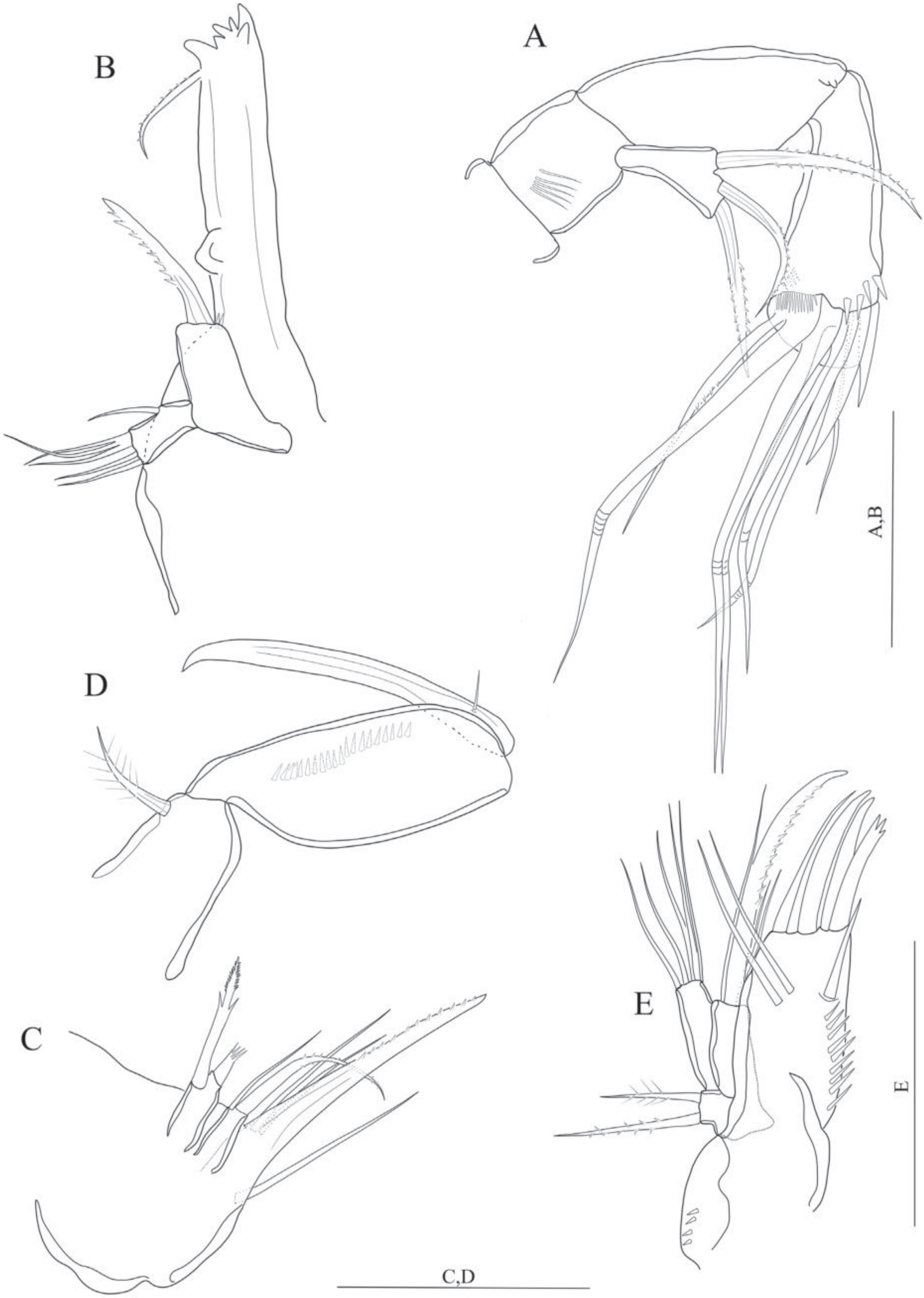

**Figure 10.** *Nitocra sonmezi* sp. nov. female holotype **A** antenna **B** mandible **C** maxilla **D** maxilliped **E** maxillule. Scale bars: 25 µm.

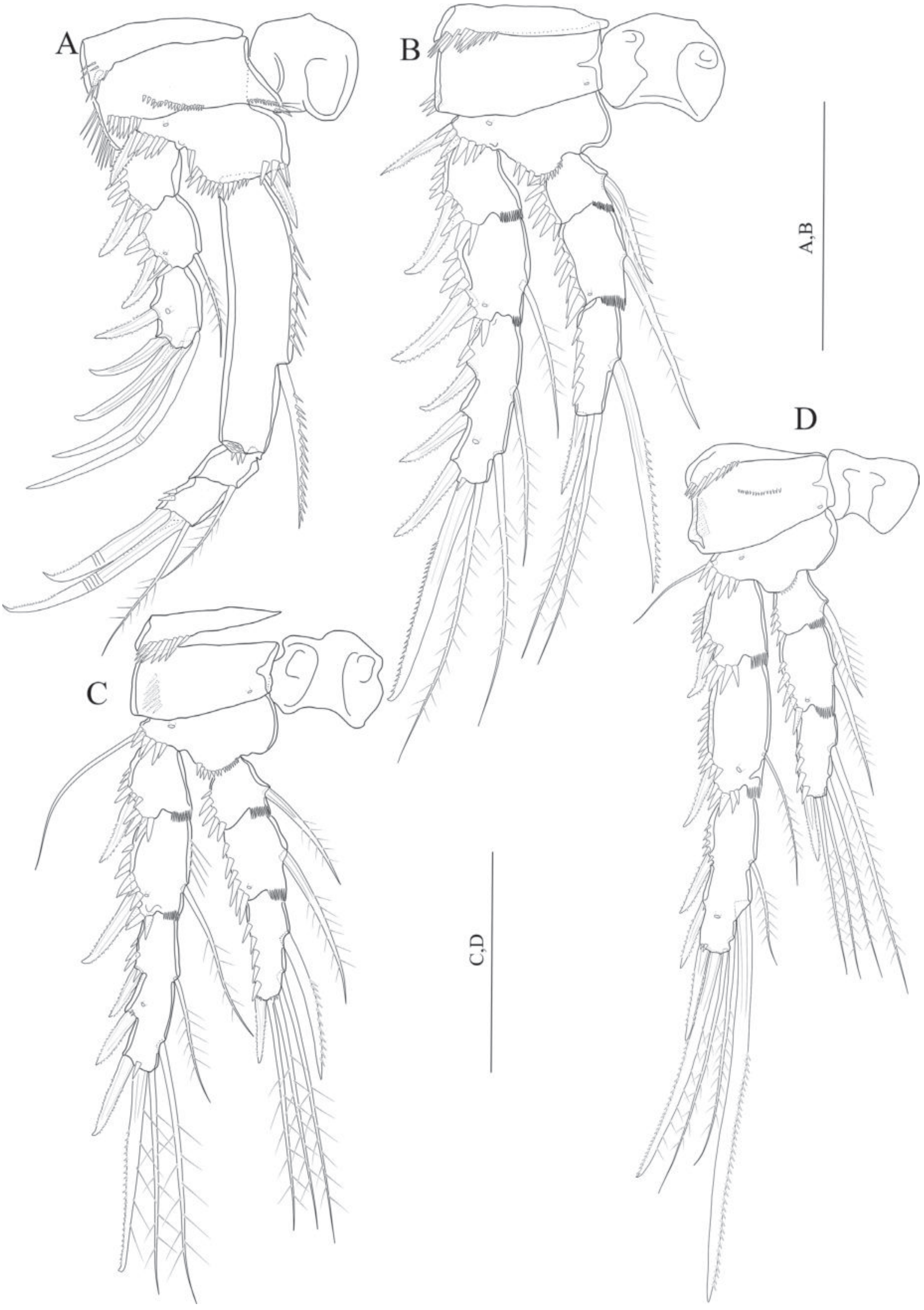

**Figure 11.** *Nitocra sonmezi* sp. nov. female holotype **A** P1, anterior **B** P2, anterior **C** P3, anterior **D** P4, anterior. Scale bars: 50 µm.

Antennule eight-segmented, setal formula 1-[1, plumose], 2-[8 +1 plumose], 3-[8], 4-[3 +1 ae], 5-[2], 6-[3], 7-[4], 8-[5 +acrothek)]. Maximum length/maximum width ratio of antennular segments 1:1.1:1.4:1.8:1.2:2:1.4:2.8.

Antenna (Fig. 10A) comprising coxa, allobasis, one-segmented endopod and one-segmented exopod same as in *N. loweae* sp. nov. except for allobasis without spinule rows proximally. Endopod without longitudinal row of spinules along inner margin. Exopod with a weakly pinnate subdistal seta.

Mandible (Fig. 10B) coxal gnathobase with coarse teeth ventrally, one unipinnate seta dorsally, palp uniramous; two-segmented, comprising basis and one-segmented endopod same as in *N. loweae* sp. nov. except for endopod lateral seta is naked, basis without lateral spinule row.

Maxilla (Fig. 10C) with syncoxa and two well-developed endites same as in *N. loweae* sp. nov. except for syncoxa without spinule row; distal endite of syncoxa cylindrical with one naked, and one stronger and longer semi-pinnate apical setae, allobasis without spinules along convex margin near the base of endopod.

Maxilliped (Fig. 10D) subchelate same as in *N. loweae* sp. nov. except for syncoxa unornamented; basis without spinules on outer distal corner.

Maxillule (Fig. 10E) praecoxa, coxal endite, basis same as in *N. loweae* sp. nov. except for endopod with one plumose and one bipinnate seta, curved seta of coxal endite long and unipinnate.

P1–P4 (Fig. 11A–D) exopod and endopod three-segmented. Intercoxal sclerite squarish and unornamented. Praecoxa triangular, outer margin with row of spinules. Exp-1 without inner seta.

P1 (Fig. 11A) same as in *N. loweae* sp. nov. except for basis without spinules along inner margin; inner margin of exp-1, 2 unornamented; innermost geniculate seta of exp-3 naked; exopod reaching slightly above the middle of enp-1 and aligned with the insertion of the inner seta of enp-1; enp-1 ~ 4.3 × as long as maximum width; subdistal seta of enp-1 unipinnate and located more proximally than that of *N. loweae* sp. nov. enp-2 without spinules on outer distal margin; enp-3 with two small spinules on outer margin.

P2 (Fig. 11B) similar to that of *N. loweae* sp. nov. except for exp-2 without setules along inner margin; inner seta of enp-3 unipinnate and stronger than in *N. loweae* sp. nov.

P3 (Fig. 11C) similar to that of *N. loweae* sp. nov. except for exp-2 with setules along inner margin; innermost seta of enp-3 unipinnate and stronger than in *N. loweae* sp. nov.

P4 (Fig. 11D) similar to that of *N. loweae* sp. nov. except for exp-2 without setules along inner margin; middle inner seta of exp-3 unipinnate, longest and stronger than that of *N. loweae* sp. nov.; innermost seta of enp-3 longest and plumose.

P5 (Fig. 9D) similar to that of *N. loweae* sp. nov. except for inner baseoendopod lobe narrower and extends halfway along the exopod, innermost seta shortest (seta I); outermost seta of exopod (seta VI) longer than in *N. loweae* sp. nov.

Armature formula of swimming legs same as in *N. loweae* sp. nov.

**Male.** Unknown.

**Etymology.** The specific name is given in honour of Associate Prof Dr Serdar Sönmez from Adıyaman University for his contribution to copepod taxonomy in Türkiye. It is a noun in the genitive case.

## ***Nitocra alperi*** **sp. nov.**

https://zoobank.org/A86AFF9C-0926-4A71-8E83-040A556CF894
Figs 12–14

**Type material.** ***Holotype*:** India • 1 ♀ (dissected on 7 slides) (NHMUK reg. no. 2023.0000). Indian Ocean, Aldabra; large tide salted lagoon; W. of Point Hadroul. Coll. Pres. K.G. Mc Kenzie, 1968; J.B.J. Wells det. (material originally registered as *N. affinis* under NHMUK reg. no. 1972.6.13.17-21).

**Description (adult female holotype).** Body (Fig. 12A, B) similar to *N. loweae* sp. nov., except for total body length 476 μm (*n* = 1) measured tip of the rostrum to posterior end of the caudal rami. Pores and sensilla as figured (Fig. 12A, B).

Anal somite (Figs 12A, 13A, B), with anal operculum bearing seventeen posterior spinules; with row of robust spinules flanking each side of the anal operculum; with a posterior row of small spinules, and two pair of pores on ventrally.

Antennule eight-segmented as in *N. affinis*. Setal formula 1-[1, plumose], 2-[8 +1 plumose], 3-[8], 4-[3 +1 ae], 5-[2], 6-[3], 7-[4], 8-[5 +acrothek)]. Maximum length/maximum width ratio of antennular segments as 1:1.3:1.3:1.6:1.3:1.1:1.1:1.6.

Antenna (Fig. 13C) similar to that of *N. loweae* sp. nov. except for allobasis with spinules only on midway inner margin; subdistal seta of exopod weakly pinnate.

Mandible (Fig. 13D) similar to that of *N. loweae* sp. nov. except for exopod with four naked apical setae (two of them basally fused at base) and without spinules.

Maxilla (Fig. 13E) similar to that of *N. loweae* sp. nov. except for allobasis without spinules along convex margin near the base of endopod; endopod with one long naked seta.

Maxilliped (Fig. 13F) similar to that of *N. loweae* sp. nov. except for syncoxa unornamented.

Maxillule (Fig. 13G) similar to that of *N. loweae* sp. nov. except for coxal endite without spinule row.

P1 (Fig. 14A) similar to that of *N. loweae* sp. nov. except for coxa without spinules on/near inner margin; basis without setules along inner margin; exopod slightly extends the enp-1; enp-1 ~ 2.6 × as long as maximum width, inner margin with less spinules along inner margin, subdistal seta unipinnate and located more proximally than in *N. loweae* sp. nov.; inner margin of enp-2 with one setule, outer distal margin with few fine spinules not extending to inner margin.

P2 (Fig. 14B) similar to that of *N. loweae* sp. nov. except for intercoxal sclerite with spinules on anterior surface; basis with setules along inner margin; inner seta of enp-3 uni-plumose and stronger than in *N. loweae* sp. nov.

P3 (Fig. 14C) similar to that of *N. loweae* sp. nov. except for intercoxal sclerite with spinules on anterior surface; basis with setules along inner margin; exp-2 with setules along inner margin; innermost seta of enp-3 unipinnate and stronger than in *N. loweae* sp. nov.

P4 (Fig. 14D) similar to that of *N. loweae* sp. nov. except for exp-1 with two fine setules along inner margin; middle inner seta of exp-3 bipinnate distal half, longest and stronger than that of *N. loweae* sp. nov.; innermost seta of enp-3 uni-plumose and stronger than in *N. loweae* sp. nov.

P5 (Fig. 14E) similar to that of *N. loweae* sp. nov. except for inner baseoendopod lobe reaching middle of the exopod; exopod tapering apically, and ~ 1.5 × as long as maximum width, outermost seta much longer, seta next to outermost seta slender and naked.

**Figure 12.** *Nitocra alperi* sp. nov. female holotype **A** habitus, dorsal **B** habitus, lateral. Scale bars: 50 µm.

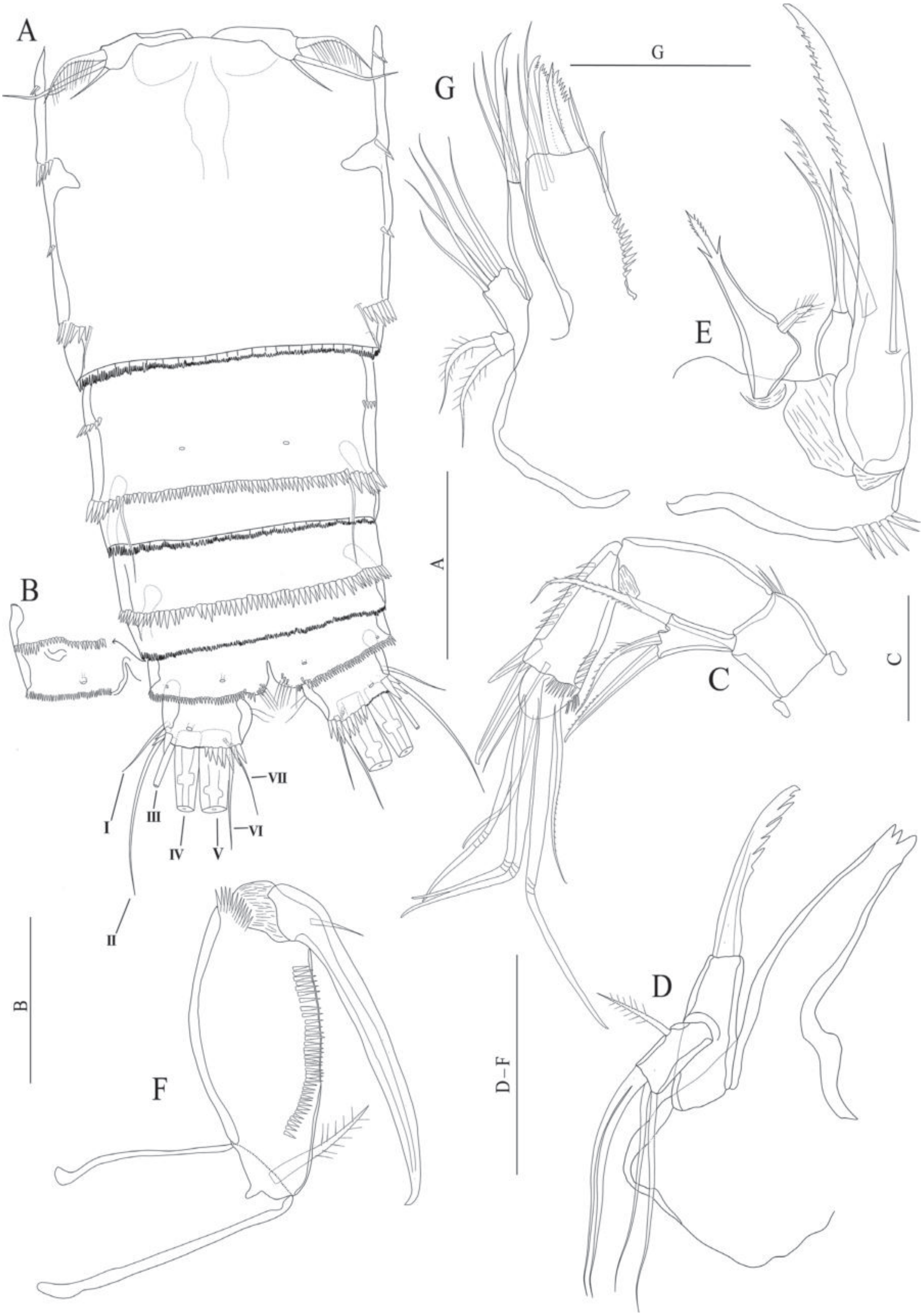

**Figure 13.** *Nitocra alperi* sp. nov. female holotype **A** urosome, ventral (P5-bearing somite omitted) **B** right part of anal somite showing spinule ornamentation, ventral **C** antenna **D** mandible **E** maxilla **F** maxilliped **G** maxillule. Scale bars: 50 µm (**A–C**); 25 µm (**D–G**).

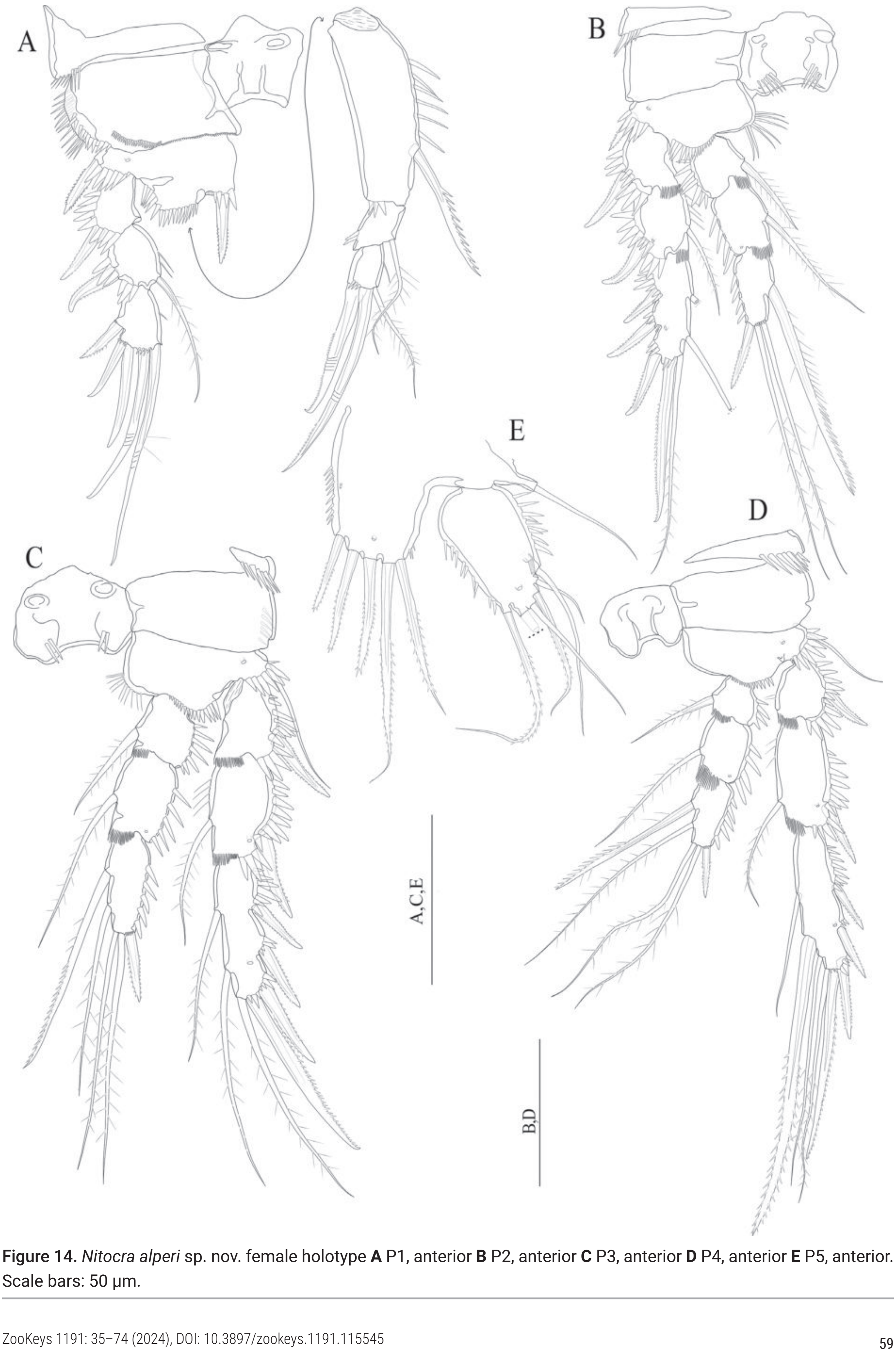

**Figure 14.** *Nitocra alperi* sp. nov. female holotype **A** P1, anterior **B** P2, anterior **C** P3, anterior **D** P4, anterior **E** P5, anterior. Scale bars: 50 µm.

Armature formula of swimming legs (not shown) same as in *N. loweae* sp. nov.

**Male.** Unknown.

**Etymology.** The specific name is given in honours of Associate Professor Dr Alp Alper from Balıkesir University for his contribution to copepod taxonomy. It is a noun in the genitive case.

### *Nitocra serdarsaki* sp. nov.

https://zoobank.org/75F4D4A1-3CE2-404E-974D-D11A1F9D4982

Figs 15–17

**Type material.** ***Holotype*:** TÜRKIYE • 1 ♂ (dissected on 7 slides) (reg. no. TCRC-2013/16). Ertuğrul Bay, Seddülbahir Beach; 40°2.5608'N, 26°11.0772'E; 29/09/2013; Drs Serdar Sak, Alp Alper, Orkan Metin Leg. This specimen was previously deposited in the collection of Biology Department of Balıkesir University which was labelled as *N. affinis* as a result of the faunistic project from Saros Bay, under the project number TÜBİTAK TBAG-212T105).

**Description (adult male holotype):** Body (Fig. 15A, B) semi-cylindrical, total body length measured from tip of the rostrum to posterior end of the caudal rami 582 μm (*n* = 1). Sensilla and pores as figured (Fig. 15A–D). Rostrum small, with two sensilla on distal margin, without rostral extension apically (Fig. 15E). Anal somite with two sensilla on both sides of anal operculum; posterior end covered with robust spinules; inner distal and lateral margin with small spinules and a pair of pores medially on ventral surface. Anal operculum (Fig. 15C) with eleven robust spinules along posterior margin. Caudal rami small and squarish; with transverse fine setules dorsally extending inner margin dorsally, and with a row of spinules laterally; ventrally with pores on near anterior and posterior margin (Fig. 15D).

Antennule (Fig. 16A). Setal pattern and structure similar to that of *N. loweae* sp. nov. except for segments weaker developed than in *N. loweae* sp. nov.

Antenna (Fig. 16B) comprising coxa, allobasis, one-segmented endopod and one- segmented exopod similar to that of *N. loweae* sp. nov. except for allobasis with spinules only on the middle of inner margin; spinule row along inner margin of free endopodal segment; more sparsely distributed than in *N. loweae* sp. nov.; inner apical seta of free endopodal segment 1.5 × as long as the adjacent apical seta; subdistal seta of exopod weakly pinnate.

Mandible (Fig. 16C) similar to that of *N. loweae* sp. nov. except for exopod with four naked apical setae (two of them fused basally) and without spinules.

Maxilla (Fig. 16D) similar to that of *N. loweae* sp. nov. except for allobasis without spinules along convex margin near the base of endopod; endopod with one long seta.

Maxilliped (Fig. 16E) similar to that of *N. loweae* sp. nov. except for syncoxa ~ 2.6 × as long as maximum width; basis ~ 2.7 × as long as maximum width.

Maxillule similar to that of *N. loweae* sp. nov.

P1 (Fig. 17A) similar to that of *N. loweae* sp. nov. except for exopod extends the level of inner seta of enp-1; enp-1 ~ 4.5 × as long as maximum width, inner margin with four well-developed spinules along inner margin, subdistal unipinnate seta located more proximally than in *N. loweae* sp. nov.; exp-3 with one spinule on outer proximal margin.

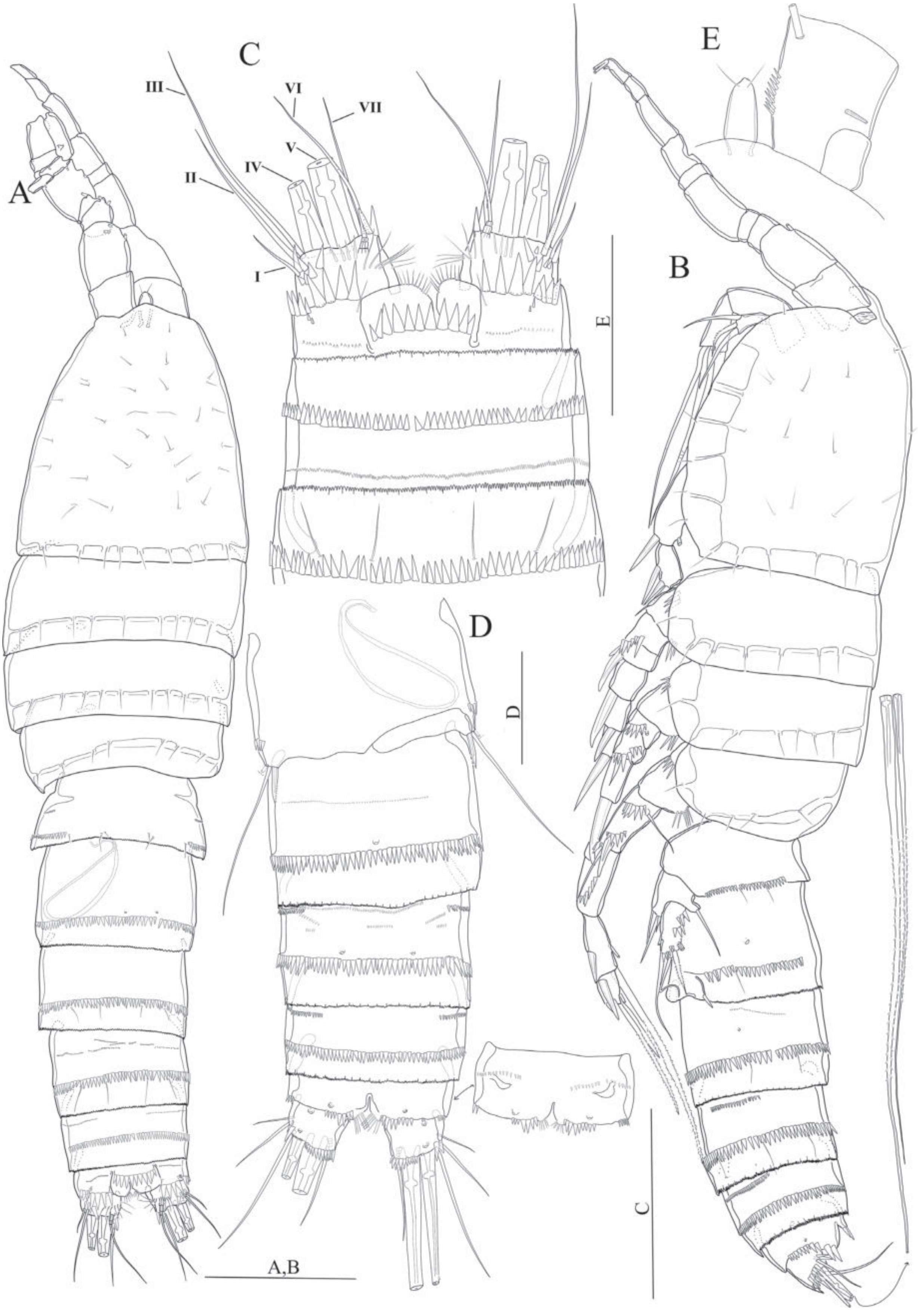

**Figure 15.** *Nitocra serdarsaki* sp. nov. male holotype **A** habitus, dorsal **B** habitus, lateral **C** penultimate and anal somites, dorsal **D** urosome, ventral (P5-bearing somite omitted) **E** rostrum and first segment of antennule. Scale bars: 50 µm.

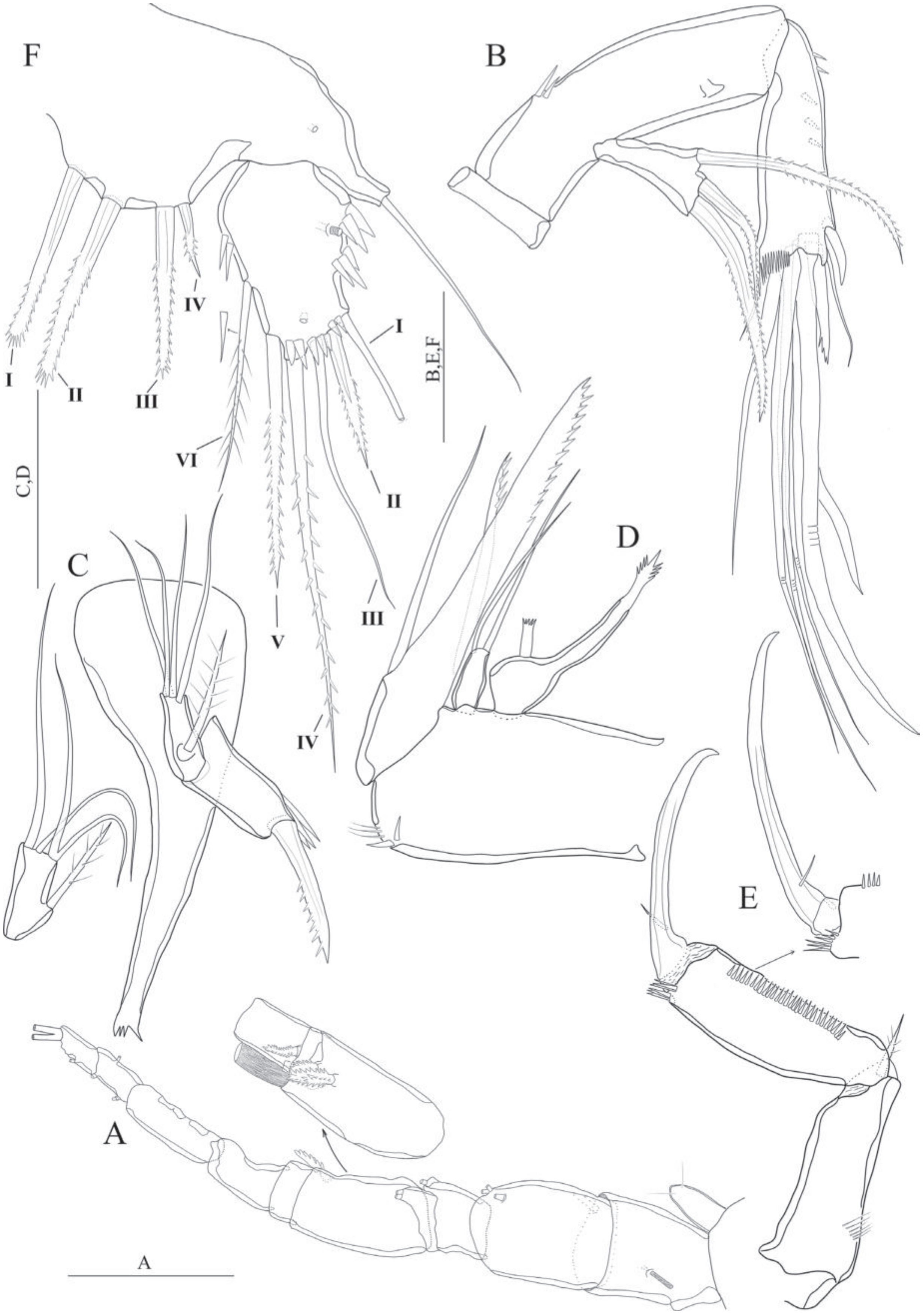

**Figure 16.** *Nitocra serdarsaki* sp. nov. male holotype **A** antennule **B** antenna **C** mandible **D** maxilla **E** maxilliped **F** P5, anterior. Scale bars: (**A**) 50 µm; (**C–F**) 25 µm.

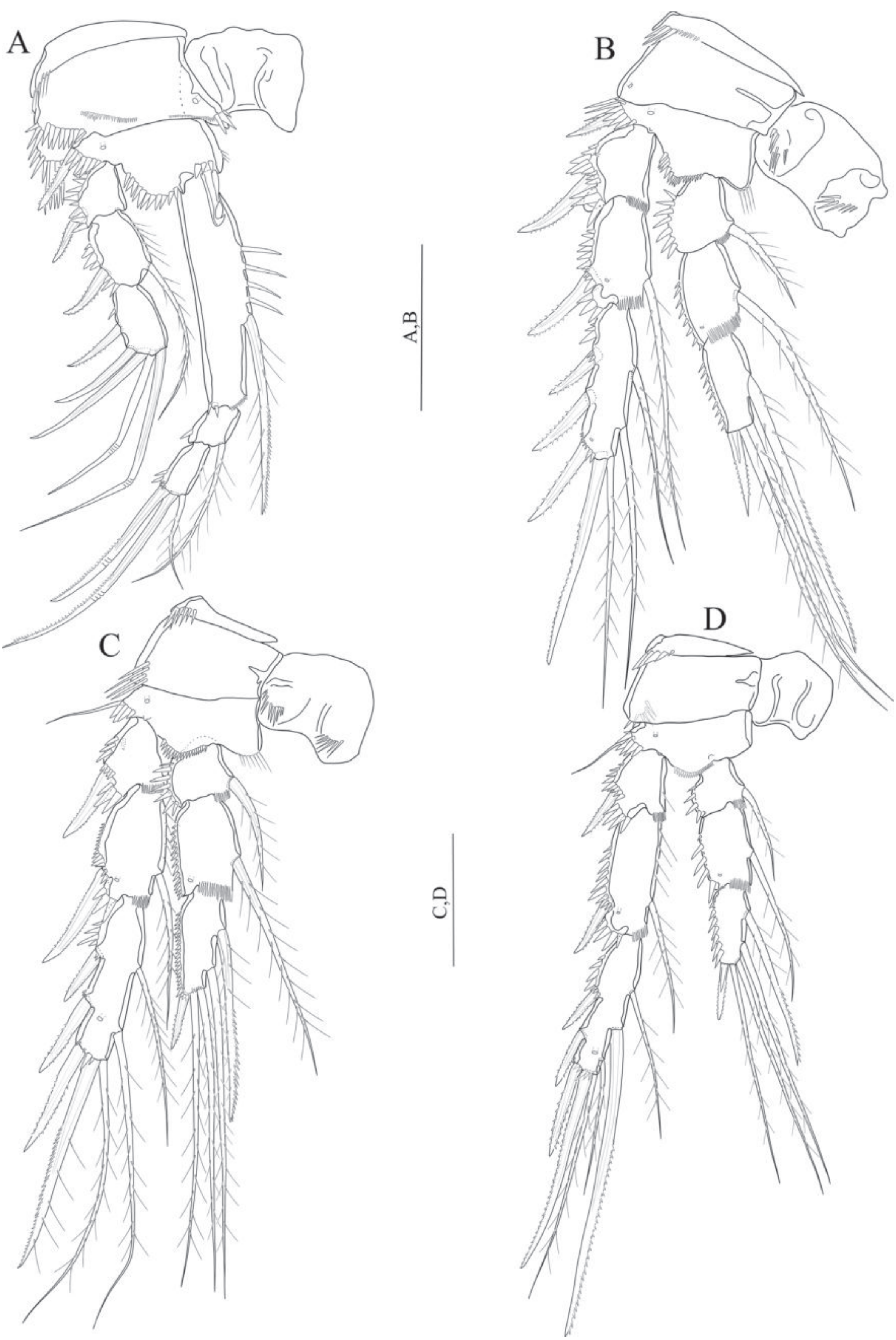

**Figure 17.** *Nitocra serdarsaki* sp. nov. male holotype **A** P1, anterior **B** P2, anterior **C** P3, anterior **D** P4, anterior. Scale bars: 50 µm.

P2 (Fig. 17B) similar to that of *N. loweae* sp. nov. except for intercoxal sclerite with spinules on anterior surface; coxa unornamented; basis with setules along inner margin; inner margin of exp-3 unornamented; spinules along outer margin of exp-2, 3 weaker than in *N. loweae* sp. nov.; inner seta of enp-3 unipinnate at distal half and stronger than in *N. loweae* sp. nov.

P3 (Fig. 17C) similar to that of *N. loweae* sp. nov. except for intercoxal sclerite with spinules on anterior surface; basis with setules along inner margin; Innermost seta of enp-3 unipinnate at distal half and stronger than in *N. loweae* sp. nov.; inner apical seta naked and as long as outer spine.

P4 (Fig. 17D) similar to that of *N. loweae* sp. nov. except for spinulose row near the base of endopod weakly developed; exp-1 with two fine setules along inner margin; middle inner seta of exp-3, longest and stronger than that of *N. loweae* sp. nov.; innermost seta of enp-3 stronger than in *N. loweae* sp. nov.; subdistal inner seta of enp-3 shorter than in *N. loweae* sp. nov.

P5 (Fig. 16F) similar to that of *N. loweae* sp. nov. except for baseoendopod with four bipinnate setae, the outermost seta short and ~ 1/2 as long as the other setae.

**Female.** Unknown

**Etymology.** The specific name is given in honour of Prof Dr Serdar Sak from Balıkesir University for his contribution to copepod taxonomy in Türkiye. It is a noun in the genitive case.

## Discussion

The family Ameiridae ranks third within the order Harpacticoida in terms of species number (Boxshall and Halsey 2004). Members of the family inhabit a wide range of sediment types and occur in virtually all salinity regimes besides living as associates of some invertebrates (Karanovic et al. 2015). The taxonomy and phylogeny of the family Ameiridae are still problematic due to numerous ill-defined genera and lack of detailed descriptions of a great deal of species (Conroy-Dalton and Huys 1996, 1998; Karanovic et al. 2015). The genus *Nitocra*, which also has a notoriously challenging and problematic taxonomy, is the largest ameirid genus, at present comprising 81 valid species and subspecies (Karanovic et al. 2015; Huys 2021; Fuentes-Reinés et al. 2022). Several factors are responsible for the origin of the current taxonomic confusion surrounding the genus *Nitocra*. The primary issue lies in the classification of *Nitocra*, which encountered initial difficulties when Boeck (1865) provided an insufficient definition of the genus, offering only fragmentary descriptions devoid of illustrations. Furthermore, the majority of conventional marine genera described and outlined in the early years of the 20th century (Sars 1907, 1911a, b, c; Lang 1935, 1936) did not substantially enhance the precise delineation of either the type genus *Ameira* or the genus *Nitocra*. The third factor blurring the generic boundary of the genus *Nitocra* is the arbitrary addition of new species, which resulted in the amalgam of phylogenetically unrelated species into the genus. Due to the taxonomic confusion within the genus *Nitocra* arising from these factors, resolving the complexity through a single study has become an impossible task. Consequently, urgently conducting modern standard redescriptions of numerous species within the genus with insufficient descriptions will significantly contribute to solving the problem (Karanovic and Pesce 2002).

Therefore, within this scope, the redefinition of *N. affinis*, one of the important polytypic species in the genus, based on lectotype material in this study has provided significant contributions to resolving the *N. affinis* species complex and solving the taxonomic problem within the genus. On the other hand, it is crucial to delineate species groups within the genus from a phylogenetic perspective. Despite being the largest genus within the family Ameiridae, with a notoriously difficult and problematic taxonomy, no attempts have been made to delineate species groups within the genus *Nitocra* until Gómez et al. (2012) who attempted to establish species groups within the genus *Nitocra* in order to ground the classification of the genus on a phylogenetic basis although they have not conducted a phylogenetic tree-based study. Gómez et al. (2012) recognised three species groups based on the setal formula of P1 exp-2, 3. The first group of species contained *Nitocra sewelli* and *N. platypus bakeri* which bear one inner seta on P1 exp-2 and four setae on P1 exp-3; the second group of species comprised *N. reducta reducta*, *N. delaruei*, *N. blochi*, *N. gracilimana*, *N. phlegrea*, and *N. chelifer* which lack an inner seta on P1 exp-2, but bear five setae on P1 exp-3; the third group of species accommodated the rest of the species with one inner seta on P1 exp-2 and five setae on P1 exp-3. Gómez et al. (2012) also recognised a distinct subgroup of species within the third group, based on the setal formula of P2–P4 exp-3 (7-7-7), P2–P4 enp-3 (4-5-5), and P2–P4 enp-1 (1-1-1). *Nitocra affinis*, *N. colombiensis*, *N. rijekana*, *N. stygia*, *N. hamata*, *N. elegans*, *N. sonmezi* sp. nov., *N. loweae* sp. nov., *N. serdarsaki* sp. nov., and *N. alperi* sp. nov., constitute another subgroup of species within the group which can be called the *affinis* group on the basis of a) by having a spinulose, long, spine-like inner middle seta on P4 exp-3, b) by having the same setal formula on the P2–P4 exp-3 (7-7-8) and P2–P4 enp-3 (4-5-5), c) by the number of seta on the P2–P4 exp-2, P2–P4 enp-1, 2 (1-1-1), d) by the elongated P1 enp-1.

*Nitocra affinis* is clearly distinguished from other congeners in the *affinis* group by the combination of the following characters in female; rostral projection reaching ~ 1/2 of the rostral length, anal operculum with 14 spinules, the reduced maxillary endopod with one slender seta, inner middle seta of P4 exp-3 strongly spinulose and long, female P5 baseoendopod with five and exopod with six setae respectively. Male P5 baseoendopod with four and exopod with six setae, respectively. *Nitocra affinis* has subsequently been reported from several other localities: Willey (1930) recorded it from Mangrove Lake in Bermuda, presenting only the setal formula of swimming legs and the number of spinules (fifteen) on the anal operculum. Vervoort (1964) reported *N. affinis* from Ifaluk Atoll in the Pacific Ocean, describing the P4 exp-3 middle inner seta as strong and long, anal operculum as spinulose, antenna exopod as one-segmented, and P1 enp-1 as slightly longer than the exopod. Unfortunately, the specific identity of the above-mentioned populations cannot be verified due to insufficient morphological data and should therefore be considered as unverified records. However, considering the isolated environments of *Nitocra affinis* from Bermuda and Ifaluk Atoll, it is strongly possible that each of these populations of *N. affinis* may represent distinct species.

Rajthilak et al. (2015) recently recorded *Nitocra affinis* from South-east India, providing both morphological and molecular data. But, based on the morphological information provided by Rajthilak et al. (2015), even the familial identification of the south-east Indian population of *N. affinis* is uncertain and therefore this record cannot be verified.

It has been demonstrated several times that many so-called cosmopolitan harpacticoid species in fact represent species complexes (Gómez et al. 2012; Karanovic et al. 2015; George 2018; Karaytuğ et al. 2021). Vervoort (1964) and Fuentes-Reinés and Suárez-Morales (2014) proposed the potential existence of a species complex within *N. affinis*. Through comprehensive morphological assessments of specimens gathered from diverse geographical locations initially labelled as *N. affinis*, this investigation has unveiled the presence of four new species in this study, thus affirming *N. affinis* as a species complex.

Lack of original descriptions or insufficient taxonomic information are the main reasons for the formation of species complexes. The swimming legs segmentation and their setal formula, the number of segments in the antennule and the structure of antennary exopod are the most commonly used morphological characters for delineation of the species in harpacticoid taxonomy (Wells 2007). Therefore, in recent studies, most researchers have concentrated on finding microcharacters such as spinule ornamentation (Alper et al. 2023) or pore signature (Karanovic et al. 2015; Karanovic and Cho 2016) which proved to be helpful in differentiating closely related morphospecies. So, it was not surprising that similar results emerged in the ameirid taxonomy. For example, Karanovic and Cho (2012) distinguished two *Ameira* species based on setules, spinules or pore ornamentations on the somites or appendages. In this study, within the *N. affinis* complex four new species namely *N. sonmezi* sp. nov., *N. serdarsaki* sp. nov., *N. alperi* sp. nov., and *N. loweae* sp. nov., were revealed mostly based on micro-morphological characters which, once again, demonstrated their importance in copepod taxonomy.

*Nitocra loweae* sp. nov. was collected from Brighton and identified as *N. affinis* (Ventham 2011). *Nitocra loweae* sp. nov. is described on the basis on one female and a male specimen and can be easily distinguished from other congeners in the *affinis* group by (a) the robust, spinulose ornamentations of urosomites, (b) by the presence of twelve large dorsal spinules on the anal operculum, c) the maxilla endopod with two slender setae. Details of the specific differences are given in Table 1. *Nitocra loweae* sp. nov. and *N. affinis* can be easily differentiated by the following characters: the antennule of *N. loweae* sp. nov. differs from that of *N. affinis* in having two plumose setae and one plumose seta on the second and third segment, respectively; the two inner setae on the seventh segment set close to each other in *N. affinis* but widely separated in *N. loweae* sp. nov.; the proximal-most inner seta on the eighth segment in *N. affinis* is located more distally than that of *N. loweae* sp. nov.; *N. loweae* sp. nov. lacks the rostral projection on the rostrum and has five setae on the P5 baseoendopod of the male, whilst according to Gurney's (1927) description, *N. affinis* has four setae on the P5 baseoendopod of the male. *Nitocra loweae* sp. nov. has four naked distal setae and two naked lateral setae on the mandibular endopod, and two slender setae on the maxilla endopod, whereas all other species in the *affinis* group have four naked distal setae and one lateral seta on the mandibular endopod, and one slender seta on the maxilla endopod. In comparison to other species within the *affinis* group, *N. loweae* sp. nov. is regarded as exhibiting a more primitive state with respect to these characters.

**Table 1.** Differentiating characters of the affinis species group. +: present; -: absent; ?: unknown.

| | number of spinules on anal operculum | apical rostral projection | ♂ P5 setae on endopod and exopod of male | inner ornamentation of the caudal rami | ornamentation of the inner seta of P1 enp-1 | Body length (mm) ♀ | Body length (mm) ♂ | seta of mandibular endopod | seta of maxillary endopod |
|---|---|---|---|---|---|---|---|---|---|
| ***N. affinis*** | 14 | + | 4:6 | fine setules | bipinnate | 0.61 (Gurney 1927) | 0.48 (Gurney 1927) | 4 naked on distal; 1 plumose on lateral | 1 long seta |
| ***N. californica* Lang, 1965** | 14 | - | 4:6 | fine setules | plumose | 0.70 | ? | 4 naked on distal; 1 plumose on lateral | 1 long seta |
| ***N. colombiensis* Fuentes-Reinés, Suárez-Morales, 2014** | 16 | + | 3:6 | small, spinules | plumose | 0.70 | 0.51 | 4 naked on distal; 1 plumose on lateral | 1 long seta |
| ***N. stygia* Por, 1968** | 20 | ? | 4:6 | ? | plumose | 0.40 | ? | ? | ? |
| ***N. rijekana* Petkovski, 1954** | 18 | ? | 5:6 | ? | ? | 0.60 | 0.50 | ? | ? |
| ***N. sonmezi* sp. nov.** | 15 | - | ? | fine setules | unipinnate, spine-like | 0.40 | ? | 4 naked on distal; 1 naked on lateral | 1 long seta |
| ***N. serdarsaki* sp. nov.** | 11 | - | 4:6 | fine setules | semiplumose-semipinnate | ? | 0.58 | 4 naked on distal; 1 plumose lateral | 1 long seta |
| ***N. alperi* sp. nov.** | 17 | + | ? | fine setules | unipinnate, spine-like | 0.47 | ? | 4 naked on distal; 1 plumose on lateral | 1 long seta |
| ***N. loweae* sp. nov.** | 12 | - | 5:6 | robust spinulose | plumose | 0.57 | 0.38 | 4 naked on distal; 2 naked on lateral | 2 long setae |

*Nitocra sonmezi* sp. nov. was described on the basis on one female specimen from mediolittoral zone of coast of Hatay, Turkey. *Nitocra sonmezi* sp. nov. is differentiated from other species of the *affinis* group by (a) the number of spinules on the anal operculum, (b) in the shape of P1 enp-1 which is ~ 4.3 × as long as maximum width, (c) by the ornamentation of the subdistal inner seta of P1 enp-1, (d) in the ornamentation of P5 endopodal and exopodal setae, e) in the ornamentation of urosomites and (f) in the ornamentation of the setae of P2–P4. Details of the specific differences are given in Table 1.

*Nitocra alperi* sp. nov. was identified as *N. affinis* from the Indian Ocean (Wells and Rao 1987). *Nitocra alperi* sp. nov. can be distinguished from other congeners of the *affinis* group by (a) the total length of P4 endopod segments; (b) the ornamentation of the inner seta P2–P4 enp-3; (c) the ornamentation of the inner seta of P1 enp-1, length to width ratio of this segment; (d) the surface ornamentation of somites and number of spinules on the anal operculum (seventeen) (see Table 1 for detailed comparisons). *Nitocra alperi* sp. nov. shares the rostral projection on its rostrum with *N. affinis*, *N. colombiensis*, and *N. loweae* sp. nov.

*Nitocra serdarsaki* sp. nov. was identified from the Aegean coast of Türkiye on the basis of the one male specimen. *Nitocra serdarsaki* sp. nov. can be distinguished from other new species by (a) the number of spinules on the anal operculum; (b) the ornamentation of P5 exopod and baseoendopod; (c) the ornamentation of inner setae of P2–P4 endopod-3, (d) the P1 enp-1 inner seta ornamentation; (e) the length and (f) ornamentation of the middle inner seta of P4 exp-3 (see Table 1 for detailed comparisons). *Nitocra affinis* has four setae on the P5 baseoendopod of the male, whereas *N. serdarsaki* sp. nov. has five setae on the P5 baseoendopod of the male.

These new species can also be easily distinguished from *N. hamata* and *N. elegans* which are in the *affinis* group, by following characters; (a) shape of female P5 exopod, (b) ornamentations of the abdominal somites and (c) the ornamentations of mouthparts (Bodin 1970; Gee 2009). *Nitocra hamata* is distinguished from other *affinis* species group by the shape of female P5 exopod which is longer and slender (Bodin 1970), P1 enp-1 length and the structure of P3 enp-3.

The status of subspecific taxa within the genus *Nitocra* (*N. reducta fluviatilis* and *N. sewelli husmanni*) have been revised by Gómez et al (2012) to recognise them as species, based on consistent morphological differences. In this context, we have also re-evaluated the status of the subspecies of *N. affinis* below:

### Establishment of *Nitocra rijekana* Petkovski, 1954

*Nitocra rijekana* was originally described as a form of *N. affinis* by Petkovski (1954) from Rijeka, Northern Adriatic (Mediterranean Sea), and has not been recorded since its original description. In the same study, Petkovski (1954) examined the material of *N. affinis* from Dubrovnik and compared it with that of Rijeka, determining significant morphological differences between them. The differences between *Nitocra rijekana* and *N. affinis* are as follows: (a) inner middle seta of P4 exp-3 of *Nitocra rijekana* is not as long as and not as strong as that of *Nitocra affinis*, (b) the male P5 baseoendopod with five and exopod with six setae (in *Nitocra affinis* 4:6). *Nitocra rijekana* can also be easily distinguished from its congeners by having a long but plumose inner middle seta of P4 exp-3. We believe that morphological differences between *Nitocra affinis rijekana* Petkovski, 1954 and *Nitocra affinis* are significant enough to warrant upgrading *Nitocra affinis rijekana* to a specific rank. The detailed comparison is provided in Table 1.

### Establishment of *Nitocra californica* Lang, 1965

Lang (1965) originally described *Nitocra affinis californica* in a tidal pool from Monterey Bay, California. Later on, Kunz (1975) recorded *Nitocra affinis californica* from Gonubie, South Africa, by examining 62 specimens collected from the reef area. Kunz (1975) observed variabilities on the P5, which may indicate that Kunz (1975) was dealing with more than one species. Unfortunately, Kunz (1975) only described the P1 and P5, thus making it impossible to confirm the specific status of Kunz' (1975) specimens. After Kunz (1975) Apostolov (1980) recorded *N. affinis californica* from Bulgaria. Fuentes-Reinés and Suárez-Morales (2014) mentioned that the Bulgarian and South African specimens may represent different species. This observation is supported by the notably shorter P1 exopod found in both the Bulgarian and South African specimens, whose exopodal ramus extends to ~ ¾ of the length of the first endopodal segment, distinctly deviating from the characteristic of *N. a. californica*, where the exopod and the first endopod segment exhibit equal lengths.

Lang's (1965) subspecies is here upgraded to full species rank since it differs sufficiently from Gurney's (1927) population and its congeners to warrant such status on the basis of the following characters: (a) P1 exp-3 ~ as long as exopod and exceeds the origin of P1 enp-1 inner seta (in all other species, the P1 exp-3 does not exceeds the origin of P1 enp-1 inner seta); (b) the setal ornamentation of swimming legs; (c) male P5 baseoendopod with four setae. Detailed comparison is provided in Table 1.

## Establishment of *Nitocra stygia* Por, 1968

Por (1968) described *Nitocra affinis stygia* from land-locked basins in the Red Sea. In the original description, the female P5, the abdominal segment, the caudal rami, P1, P4 exopod and male P5 were illustrated. Por's (1968) subspecies is here upgraded to full species rank since it differs sufficiently from Gurney's (1927) population and its congeners to warrant such status on the basis of the following characters: (a) large hyaline field on female P5 and its large dimensions, (b) inner middle seta of P4 exp-3 is not as long as and not as strong as in *N. affinis*, (c) penultimate somite surrounded by spinule (only from dorsal to lateral in *N. affinis*), (d) female baseoendopodal setae are almost equal in length, (e) male baseoendopod with four setae. Detailed comparison is provided in Table 1.

## Establishment of *Nitocra colombiensis* Fuentes-Reinés & Suárez-Morales, 2014

*Nitocra colombiensis* is originally described as *Nitocra affinis colombiensis* from a lagoon in Colombia (Fuentes-Reinés and Suárez-Morales 2014). This subspecies from Colombia is here upgraded to full species rank since it differs sufficiently from Gurney's (1927) population and its congeners to warrant such status on the basis of the following characters: (a) number of setae of the male P5 endopod of; (b) number of spinules on the anal operculum; (c) shape and ornamentation of the middle inner seta P4 exp-3; (d) ratio of the P1 enp-1; (e) body ornamentation; (f) antennular setal formula; (g) maxillule basis with four setae. In the original description of *Nitocra colombiensis*, apical rostral projection is given as diagnostic character for the species. But the rostral projection is also observed both in *N. affinis* and *N. alperi* sp. nov.

Fuentes-Reinés and Suárez-Morales (2014) provided an identification key for *affinis* group. The key distinguished *Nitocra colombiensis* from other species with the apical rostral projection. We observed the apical rostral projection both in *N. affinis* and *N. alperi* sp. nov. in this study. Therefore, here we revised the identification key for taxa contained in the *N. affinis* group.

## A key to the *Nitocra affinis* species group

1 Inner middle seta of P4 exopod-3 not strong and longer than other setae. ........................................ ***N. rijekana***
– The inner middle seta of P4 exopod-3 long, strong and spinulose ............**2**
2 Rostrum with rostral projection........................................**3**
– Rostrum without rostral projection ........................................**4**
3 P1 enp-1 with a plumose inner seta; male P5 baseoendopod with 3 setae ........................................ ***N. colombiensis***
– P1 enp-1 with a spinulose inner seta; male P5 baseoendopod with 4 setae........................................ ***N. affinis***

– P1 enp-1 with unipinnate seta ........................................... ***N. alperi* sp. nov.**

4 P1 exopod not reaching beyond the insertion site of the inner seta of P1 enp-1; male P5 baseoendopod with 4 setae ........................... ***N. californica***

– P1 exopod reaching beyond the insertion site of the inner seta of P1 enp-1 ........................................................................................................ **5**

– P5 baseoendopod with large hyaline field; male P5 baseoendopod with 4 setae.................................................................................................. ***N. stygia***

– P5 baseoendopod without large hyaline field ............................................ **6**

5 Mandibular endopod with 1 plumose seta laterally, and 5 naked setae apically ........................................................................................................ **7**

– Mandibular endopod with 1 plumose seta laterally, and 4 naked setae apically ........................................................................... ***N. serdarsaki*. sp. nov.**

6 Penultimate somite with robust spinules on ventral, spinules on lateral side (not surrounded dorsoventrally); caudal rami inner margin covered with robust spinules; inner proximal seta P3 endopod-3 naked and not longer than other ............................................................ ***N. loweae* sp. nov.**

7 Penultimate somite ornamented with spinules along somite (surrounded dorsoventrally) ventral; caudal rami inner margin naked; inner proximal seta of P3 endopod-3 not longer than other setae and unipennate ........... ........................................................................................ ***N. sonmezi* sp. nov.**

## Conclusion

The growing significance of microcharacters in copepod taxonomy has revealed that numerous species lacking comprehensive descriptions are, in fact, part of species complexes. In this study, *Nitocra affinis* was redescribed based on lectotype material which facilitated us through detailed comparison with specimens recorded and labelled as *N. affinis* from distantly related localities. The results clearly indicated that each of these specimens attributed to *N. affinis* corresponds to a distinct species. Four new species have been described from different localities, and named as *N. sonmezi* sp. nov., *N. loweae* sp. nov., *N. alperi* sp. nov., and *N. serdarsaki* sp. nov. The status of subspecific taxa of *N. affinis* has been re-evaluated based on the literature and four subspecies of *N. affinis* have been reinstated to specific rank, and named as *N. stygia*, *N. rijekana*, *N. californica*, and *N. colombiensis*. The description of the majority of the species/subspecies within the *Nitocra* genus is notably insufficient. While the morphological examination of mouthparts in ameirid taxa can be challenging, a detailed morphological analysis of mouthparts may significantly contribute to resolving the problematic taxonomy of the genus. Indeed, in this study, although setal formulae of the swimming legs of the four newly described species are the same as in *N. affinis* species, new morphological differences have been detected. For instance, there is a distinct apical extension of the rostrum of *N. affinis* and *N. alperi*. While in *N. loweae*, the maxilla endopod is represented by two setae of equal length, it is represented by a single seta in other species within the *affinis* group. These findings clearly underscore the significant contributions that detailed species descriptions will make to resolve the challenging taxonomy of the genus *Nitocra*. In addition to morphological studies, the phylogenetic analysis of molecular data to be obtained will provide valuable insights into both the taxonomy of the genus *Nitocra* and the phylogenetic relationships among genera within the family Ameiridae.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# Revision of the orb-weaver spider genus *Gea* C.L. Koch, 1843 (Araneae, Araneidae) from China

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## Abstract

The orb-weaver spider genus *Gea* C.L. Koch, 1843 from China is revised, and three species including one new species, are recognized: *Gea jingdong* Mi, Wang & Gan, **sp. nov.** (♂♀) from Yunnan; *Gea spinipes* C.L. Koch, 1843 (♂♀) from Guangdong, Guangxi, Guizhou, Hainan, Taiwan, and Yunnan; and *Gea subarmata* Thorell, 1890 (♂♀) from Guangxi and Hainan. *Gea subarmata* is newly recorded in China.

**Key words:** Arachnida, Argiopinae, diagnosis, morphology, new species, taxonomy

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## Introduction

The orb-weaver spider subfamily Argiopinae consists of three genera, *Gea* C.L. Koch, 1843, *Argiope* Audouin, 1826, and *Neogea* Levi, 1983 (Levi 1983). This subfamily differs from other araneid subfamilies in having the posterior eye row procurved in dorsal view, and it is also characterized by sexual dimorphism (Levi 1983). The subfamily Argiopinae of the Western Pacific region has been revised by Levi (1983), who included in it 49 *Argiope* species, seven *Gea* species, and two *Neogea* species; eight species of *Argiope* occur in China, but no species of *Gea* were known from China.

The genus *Gea* contains 13 species and subspecies, which are mainly distributed in Africa, Asia, and Australia, and *Gea heptagon* (Hentz, 1850) is introduced to the USA to Argentina (WSC 2024). *Gea spinipes* has been almost concurrently reported from Guizhou and Yunnan (Yin et al. 1997) and Taiwan (Chang and Chang 1997) and is the only known *Gea* species known from China at present (Song et al. 1999; WSC 2024).

The *Gea* specimens collected in China were examined, and three species including a new species, are identified. They are described in this paper.

## Material and methods

All specimens were collected by beating shrubs or by hand and are preserved in 75% ethanol. The specimens are deposited in the Museum of Tongren University, China (**TRU**). Methods follow Mi et al. (2023).

All measurements are given in millimeters. Leg measurements are given as total length (femur, patella + tibia, metatarsus, tarsus). Abbreviations used in the text and figures are as follows: **ALE** anterior lateral eye; **AME** anterior median eye; **C** conductor; **CD** copulatory duct; **CO** copulatory opening; **E** embolus; **FD** fertilization duct; **LP** lateral plate; **MA** median apophysis; **MOA** median ocular area; **PLE** posterior lateral eye; **PME** posterior median eye; **Sp** spermatheca.

## Taxonomy

### Family Araneidae Clerck, 1757

### Genus *Gea* C.L. Koch, 1843

*Gea* C.L. Koch, 1843: 101.

**Type species.** *Gea spinipes* C.L. Koch, 1843.

**Diagnosis.** *Gea* is distinguished from *Argiope* by having the posterior eyes about equally spaced, while *Argiope* has the posterior median eyes farther from the posterior lateral eyes than the posterior median eyes from each other (Levi 1983: figs 27, 45, 64). *Gea* differs from *Neogea* in having the cephalic region behind the eyes not swollen, while in *Neogea* this region of the head is swollen (Levi 1983: figs 290, 292).

**Description.** Small to medium-sized spiders with female total length of 3.65–9.00 mm and male total length of 3.00–4.30 mm. Carapace pear-shaped, yellow to yellowish brown. Legs yellow to yellowish brown, always with dark annuli; coxa I of male without hook; femur II of male without groove; tibia II of male not expanded. Abdomen shield-shaped dorsal often with a pair of low anterolateral humps in females, pale with a pair of dark patches close to humps and dark folium posteriorly or dark with white spots. Ventral abdomen pale with irregular dark patches or white spots.

***Pedipalp*** of male without basal femoral protrusion; patella with only one bristle; paracybium fingerlike or flattened fingerlike; median apophysis bifurcated; dorsal ramus often weaker than ventral ramus; embolus extremely long and curved, thick at base, tapering to filiform end; conductor broad, curved, wrapped distal part of embolus.

***Epigynum*** weakly sclerotized; median septum separating two depressions; copulatory openings situated on edges of depressions; copulatory ducts twisted, a bit longer than spermatheca; spermathecae elongate kidney-shaped, S-shaped, or bean-shaped, either touching or not.

**Comment.** Spination of femur I is not useful to characterize these *Gea* species.

### *Gea jingdong* Mi, Wang & Gan, sp. nov.

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Figs 1, 2, 7A–D, 8

**Type materials.** ***Holotype***: China • ♂; Yunnan Province, Dali Bai Autonomous Prefecture, Jingdong Yi Autonomous County, Jinping Township, Yubishan Park; 24°27.01'N, 101°49.53'E; ca 1270 m elev.; 16.VIII.2015; X.Q. Mi et al. leg.;

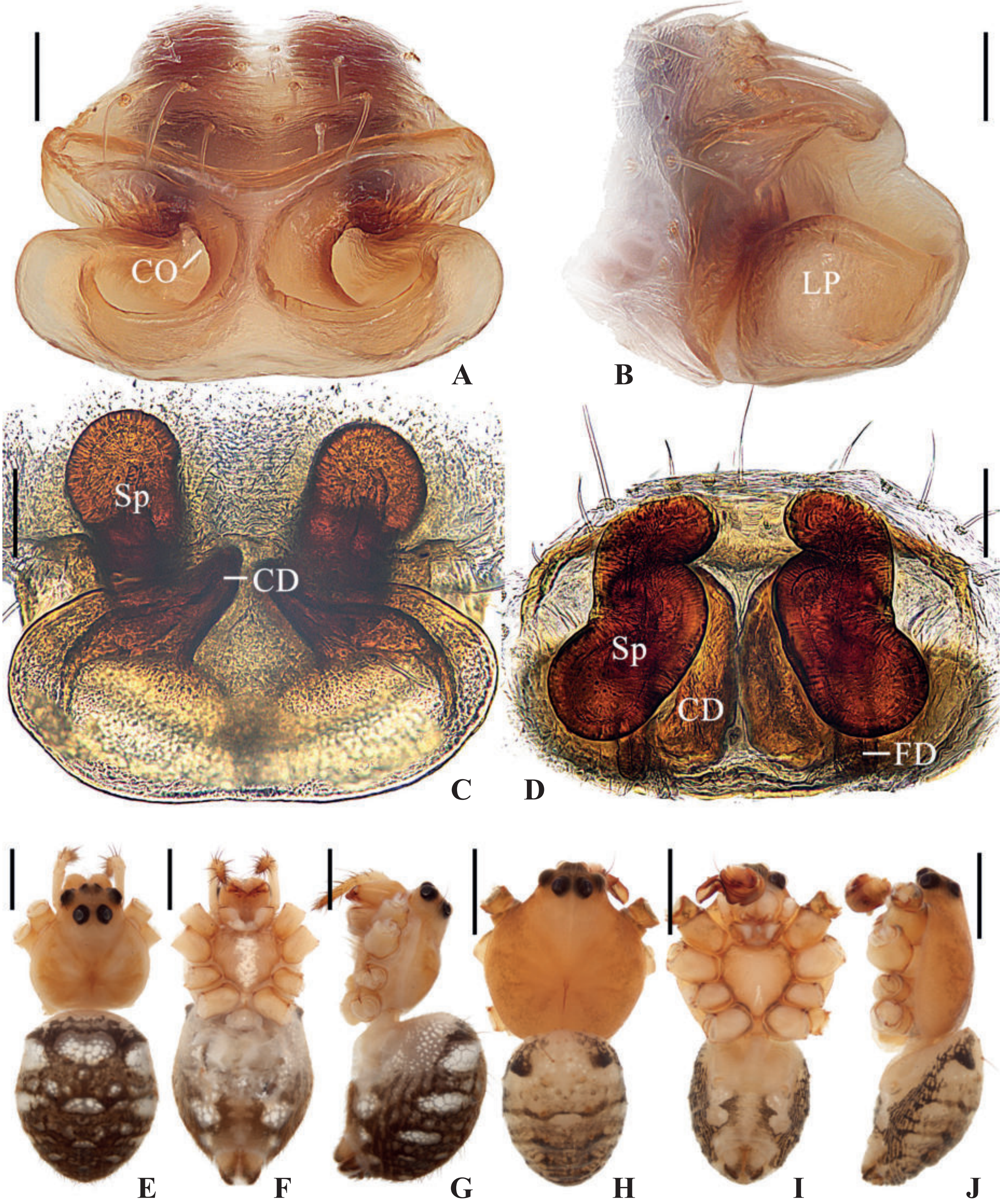

**Figure 1.** *Gea jingdong* Mi, Wang & Gan, sp. nov. **A–G** female paratype TRU-Araneidae-269 **H–J** male holotype **A** epigyne, ventral view **B** ibid., lateral view **C** vulva, posterior view **D** ibid., dorsal view **E, H** habitus, dorsal view **F, I** ibid., ventral view **G, J** ibid., lateral view. Scale bars: 0.1 mm (**A–D**); 1 mm (**E–J**). Abbreviations: CD copulatory duct, CO copulatory opening, FD fertilization duct, LP lateral plate, Sp spermatheca.

TRU-Araneidae-268. ***Paratypes*:** 3♀♀; same data as for holotype; TRU-Araneidae-269–271.

**Etymology.** The specific name is a noun in apposition and refers to the type locality.

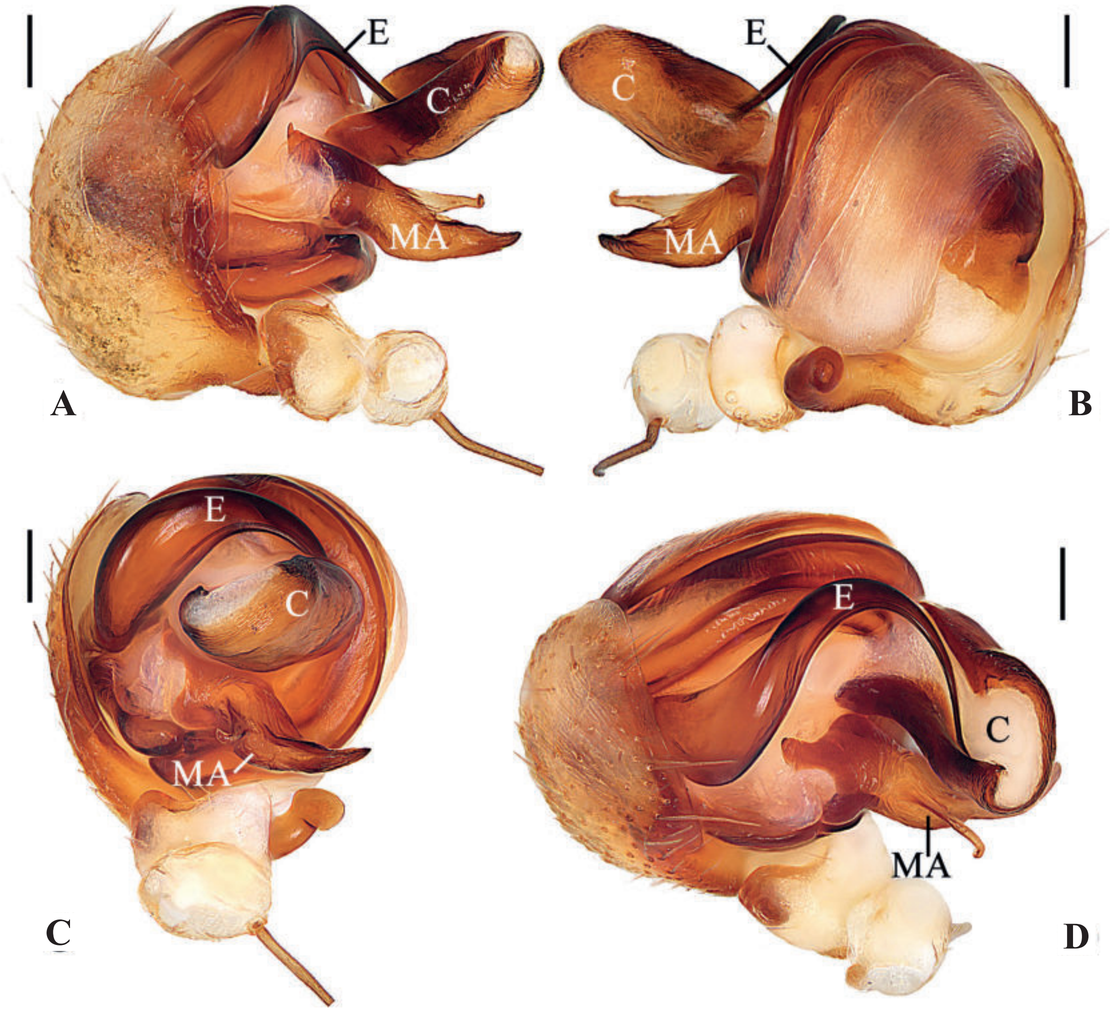

**Figure 2.** *Gea jingdong* Mi, Wang & Gan, sp. nov. male holotype **A** pedipalp, prolateral view **B** ibid., retrolateral view **C** ibid., ventral view **D** ibid., apical view. Scale bars: 0.1 mm. Abbreviations: C conductor, E embolus, MA median apophysis.

**Diagnosis.** The new species resembles *G. spinipes* in appearance and genitalia structures, but it can be distinguished as follows: 1) median apophysis not exceeding the conductor in prolateral view and retrolateral view (Fig. 2A, B) vs exceeding the conductor (Fig. 4A, B); 2) visible part of embolus curled about 90° in ventral view (Fig. 2C) vs about 180° (Fig. 4C); 3) conductor shorter, extending ventrally and not exceeding prolateral margin of pedipalp in ventral view (Fig. 2C) vs longer, extending ventro-prolaterally and the tip exceeding the prolateral margin of pedipalp (Fig. 4C); 4) copulatory openings situated on inner edges of the depressions (Fig. 1A) vs on anterior lateral edges (Fig. 3A); 5) lateral epigynal plates not covering the anterior rim in lateral view (Fig. 1B) vs covering the anterior rim (Fig. 3B); and 6) female carapace lacking dark brown patches (Fig. 1E, G) vs having dark brown patches (Fig. 3G, I).

**Description. Male** (holotype, Figs 1H–J, 2, 7A–D). Total length 3.80. Carapace 2.25 long, 1.90 wide. Abdomen 1.90 long, 1.45 wide. Clypeus 0.05 high. Eye sizes and interdistances: AME 0.15, ALE 0.08, PME 0.15, PLE 0.15, AME–AME 0.13, AME–ALE 0.03, PME–PME 0.20, PME–PLE 0.18, MOA length 0.53, anterior width 0.38, posterior width 0.45. Leg measurements: **I** 8.85 (2.75, 2.65, 2.40, 1.05), **II** 8.35 (2.60, 2.45, 2.30, 1.00), **III** 4.55 (1.55, 1.30, 1.10, 0.60), **IV** 7.05 (2.35, 2.00, 1.90, 0.80). Carapace yellow, with inconspicuous gray patches in thoracic region; base of eyes black. Cervical groove inconspicuous; fovea longitudinal. Chelicerae yellow, with four promarginal and three retromarginal teeth. Endites wider than long, yellow, with very narrow, dark anterior edges. Labium triangular, yellow. Sternum cordiform, yellow, with a wedge-shaped white patch posteriorly. Legs yellow to yellowish brown, with inconspicuous annuli; femur I with 12 macrosetae; tibia I with 12 macrosetae; tibia II with seven macrosetae; tibia III with seven macrosetae; tibia IV with seven macrosetae. Abdomen shield-shaped, ~1.31× longer than wide, grayish yellow, dorsal with a pair of dark brown patches anterolaterally and a dark brown folium posteriorly. Venter abdomen yellow with gray patches. Spinnerets yellow with gray tip.

***Pedipalp*** (Fig. 2): paracybium fingerlike; median apophysis bifurcated; dorsal ramus weaker than the ventral one; embolus thick at base, twisted and tapered into a fine tip; conductor membranous, curled, about 2× longer than wide in retrolateral view.

**Female** (paratype TRU-Araneidae-269, Fig. 1A–G). Total length 5.05. Carapace 2.35 long, 2.00 wide. Abdomen 3.00 long, 2.35 wide. Clypeus 0.08 high. Eye sizes and interdistances: AME 0.15, ALE 0.08, PME 0.18, PLE 0.18, AME–AME 0.15, AME–ALE 0.03, PME–PME 0.33, PME–PLE 0.35, MOA length 0.58, anterior width 0.43, posterior width 0.65. Leg measurements: I 8.45 (2.45, 2.80, 2.20, 1.00), II 8.35 (2.45, 2.75, 2.15, 1.00), III 5.10 (1.65, 1.60, 1.15, 0.70), IV 8.00 (2.60, 2.55, 2.00, 0.85). Habitus similar to that of male, but abdomen with a pair of low anterolateral humps and sternum with a throughout paler patch.

***Epigyne*** (Fig. 1A–D): ~1.36× wider than long in ventral view, with a distinct median septum separating two depressions; copulatory openings situated on inner edges of the depressions; copulatory ducts widest at the beginning part, a bit longer than spermatheca; spermathecae almost S-shaped in dorsal view, not touching.

**Variation.** Total length: ♀ 5.05–6.70 (*n* = 3).

**Distribution.** China (Yunnan).

### *Gea spinipes* C.L. Koch, 1843

Figs 3, 4, 7E–H, 8

*Gea spinipes* C.L. Koch 1843: 101, fig. 823; Yin et al. 1989: 67, fig. 7A–C; Chang and Chang 1997: 83, figs 1–4; Yin et al. 1997: 90, fig. 21a–f; Song et al. 1999: 282, fig. 169B–D. (type material not examined).

**Materials examined.** China – Guangxi Zhuang Autonomous Region • 1♂; Beihai City, Yinhai District, Yajishan Forestry Station; 21°35.37'N, 109°18.41'E; ca 30 m elev.; 12.VIII.2017; X.Q. Mi et al. leg.; TRU-Araneidae-272 • 1♂; Fangchenggang City, Shangsi County, Shiwandashan National Forestry Park; 21°53.87'N, 107°54.26'E; ca 370 m elev.; 14.VIII.2017; X.Q. Mi et al. leg.; TRU-Araneidae-273 • 1♂; Beihai City, Tieshangang District, Xinggang Township, Xiaomatou Village, Caobiaotang; 21°33.11'N, 109°29.22'E; ca 10 m elev.; 4.XII.2018, X.Q. Mi et al. leg.; TRU-Araneidae-275 • 2♀♀; Chongzuo City, Jiangzhou District, Zuozhou Township, Guanghe Village; 22°34.72'N, 107°24.94'E; ca 160 m elev.; 4.VII.2019; C. Wang et al. leg.; TRU-Araneidae-276–277. – Guangdong Province • 1♀; Maoming City, Xinyi City, Dawuling Natural Reseve; 22°17.05'N, 111°10.87'E; ca 700 m elev.; 2.XII.2018, X.Q. Mi et al. leg.; TRU-Araneidae-274. – Hainan Province • 1♀;Wuzhishan City, A'tuol-

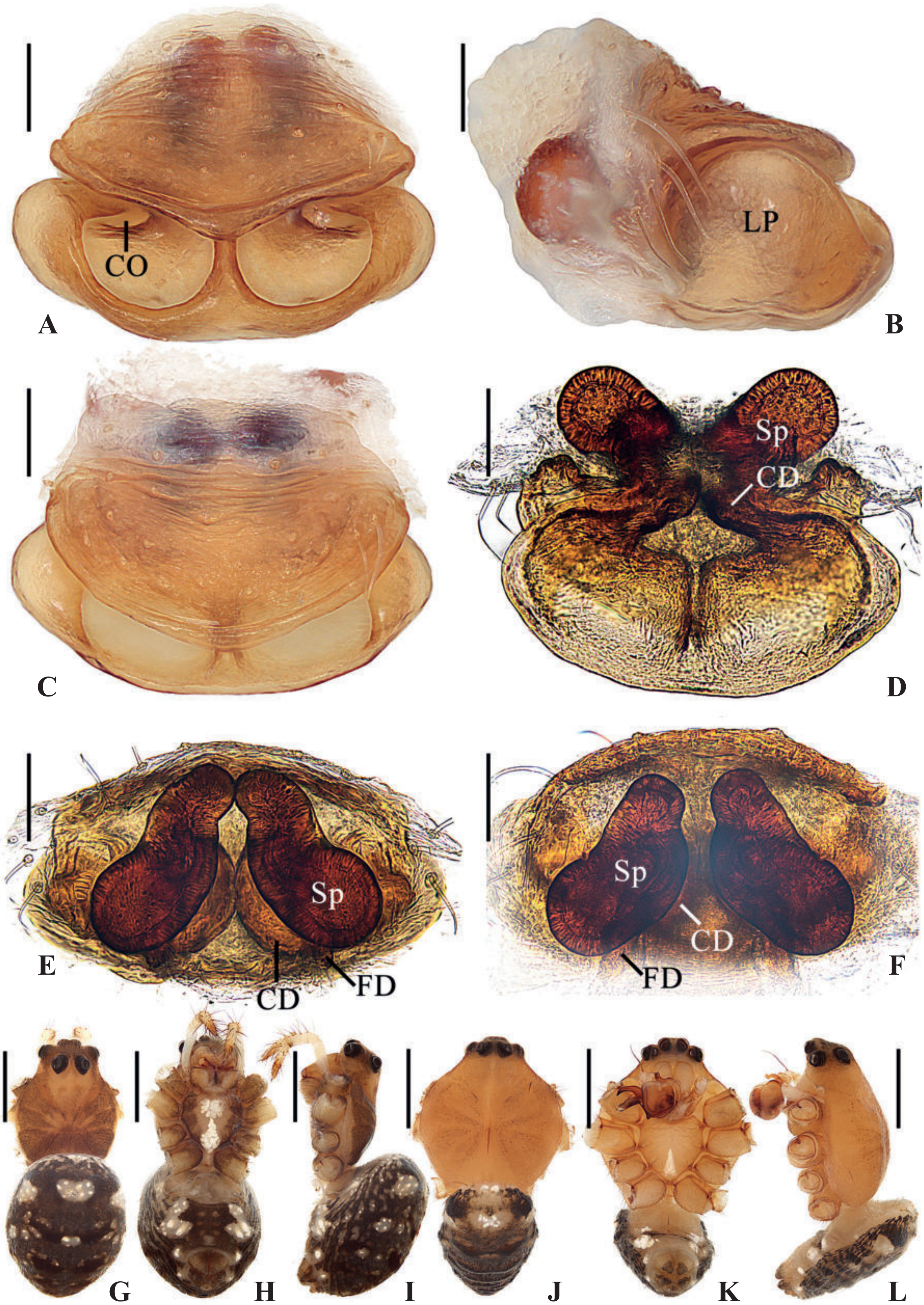

**Figure 3.** *Gea spinipes* C.L. Koch, 1843 **A–E, G–I** TRU-Araneidae-274 **F** TRU-Araneidae-276 **J–L** TRU-Araneidae-272 **A** epigyne, ventral view **B** ibid., lateral view **C** ibid., anterior view **D** vulva, posterior view **E** ibid., dorsal view **F** ibid., dorsal view **G, J** habitus, dorsal view **H, K** ibid., ventral view **I, L** ibid., lateral view. Scale bars: 0.1 mm (**A–F**); 1 mm (**G–L**). Abbreviations: CD copulatory duct, CO copulatory opening, FD fertilization duct, LP lateral plate, Sp spermatheca.

ing; 18°50.17'N, 109°30.61'E; ca 790 m elev.; 9.VIII.2020 X.Q. Mi et al. leg.; TRU-Araneidae-278 • 1♀; Wuzhishan City, Shuiman Township, around Yataiyulin Hotel; 18°54.37'N, 109°40.70'E; ca 750 m elev.; 11.VIII.2020; X.Q. Mi et al. leg.; TRU-Araneidae-279 • 1♀; Dongfang City, Gancheng Township, Tuotou Village; 18°50.57'N, 108°50.87'E; ca 110 m elev.; 29.VII.2023; X.Q. Mi et al. leg.; TRU-Araneidae-280 • 1♂; Dongfang City, Gancheng Township, Tuotou Village, Shi'anlao; 18°50.56'N, 108°50.72'E; ca 110 m elev.; 30.VII.2023; X.Q. Mi et al. leg.; TRU-Araneidae-281 • 1♂1♀; Lingshui Li Autonomous County, Diaoluoshan National Nature Reserve, Popular Science Base; 18°40.25'N, 109°53.66'E; ca 490 m elev.; 26.VII.2023; C. Wang et al. leg.; TRU-Araneidae-282–283 • 1♂; Lingshui Li Autonomous County, Diaoluoshan National Nature Reserve, Shidai Village, Heliuling; 18°47.55'N, 109°44.03'E; ca 610 m elev.; 27.VII.2023; C. Wang et al. leg.; TRU-Araneidae-284 • 1♂; Lingshui Li Autonomous County, Diaoluoshan National Nature Reserve, Houshan; 18°43.57'N, 109°52.04'E; ca 930 m elev.; 28.VII.2023; C. Wang et al. leg.; TRU-Araneidae-285 • 1♂; Changjiang Li Autonomous County, Qicha Township, Bawangling National Nature Reserve, Dongyi Forest Station; 19°7.23'N, 109°7.64'E; ca 490 m elev.; 3.VIII.2023; X.Q. Mi et al. Leg; TRU-Araneidae-286 • 1♀; Baoting Li and Miao Autonomous County, Maogan Township, X124 roadside; 18°39.32'N, 109°32.45'E; ca 530 m elev.; 4.VIII.2023; C. Wang et al. leg; TRU-Araneidae-287.

**Diagnosis.** See the Diagnosis of *G. jingdong* Mi, Wang & Gan, sp. nov.

**Description. Male** (Figs 3J–L, 4, 7E–H). Total length 3.25. Carapace 1.95 long, 1.70 wide. Abdomen 1.85 long, 1.20 wide. Clypeus 0.05 high. Eye sizes and interdistances: AME 0.13, ALE 0.08, PME 0.13, PLE 0.13, AME–AME 0.13, AME–ALE 0.03, PME–PME 0.20, PME–PLE 0.23, MOA length 0.53, anterior width 0.38, posterior width 0.43. Leg measurements: I 8.55 (2.50, 2.60, 2.40, 1.05), II 7.90 (2.35, 2.30, 2.25, 1.00), III 4.65 (1.55, 1.30, 1.15, 0.65), IV 7.20 (2.35, 2.00, 2.00, 0.85). Carapace yellow, with inconspicuous, radial, dark patches; eyes with dark base. Cervical groove inconspicuous; fovea longitudinal. Chelicerae yellow, with four promarginal and three retromarginal teeth. Endites wider than long, yellow, with very narrow, dark anterior edges. Labium triangular, yellow. Sternum cordiform, yellow, with a white, wedge-shaped patch. Legs yellow to yellowish brown; legs III and IV with dark annuli; femur I with 11 macrosetae; tibia I with 13 macrosetae; tibia II with 13 macrosetae; tibia III with seven macrosetae; tibia IV with 11 macrosetae. Abdomen shield-shaped, ~1.54× longer than wide; dorsum dark, with two white spots anteriorly. Venter abdomen yellow, with white patches. Spinnerets yellow with gray tip.

***Pedipalp*** (Fig. 4): paracybium fingerlike; median apophysis bifurcated, dorsal ramus weaker, ventral ramus extremely long, exceeding length of conductor in prolateral and retrolateral view; embolus stout at base, twisted approximately 360° and tapering into a fine tip; conductor prominent, curled bilaterally.

**Female** (Fig. 3A–I). Total length 3.65. Carapace 2.05 long, 1.60 wide. Abdomen 2.40 long, 1.75 wide. Clypeus 0.05 high. Eye sizes and interdistances: AME 0.18, ALE 0.08, PME 0.18, PLE 0.18, AME–AME 0.10, AME–ALE 0.05, PME–PME 0.25, PME–PLE 0.35, MOA length 0.65, anterior width 0.38, posterior width 0.55. Leg measurements: I 6.60 (2.00, 2.05, 1.75, 0.80), II 6.50 (2.05, 2.00, 1.70, 0.75), III 4.05 (1.30, 1.25, 0.95, 0.55), IV 6.30 (2.10, 2.00, 1.60, 0.60). Habitus similar to that of male but with darker patches on thoracic region.

***Epigyne*** (Fig. 4A–F): ~1.3× wider than long in ventral view, with a distinct median septum separating two depressions in ventral view; copulatory openings

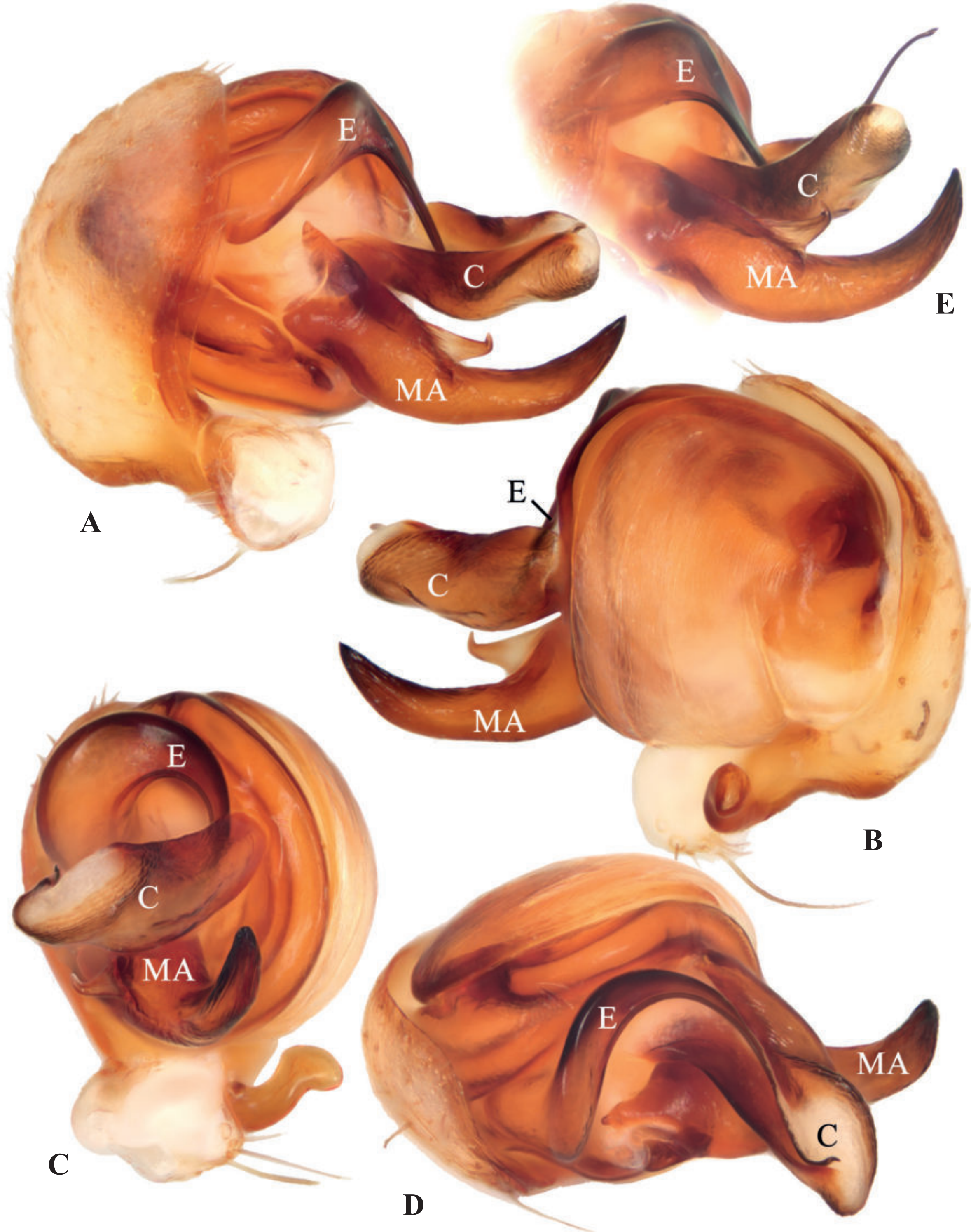

**Figure 4.** *Gea spinipes* C.L. Koch, 1843 **A–D** TRU-Araneidae-272 **E** TRU-Araneidae-279 **A** pedipalp, prolateral view **B** ibid., retrolateral view **C** ibid., ventral view **D** ibid., apical view **E** part of pedipalp (show the unbroken tip of embolus), prolateral view. Scale bars: 0.1 mm. Abbreviations: C conductor, E embolus, MA median apophysis.

situated on anterolateral edges of depressions; copulatory ducts twisted, a bit longer than spermatheca; spermathecae elongate kidney-shaped, touching or nearly touching at midline.

**Variation.** Total length: ♂ 3.25–4.00 (*n* = 8); ♀ 3.65–6.90 (*n* = 8). Tip of embolus always broken.

**Distribution.** China (Guangdong, Guangxi, Guizhou, Hainan, Taiwan, Yunnan), Pakistan, India, Indonesia, Malaysia, Myanmar, and Singapore.

**Comment.** *Gea spinipes* is widely distributed from Pakistan to Indonesia, and shows some differences in epigynal structure of specimens collected from different sites (Levi 1983: figs 362–370) and that may indicate they are not conspecific. So, further taxonomic study about this species is necessary, especially getting more male specimens from different sites. *G. zaragosa* described by Barrion and Litsinger (1995) is similar to *G. spinipes* both in habitus and genitalia structures, but no detailed diagnosis was provided. Judging from the illustrations, *G. zaragosa* Barrion & Litsinger, 1995 is probably synonymized with the former.

### *Gea subarmata* Thorell, 1890

Figs 5, 6, 7I–L, 8

*Gea subarmata* Thorell, 1890: 101; Levi 1983: 323, figs 350–354; Okuma et al. 1993: 21, fig. 16A, B (type material not examined).

**Materials examined.** China – Guangxi Zhuang Autonomous Region • 1♂; Beihai City, Tieshangang District, Xinggang Township, Xiaomatou Village, Caobiaotang; 21°33.11'N, 109°29.22'E; ca 10 m elev.; 4.XII.2018; X.Q. Mi et al. leg.; TRU-Araneidae-288. – Hainan Province • 2♀♀; Dongfang City, Gancheng Township, Tuotou Village, Shi’anlao; 18°50.56'N, 108°50.72'E; ca 110 m elev.; 30.VII.2023; X.Q. Mi et al. leg.; TRU-Araneidae-289–290.

**Diagnosis.** Females differ from those of congeneric species by the circular epigynum frame in ventral view (Fig. 5A) and bean-shaped spermathecae (Fig. 5E); males resembles *G. eff* Levi, 1983 in having similar pedipalp structures, but differs in: 1) dorsal ramus of the median apophysis tapered (Fig. 6A, C) vs slender (Levi 1983: figs 360, 361); 2) dorsal ramus of the median apophysis shorter than ventral ramus (Fig. 6E) vs about equal length (Levi 1983: fig. 360); and 3) conductor curled into a triangular dorsal fin in retrolateral view (Fig. 6B) vs lacking a triangular dorsal fin (Levi 1983: fig. 361).

**Description. Male** (TRU-Araneidae-288, Figs 5J–L, 6, 7I–L). Total length 3.00. Carapace 1.65 long, 1.35 wide. Abdomen 1.65 long, 1.20 wide. Clypeus 0.10 high. Eye sizes and interdistances: AME 0.10, ALE 0.05, PME 0.10, PLE 0.10, AME–AME 0.10, AME–ALE 0.03, PME–PME 0.18, PME–PLE 0.20, MOA length 0.43, anterior width 0.33, posterior width 0.33. Leg measurements: I 6.55 (1.85, 2.00, 1.80, 0.90), II 6.05 (1.75, 1.80, 1.65, 0.85), III 3.20 (1.05, 0.95, 0.70, 0.50), IV 4.90 (1.60, 1.40, 1.25, 0.65). Carapace yellow, with dark patches on thoracic region. Cervical groove inconspicuous; fovea longitudinal. Chelicerae yellow, with four promarginal and three retromarginal teeth. Endites wider than long, grayish yellow, with very narrow, dark anterior edge. Labium triangular, grayish yellow, with paler at tip. Sternum cordiform, yellowish brown, with a paler longitudinal patch. Legs yellow without annuli; femur I with five macrosetae; tibia I with nine macrosetae; tibia II with eight macrosetae, tibia III with four macrosetae; tibia IV with nine macrosetae. Abdomen shield-shaped, ~1.38× longer than wide; dorsum whitish yellow, with a pair of narrow, grayish-brown patches anterolaterally and a grayish-brown folium posteriorly. Venter abdomen whitish yellow, with grayish-brown patches. Spinnerets yellowish brown.

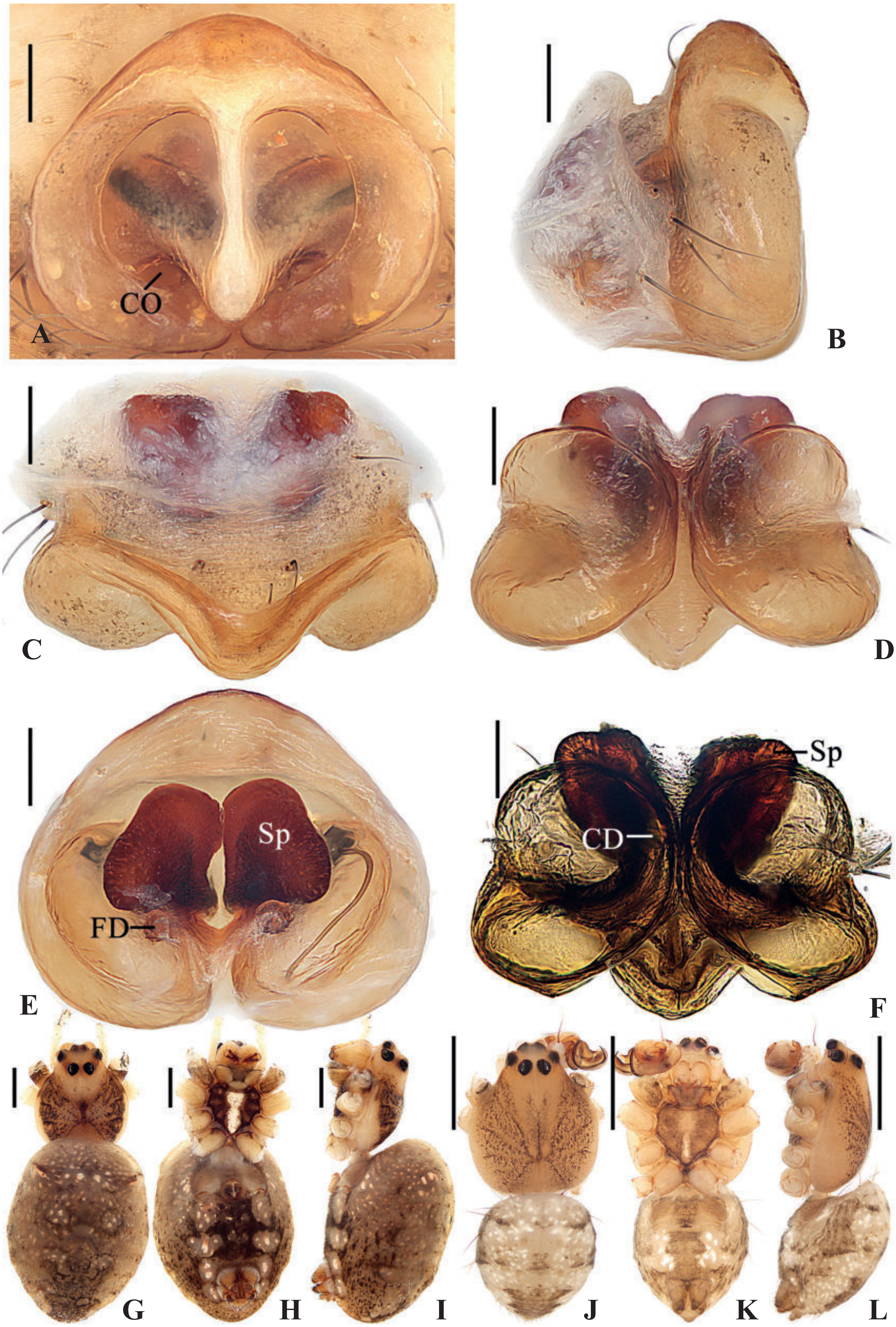

**Figure 5.** *Gea subarmata* Thorell, 1890 **A–I** TRU-Araneidae-289 **J–L** TRU-Araneidae-288 **A** epigyne, ventral view **B** ibid., lateral view **C** ibid., anterior view **D** ibid., posterior view **E** vulva, dorsal view **F** ibid., posterior view **G, J** habitus, dorsal view **H, K** ibid., ventral view **I, L** ibid., lateral view. Scale bars: 0.1 mm (**A–F**); 1 mm (**G–L**). Abbreviations: CD copulatory duct, CO copulatory opening, FD fertilization duct, Sp spermatheca.

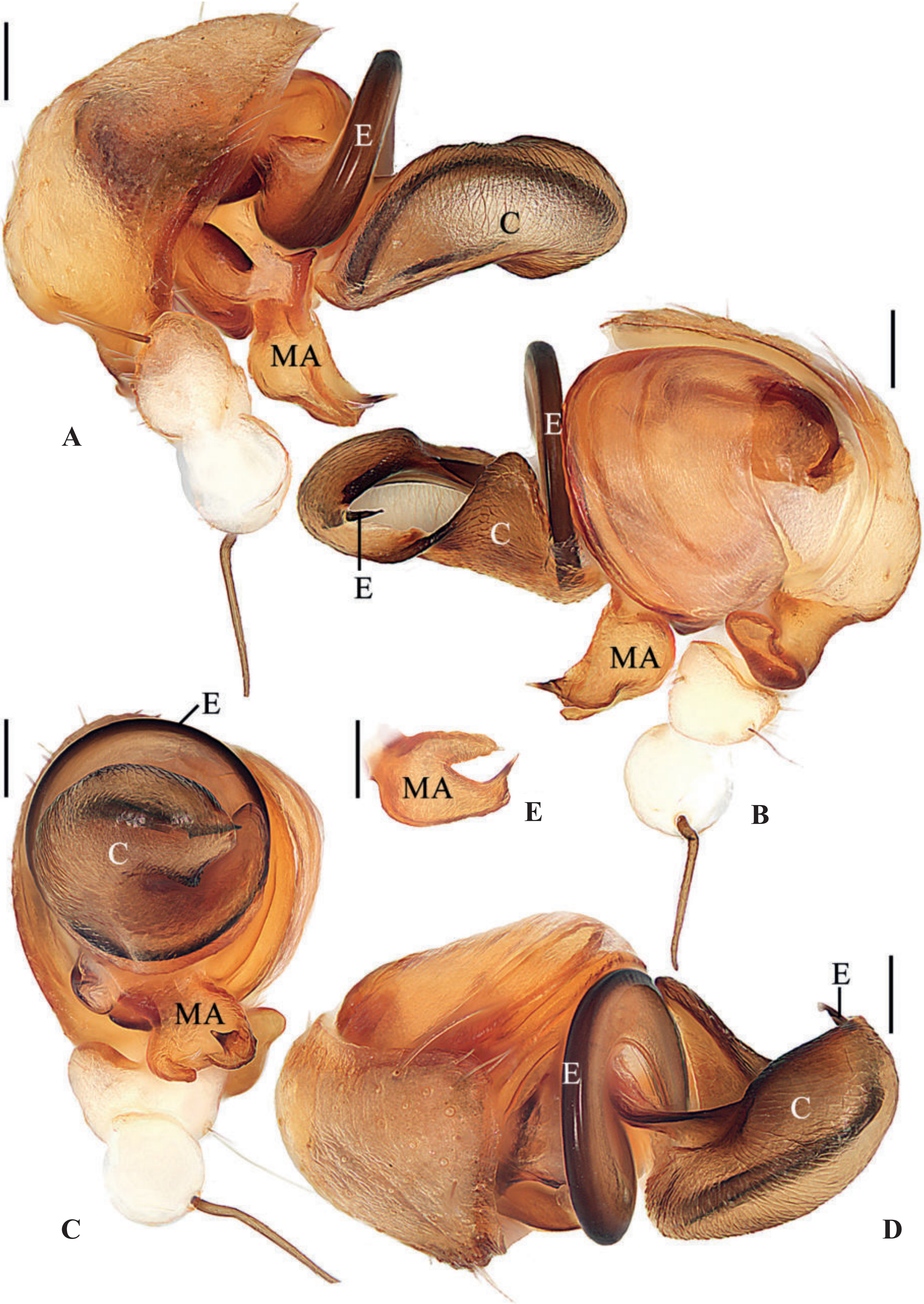

**Figure 6.** *Gea subarmata* Thorell, 1890 TRU-Araneidae-288 **A** pedipalp, prolateral view **B** ibid., retrolateral view **C** ibid., ventral view **D** ibid., apical view **E** median apophysis, dorsal view. Scale bars: 0.1 mm. Abbreviations: C conductor, E embolus, MA median apophysis.

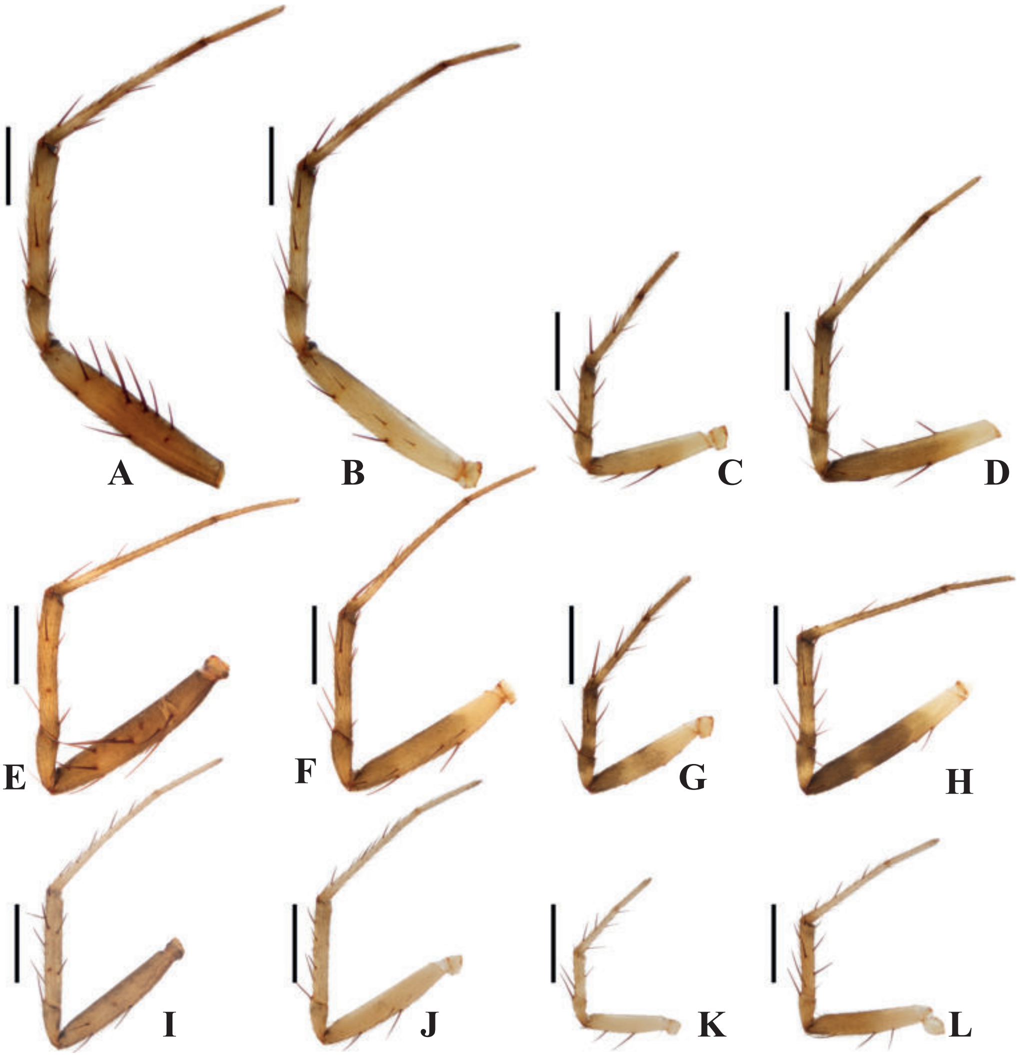

**Figure 7.** Legs of *Gea* spp., prolateral view (some macroseta fell out from the original positions) **A–D** *Gea jingdong* Mi, Wang & Gan, sp. nov. holotype **E–H** *Gea spinipes* C.L. Koch, 1843 TRU-Araneidae-272 **I–L** *Gea subarmata* Thorell, 1890 TRU-Araneidae-288 **A, E, I** legs I **B, F, J** legs II **C, G, K** legs III **D, H, L** legs IV. Scale bars: 1 mm.

***Pedipalp*** (Fig. 6): paracybium flattened, fingerlike; median apophysis bifurcate; dorsal ramus about equal length to ventral ramus; ventral ramus with a distal spur; embolus extremely long, twisted more than 360°; conductor prominent, membranous, wrapped around distal half of embolus.

**Female** (TRU-Araneidae-289, Fig. 5A–I). Total length 5.90. Carapace 2.30 long, 2.00 wide. Abdomen 3.80 long, 3.00 wide. Clypeus 0.10 high. Eye sizes and interdistances: AME 0.13, ALE 0.08, PME 0.13, PLE 0.13, AME–AME 0.25, AME–ALE 0.08, PME–PME 0.30, PME–PLE 0.35, MOA length 0.70, anterior width 0.50, posterior width 0.55. Leg measurements: **I** 8.30 (2.40, 2.75, 2.20, 0.95), **II** 7.95 (2.40, 2.65, 2.00, 0.90), **III** 4.85 (1.55, 1.55, 1.10, 0.65), **IV** 7.60 (2.40, 2.50, 1.95, 0.75). Habitus similar to that of male but abdomen with a pair of low anterolateral humps, thoracic region, sternum and abdomen a bit darker, and paler patch on sternum more obvious.

***Epigyne*** (Fig. 5A–F) ~1.2× wider than long, with circular frame and a long median septum separating two depressions in ventral view; copulatory openings located at posterior edges of depressions; copulatory ducts twisted into a C-shape, a bit longer than spermatheca; spermathecae bean-shaped, touching at midline.

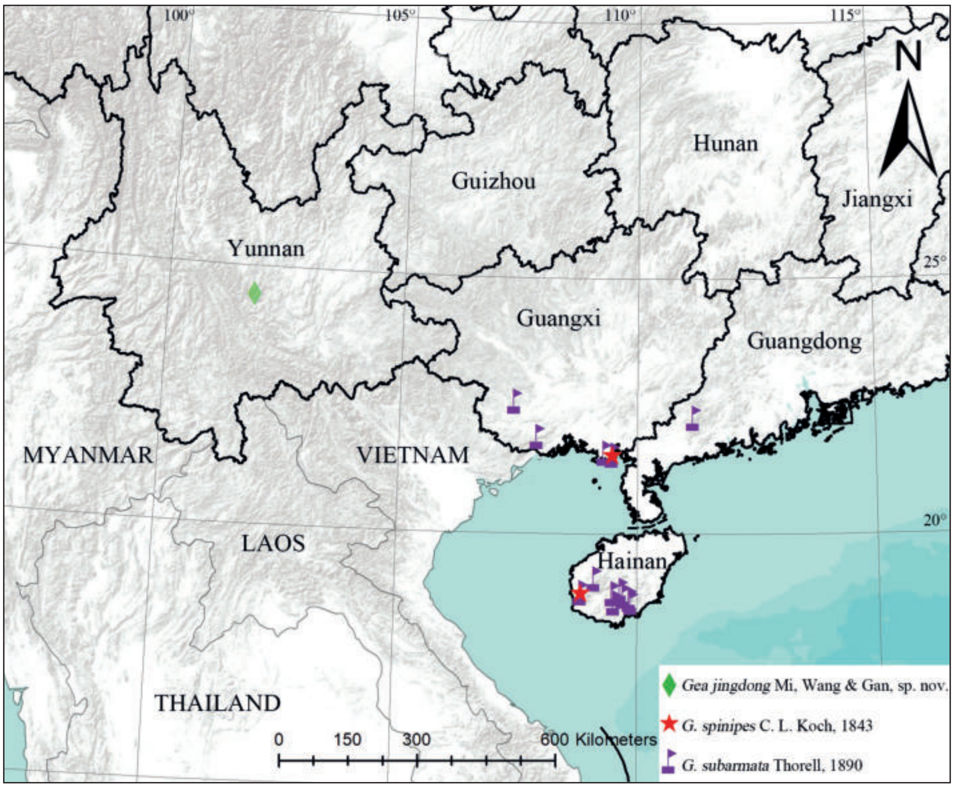

**Figure 8.** Distribution in China of the examined specimens.

**Variation.** Total length: ♀ 5.60–5.90 (*n* = 2).

**Distribution.** China (Hainan, Guangxi), Bangladesh, India, Indonesia, Japan, Malaysia, Myanmar, New Guinea, Philippines, and Singapore.

**Comment.** Male of *G. subarmata* described by Kulczyński (1911) is the male of *G. eff* Levi, 1983 as Levi (1983) proposed.

## Acknowledgements

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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## Author contributions

Data curation: WY. Funding acquisition: MX. Methodology: GJJ. Project administration: MX. Writing – original draft: LF. Writing – review and editing: WC.

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## Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# *Ghatippus paschima*, a new species and genus of plexippine jumping spider from the Western Ghats of India (Salticidae, Plexippini, Plexippina)

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## Abstract

We propose a new genus of plexippine jumping spiders from the Western Ghats of India based on the new species *Ghatippus paschima* **gen. et sp. nov.** While it bears a superficial resemblance to *Pancorius* in body form and *Hyllus* in membrane-bearing embolus, our UCE phylogenomic data—the first to resolve broad relationships within the Plexippina—as well as morphological features justify its status as a new genus. In addition to the molecular data and morphological descriptions, we provide photographs of living specimens of *Ghatippus paschima* **gen. et sp. nov.** and information on their natural history.

**Key words:** Araneae, biodiversity research, classification, phylogenomics, systematics, taxonomy

## Introduction

The Western Ghats of India, one of the hottest hotspots of biodiversity, awaits more than chance-based reporting of salticid spider diversity. Systematic surveys may reveal previously undiscovered salticids critical to understanding the region's ecosystems and the broader context of salticid diversity and phylogeny. Our 2019 surveys in a private estate in Kodagu, Karnataka, for instance, uncovered one such salticid lineage, of the subtribe Plexippina. Here, we describe that new species and propose a new genus for it based on phylogenomic evidence and morphology.

The subtribe Plexippina (Salticinae, Plexippini), an Old World group except for two New World species of *Evarcha* Simon, 1902, is species-rich, containing over 500 described species currently placed in 37 genera worldwide (Maddison 2015; Metzner 2023; World Spider Catalog 2023). Their combination of high diversity, conservative body forms, and simple genitalia have hindered the discovery of synapomorphies that could delimit genera, making the group taxonomically challenging. Placing new species in genera without evidence explicitly stated and interpreted phylogenetically has led to decisions about generic divisions (e.g. Prószyński's 2018 splitting of *Evarcha*) that are weakly supported and sometimes not broadly accepted (Kropf et al. 2019; World Spider Catalog 2023). Despite the taxonomic mess within the subtribe, what species are included in the Plexippina has remained more or less stable based on a combination of morphological (Maddison 1996, 2015) and molecular data (Maddison and Hedin 2003; Maddison et al. 2008; Bodner and Maddison 2012).

The first steps to our modern concept of Plexippina were taken by Maddison (1996), based on the form of the male endite's serrula and the palp. Molecular data subsequently showed that some of the genera he included (e.g. *Sibianor* Logunov, 2001) are instead harmochirines (Maddison and Hedin 2003; Maddison et al. 2008; Bodner and Maddison 2012), leading to Maddison's (2015) refined concept of the Plexippina. Using these studies as context, we here examine phylogenomically the relationships of the newly discovered plexippine lineage from the Western Ghats. Its placement would be unclear by morphology alone, as it is morphologically similar to *Hyllus* C.L. Koch, 1846 in male genitalia and *Pancorius* Simon, 1902 in its body form.

In the course of this work, we provide the first-ever plexippine phylogenomic tree, based on ultraconserved element data (Faircloth 2017; Zhang et al. 2023), contributing to further understanding of the relationship among plexippine genera and salticids in general (see Maddison et al. 2020a, b).

## Materials and methods

### Materials examined

The Indian specimens examined in this study are deposited in the Biodiversity Lab Research Collections of the National Centre for Biological Sciences (NCBS), Bengaluru, India (http://biodiversitycollections.in/). Individual specimens are identified by three-digit voucher codes prefixed with "**IBC-BP**" and "**IBC-BX**"; in addition, some are also identified by code numbers starting "**AS19.**". Non-Indian specimens are deposited in the University of British Columbia Spencer Entomological Collection. Codes beginning with "**WPM#19-**" indicate a collecting event of location and date, and thus may apply to more than one specimen.

### Morphology

A drawing tube attached to a Nikon ME600L compound microscope was used to prepare illustrations. Clove oil was used for clear viewing of epigyna after digesting the internal epigynal soft tissues with pancreatin. Preserved specimens were photographed using an Olympus OM-D E-M10 II mounted on an Olympus SZX12 stereoscope (for bodies) and a Nikon D7000 mounted on a Nikon ME600L compound microscope (for copulatory organs). Photographs were stacked using Helicon Focus 8.2.1 Pro. Living specimens were photographed with an Olympus OM-D E-M10 II camera with a 60 mm macro lens.

Descriptions are based on ethanol-preserved specimens. The descriptions were written with primary reference to the focal specimen indicated, which was used for measurements and carefully checked for details, but they apply as far as known to the other specimens examined. Carapace length was measured from the anterior base of the median eyes to the posterior margin of the carapace. The abdomen was measured from its anterior edge to the posterior end of the anal tubercle. All the measurements are in millimetres. Leg measurements are represented as follows: total length (femur, patella, tibia, metatarsus, and tarsus). Abbreviations used here are as follows: **ALE**, anterior lateral eye; **AME**, anterior median eye; **PME**, posterior median eye; **PLE**, posterior lateral eye; **RTA**, retrolateral tibial apophysis.

## Taxon sampling for phylogenomics

The set of 18 species (15 ingroup and 3 outgroup species) used in the phylogenomic analysis, and with their taxonomic authority indicated, is listed in Table 1. The selection of ingroup taxa was determined based on the limits of Plexippina, informed by previous phylogenetic studies (Maddison et al. 2008; Bodner and Maddison 2012) and synthesis work by Maddison (2015). The taxon sampling strategy aimed to maximize the representation of plexippine genera and their morphological diversity, including those most similar and relatively least similar to the focal species of this work. The two genera viewed as morphologically most similar to the new species, and thus candidate genera to contain it, are *Hyllus* and *Pancorius*. Thus, two distinct species of each of those were included to give them the best chance of linking to the new species. Otherwise, 11 other plexippine genera representing diverse body forms were included, for a total of 15 ingroup taxa representing 13 genera. These 13 ingroup genera represent ~86% of the plexippine genera known from India. The selection of outgroup taxa, two harmochirines and one salticine, was based on previous salticid phylogenetic studies (Maddison et al. 2008, 2014, 2017; Bodner and Maddison 2012; Maddison 2015).

**Table 1.** Specimens used in phylogenomic analysis.

| Species | Voucher | Sex | Locality | GPS coordinates (lat., long.) |
|---|---|---|---|---|
| *Anarrhotus fossulatus* Simon, 1902 | AS19.1319 | ♂ | Singapore | 1.379, 103.816 |
| *Artabrus erythrocephalus* (C.L. Koch, 1846) | AS19.2205 | ♂ | Singapore | 1.355–7, 103.774–5 |
| *Baryphas ahenus* Simon, 1902 | d536 | ♂ | South Africa | -25.95, 30.56 |
| *Bianor maculatus* (Keyserling, 1883) | NZ19.9864 | ♂ | New Zealand | -42.1691, 172.8090 |
| *Carrhotus* sp. | AS19.4650 | ♂ | India | 12.2145, 75.653–4 |
| *Epeus* sp. | DDKM21.055 | ♂ | Singapore | 1.355, 103.78 |
| *Evacin bulbosa* (Żabka, 1985) | AS19.2123 | ♂ | Singapore | 1.406, 103.971 |
| *Evarcha falcata* (Clerck, 1757) | RU18-5264 | ♂ | Russia | 53.721, 77.726 |
| *Ghatippus paschima* Marathe & Maddison sp. nov. | IBC-BP833/ AS19.3805 | ♂ | India | 12.220–1, 75.657–8 |
| *Habronattus hirsutus* (G.W. Peckham & E.G. Peckham, 1888) | IDWM.21018 | ♂ | Canada | 48.827, -123.265 |
| *Hyllus keratodes* (van Hasselt, 1882) | DDKM21.028 | ♂ | Malaysia | 3.325, 101.753 |
| *Hyllus semicupreus* (Simon, 1885) | AS19.4415 | ♂ | India | 12.2156, 75.6606 |
| *Pancorius dentichelis* (Simon, 1899) | SWK12-0042 | ♂ | Malaysia | 1.605–6, 110.185–7 |
| *Pancorius petoti* Prószyński & Deeleman-Reinhold, 2013 | SWK12-0195 | ♂ | Malaysia | 1.603–4, 110.185 |
| *Plexippus paykulli* (Audouin, 1826) | AS19.7337 | ♂ | India | 12.825–6, 78.252–3 |
| *Ptocasius weyersi* Simon, 1885 | DDKM21.069 | ♂ | Singapore | 1.36, 103.78 |
| *Telamonia festiva* Thorell, 1887 | DDKM21.048 | ♂ | China | 21.8105, 107.2925 |
| *Thyene imperialis* (Rossi, 1846) | AS19.6443 | ♂ | India | 12.216, 76.625 |

## Ultraconserved element (UCE) data

Molecular data was gathered for UCE loci using target enrichment sequencing methods (Faircloth 2017). One to four legs were used for DNA extraction using the Qiagen DNeasy Blood and Tissue Kit following the manufacturer protocol. The quality and quantity of the genomic DNA was measured using a NanoDrop 200c Spectrophotometer. For the target enrichment UCE sequencing, dual-indexed TruSeq-style libraries were prepared following methods used previously (e.g. Maddison et al. 2020b). Targeted enrichment using the RTA_v2 probeset (Zhang et al. 2023) was performed using the myBaits v. 4.01 protocol (Arbor Biosciences, https://arborbiosci.com/wp-content/uploads/2023/06/myBaits_Manual_v5.03.pdf). Libraries were sequenced on partial lanes of illumina NovaSeq 6000 S4 runs with 150-bp paired end reads.

Raw demultiplexed reads were processed with PHYLUCE v. 1.6 (Faircloth 2016), quality control and adapter removal were performed with Illumiprocessor wrapper (Faircloth 2013), and assemblies were created with SPAdes v. 3.14.1 (Nurk et al. 2013) using options at default settings. The UCE loci were recovered using RTA_v2 probeset (Zhang et al. 2023). The recovered loci were aligned with MAFFT using L-INS-i option (Katoh and Standley 2013). The aligned UCE loci were then trimmed with Gblocks (Castresana 2000; Talavera and Castresana 2007) using –b1 0.5, –b2 0.7, –b3 8, –b4 8, –b5 0.4 setting and re-aligned with MAFFT using L-INS-i option within Mesquite v. 3.61 (Maddison and Maddison 2019). As in the analysis of Maddison et al. (2020a), suspected paralogous loci were deleted based on branch lengths in RAxML (Stamatakis 2014) inferred gene trees. Loci represented in fewer than 10 taxa total were deleted.

## Phylogenetic analysis

Maximum-likelihood phylogenetic and bootstrap analyses were performed with IQ-TREE v. 1.6.12 (Nguyen et al. 2015) using the Zephyr v. 3.1 package (Maddison and Maddison 2020) in Mesquite v. 3.61 (Maddison and Maddison 2019) on the concatenated, unpartitioned UCE dataset with 15 ingroup and three outgroup taxa. For the phylogenetic tree inference, the option -m TEST (standard model selection followed by tree inference, edge-linked partition model, no partition-specific rates) was used with 10 search replicates. For the bootstrap analysis, the same option as the tree inference was used with 1000 search replicates.

## Data availability

The raw sequence reads obtained from UCE capture are stored within the Sequence Read Archive (BioProject: PRJNA1067139, https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1067139) and their accession numbers are listed in Table 1. The UCE loci matrices from SPAdes assemblies, pre-Gblocks, and the concatenated matrices used for phylogenetic and bootstrap analysis, along with trees, are available on the Dryad data repository (Link: https://doi.org/10.5061/dryad.zcrjdfnkw).

**Table 2.** Specifics of molecular data used for this phylogenomic analysis. Molecular data was generated based on RTA_v2 probeset. "**SRA**" is Sequence Read Archive accession number available through NCBI; "**Reads pass QC**" is the number of reads after the removal of adapter-contamination and low-quality bases using Illumiprocessor; "**Total UCE loci**" is the total number of UCE loci recovered with RTA_v2 probeset; **"After paralogy filter"** is the number of UCE loci after deletion of suspected paralogous loci based on branch length ratios; "**In at least 10 taxa**" is the number of UCE loci in at least 10 or more taxa after branch length criteria; "**Filtered UCE sequence length**" is the concatenated sequence length of filtered UCE loci; **"Total loci"** is the number of UCE loci represented among all taxa.

| Species | Voucher | SRA | Reads pass QC | Total UCE loci | After paralogy filter | In at least 10 taxa | Filtered UCE sequence length |
|---|---|---|---|---|---|---|---|
| *Anarrhotus fossulatus* | AS19.1319 | SRR27728361 | 15542927 | 2525 | 2492 | 2384 | 2057818 |
| *Artabrus erythrocephalus* | AS19.2205 | SRR27728359 | 14903498 | 2837 | 2800 | 2736 | 2287255 |
| *Baryphas ahenus* | d536 | SRR27728358 | 2653688 | 2255 | 2225 | 2205 | 965482 |
| *Bianor maculatus* | NZ19.9864 | SRR27728369 | 7914005 | 2954 | 2916 | 2794 | 2376468 |
| *Carrhotus* sp. | AS19.4650 | SRR27728370 | 5272657 | 2914 | 2877 | 2783 | 2284451 |
| *Epeus* sp. | DDKM21.055 | SRR27728357 | 13896435 | 2896 | 2859 | 2779 | 2403857 |
| *Evacin bulbosa* | AS19.2123 | SRR27728356 | 10851810 | 2765 | 2731 | 2628 | 2113380 |
| *Evarcha falcata* | RU18-5264 | SRR27728355 | 11538276 | 2761 | 2723 | 2659 | 2174281 |
| *Ghatippus paschima* sp. nov. | IBC-BP833/ AS19.3805 | SRR27728354 | 7881860 | 2892 | 2854 | 2779 | 2381949 |
| *Habronattus hirsutus* | IDWM.21018 | SRR27728360 | 6581974 | 2817 | 2784 | 2682 | 2187694 |
| *Hyllus keratodes* | DDKM21.028 | SRR27728353 | 11349372 | 2925 | 2886 | 2788 | 2367864 |
| *Hyllus semicupreus* | AS19.4415 | SRR27728368 | 9874003 | 2939 | 2905 | 2820 | 2377271 |
| *Pancorius dentichelis* | SWK12-0042 | SRR27728367 | 6025337 | 3092 | 3054 | 2956 | 2251455 |
| *Pancorius petoti* | SWK12-0195 | SRR27728366 | 5116119 | 2980 | 2943 | 2853 | 2245013 |
| *Plexippus paykulli* | AS19.7337 | SRR27728365 | 7445183 | 2930 | 2892 | 2799 | 2139754 |
| *Ptocasius weyersi* | DDKM21.069 | SRR27728364 | 9926900 | 2878 | 2840 | 2768 | 2279296 |
| *Telamonia festiva* | DDKM21.048 | SRR27728363 | 7908436 | 2948 | 2911 | 2831 | 2414600 |
| *Thyene imperialis* | AS19.6443 | SRR27728362 | 7797854 | 2888 | 2851 | 2763 | 2371167 |
|  |  |  | Average: | 2844.2 | 2807.9 | 2722.6 | 2204391.9 |
|  |  |  | Minimum: | 2255 | 2225 | 2205 | 965482 |
|  |  |  | Maximum: | 3092 | 3054 | 2956 | 2414600 |
|  |  |  | Total loci: | 3377 | 3335 | 3060 |  |

## Results

### Phylogenetic results

Table 2 lists the sequence data recovered from the 18 taxa. On average 2844 UCE loci per taxa (minimum 2255, maximum 3092) were initially recovered. Of these total loci, on average 2807 loci survived per taxa (min. 2225, max. 3054) after removing suspected paralogous loci based on branch lengths, and on average 2722 loci remained per taxa (min. 2205, max. 2956) after removing loci represented in fewer than 10 taxa. In total, 3060 UCE loci were represented in the resulting dataset, which were concatenated into the final matrix, in which each taxon had on average ~2.2 million base pairs of sequence data (min. 965482, max. 2414600).

The phylogenetic results are shown in Fig. 1. The subtribes Plexippina and Harmochirina are recovered as reciprocally monophyletic, consistent with the previous phylogenetic studies with much less sequence data (Maddison and Hedin 2003; Maddison et al. 2008; Bodner and Maddison 2012). Within the Plexippina, two major clades are recognized (marked in Fig. 1). Bootstrap val-

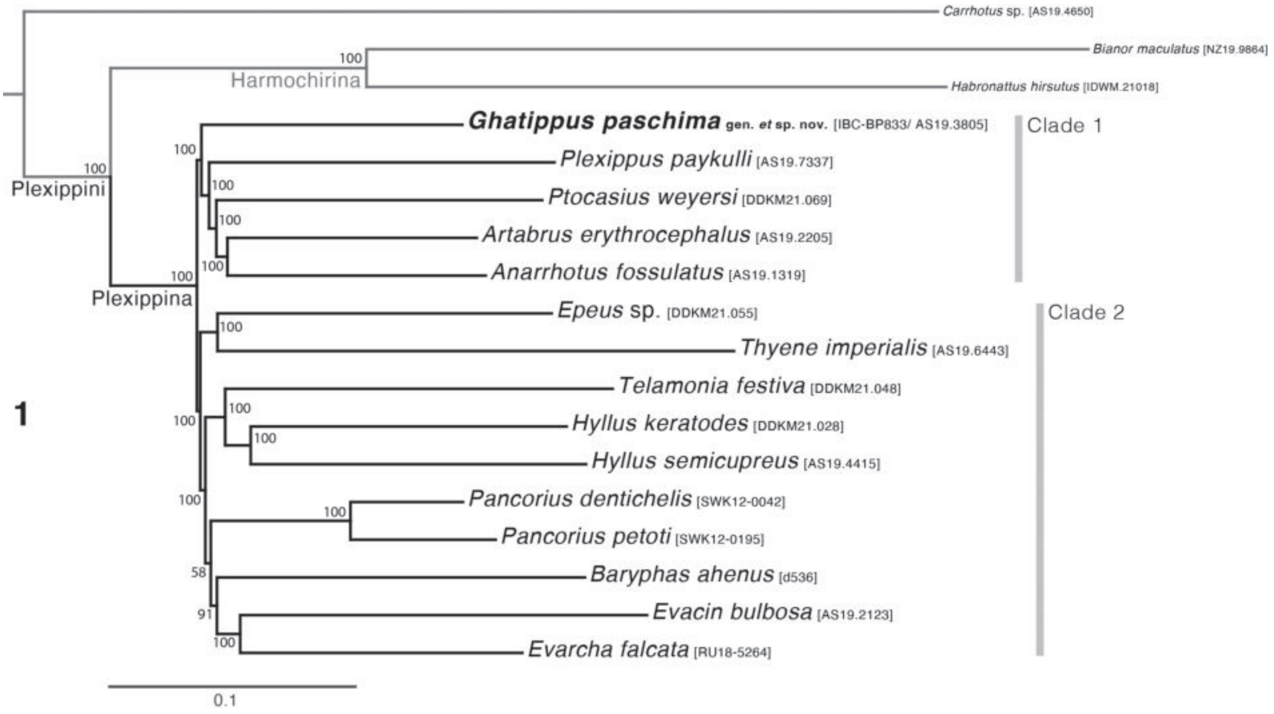


**Figure 1.** Maximum-likelihood tree, best tree of 10 replicates inferred using IQ-TREE, from concatenated dataset of 3060 ultraconserved element loci. Numbers at the nodes are percentage of 1000 bootstrap replicates recovering the clade. *Ghatippus paschima* sp. nov. is recovered distantly (see Clade 1) from morphologically similar *Hyllus* and *Pancorius* (see Clade 2).

ues are generally high, showing that the relationships are well supported, as might be expected with this volume of sequence data.

*Ghatippus* gen. nov. is recovered as sister to all the genera in clade 1 (see Fig. 1): (*Ghatippus*, (*Plexippus*, (*Ptocasius*, (*Anarrhotus*, *Artabrus*)))). This phylogenetic position of *Ghatippus* gen. nov. necessitates its recognition as a new genus. Any other taxonomic decision apart from creating a new genus, whether to include it in a phylogenetically closely related genus or in another morphologically similar plexippine genus, would render the genus in which it is placed either paraphyletic or polyphyletic. The only other phylogenetically meaningful option, besides creating a new genus, would be to lump all the genera in clade 1 into a single genus. This would generate a massive genus of highly diverse body forms that would go against all traditions of salticid generic limits. A far better choice is to recognize *Ghatippus* gen. nov. as a new genus.

The choice to establish a new genus is further substantiated by morphology. Within clade 1, *Ghatippus* gen. nov. is unique with its membrane bearing medium-long embolus. In contrast, *Anarrhotus* Simon, 1902 and *Plexippus* C.L. Koch, 1846 have a short embolus, while *Artabrus* Simon, 1902 and *Ptocasius* Simon, 1885 have a medium to long, thin embolus. Importantly, all four of these lack a membrane-bearing embolus.

## Taxonomic results

### Family Salticidae Blackwall, 1841
### Tribe Plexippini Simon, 1901
### Subtribe Plexippina Simon, 1901

### *Ghatippus* Marathe & Maddison, gen. nov.

https://zoobank.org/1E8E60B3-FBE6-4DB5-83B0-38BFFE401862
Figs 2–40
Kannada: ಘಾಟಿಪ್ಪಸ್ | Devanagari: घाटिप्पस्

**Type species.** *Ghatippus paschima* Marathe & Maddison, sp. nov.; by monotypy.

**Etymology.** The generic name *Ghatippus* gen. nov. combines the word ‘Ghat’, representing the collecting locality—the Western Ghats Mountain range—with the distinctive suffix found in several plexippine genera. The generic name is assigned to the masculine gender.

**Diagnosis.** The UCE phylogeny implies genetic diagnosability of *Ghatippus* gen. nov., but here we focus on the morphological distinctions. The membranous retrolateral edge of the embolus (Figs 2, 18) and lack of distinct epigynal coupling pockets (Figs 4, 20) differentiate *Ghatippus* gen. nov. from all members of clade 1 (Fig. 1) and other plexippines except *Hyllus*, *Thyene* Simon, 1885, and *Vailimia* Kammerer, 2006. Also, *Ghatippus* gen. nov. is the only plexippine reported to have a bifurcated male fang with nearly co-equal branch points (Figs 6, 12).

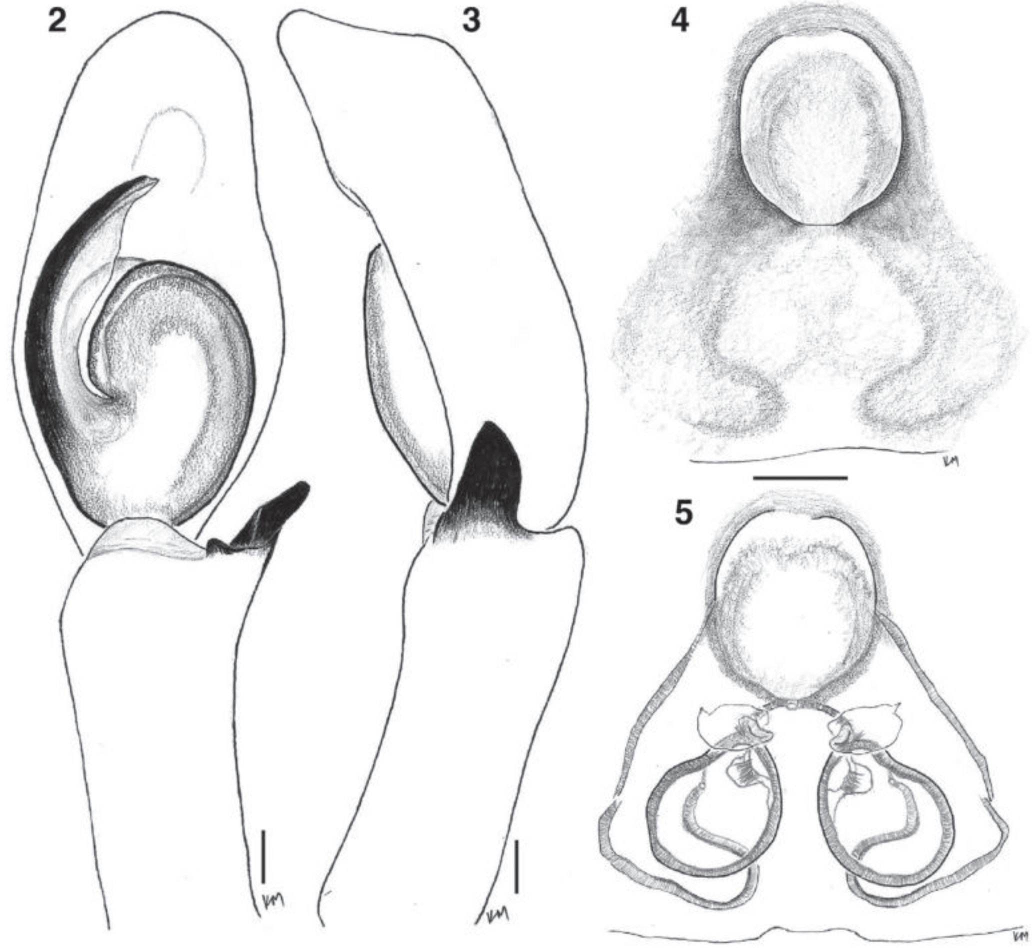
From *Hyllus*, *Ghatippus* gen. nov. differs in carapace (higher, box-shaped, PLEs on tubercles in *Ghatippus* gen. nov. vs relatively lower, rounder, no tubercles in *Hyllus*), RTA (simple, short vs serrated, wide), cymbium (laterally narrow with a narrow apex vs robust, laterally wide with a broader apex), and copulatory ducts (short vs long). From *Thyene*, *Ghatippus* gen. nov. differs in embolus length (medium in *Ghatippus* gen. nov. vs long and coiled in *Thyene*), copulatory ducts (short vs long), and carapace (higher, box-shaped, PLEs on tubercles vs relatively lower, rounder, no tubercles). From *Vailimia*, *Ghatippus* gen. nov. differs in embolus length (medium in *Ghatippus* gen. nov. vs long in *Vailimia*), RTA (simple, short vs curvy, long), and spermathecae (simple vs globular). *Ghatippus* gen. nov. also has an oval abdomen and open posture typical for salticids, unlike *Vailimia*’s pointed abdomen and unusual stance, holding the legs close to the body in a compact crouch.

*Ghatippus* gen. nov. is most likely to be confused with *Pancorius* because of the high, box-shaped carapace with PLEs on tubercles, but *Pancorius* lacks the membrane-bearing embolus and has distinct epigynal coupling pockets.

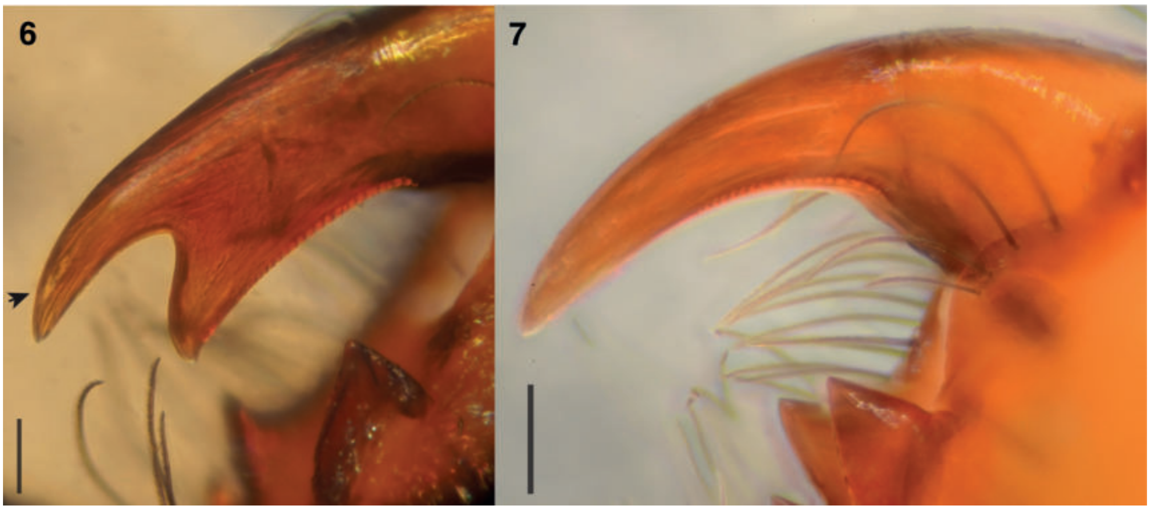
### *Ghatippus paschima* Marathe & Maddison, sp. nov.

https://zoobank.org/FAD7F75C-B5B9-4B6B-ABF4-621D8073A3C5
Figs 2–40
ಘಾಟಿಪ್ಪಸ್ ಪಶ್ಚಿಮ | घाटिप्पस पश्चिम

**Type materials.** All from India: Karnataka: Kodagu: Yavakapadi, Honey Valley area and deposited in Biodiversity Lab Research Collections, NCBS. ***Holotype*:** Male, IBC-BP817, 12.2202°N, 75.6581°E, 1190–1230 m elev., 24 June 2019, K. Marathe & W. Maddison, WPM#19-071. ***Paratypes*:** 5 ♂♂ and 5 ♀♀ (IBC-BP818 – IBC-BP827), data same as the holotype • 4 ♂♂ and 1 ♀ (IBC-BP828 – IBC-BP832), buildings and roadside, 12.22°N, 75.66°E, 1100 m elev., 23–28 June 2019, W. Maddison & K. Marathe, WPM#19-069 • 4 ♂♂ and 4 ♀♀ (IBC-BP833 – IBC-BP840), along stream, 12.220 to 12.221°N, 75.657 to 75.658°E, 1190 m

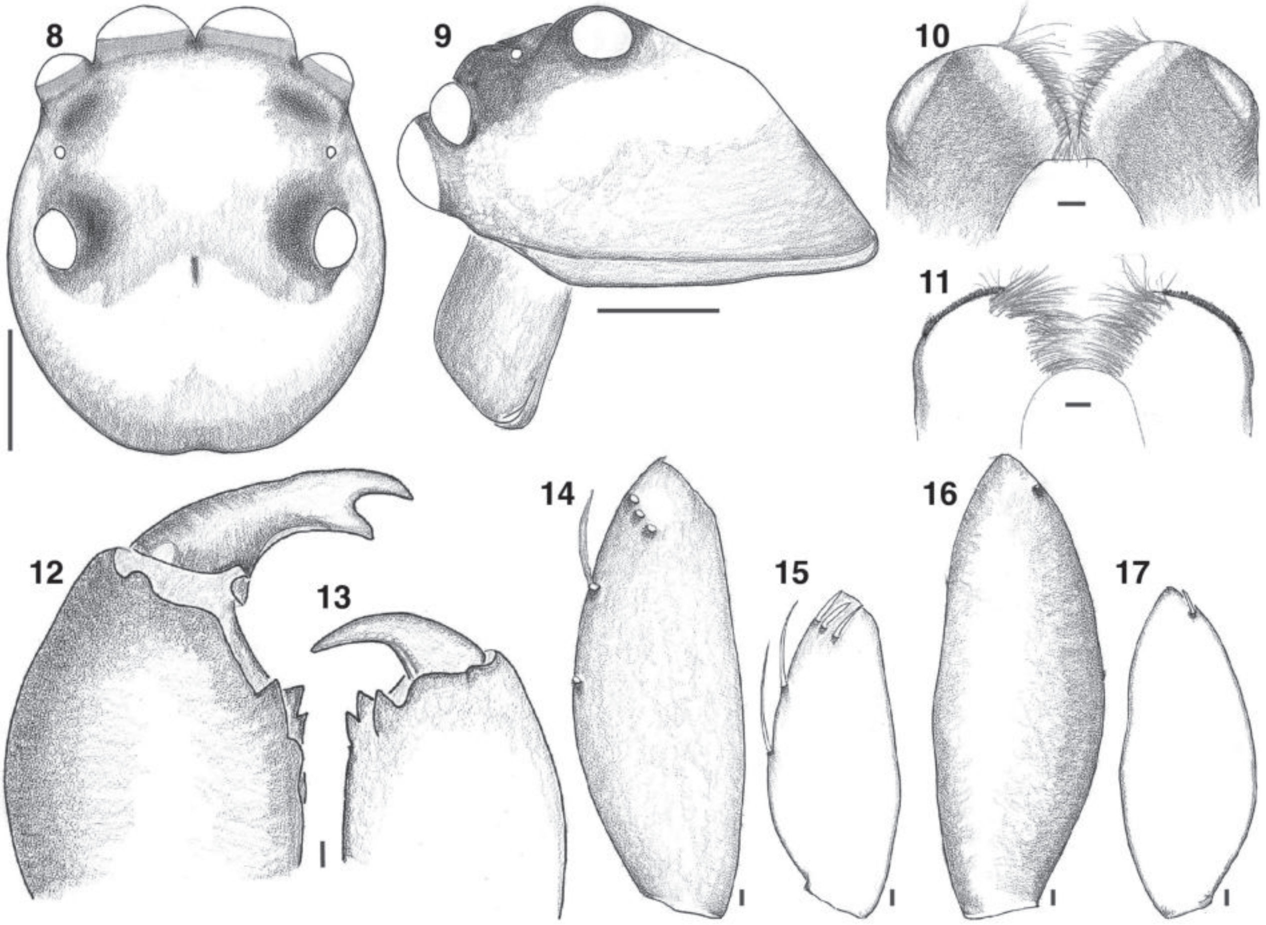


**Figures 2–5.** *Ghatippus paschima* sp. nov. genitalia **2** male left palp, ventral view (holotype IBC-BP817) **3** ditto, retrolateral view (holotype IBC-BP817) **4** epigyne, ventral view (paratype IBC-BP818) **5** vulva, dorsal view (paratype IBC-BP818). Scale bars: 0.1 mm.



**Figures 6, 7.** *Ghatippus paschima* sp. nov., dorsal view of left chelicerae **6** paratype male, IBP-BP819 **7** paratype female, IBC-BP820 (arrow points to the true tip on the male chelicera bearing the venom duct). Scale bars: 0.1 mm.

elev., 24 June 2019, W. Maddison & K. Marathe, WPM#19-070 • 3 ♂♂ (IBC-BP841 – IBC-BP843), forest & grassland, 12.2156 to 12.2157°N, 75.6597 to 75.6606°E, 1300 m elev., 25 June 2019, W. Maddison & K. Marathe, WPM#19-



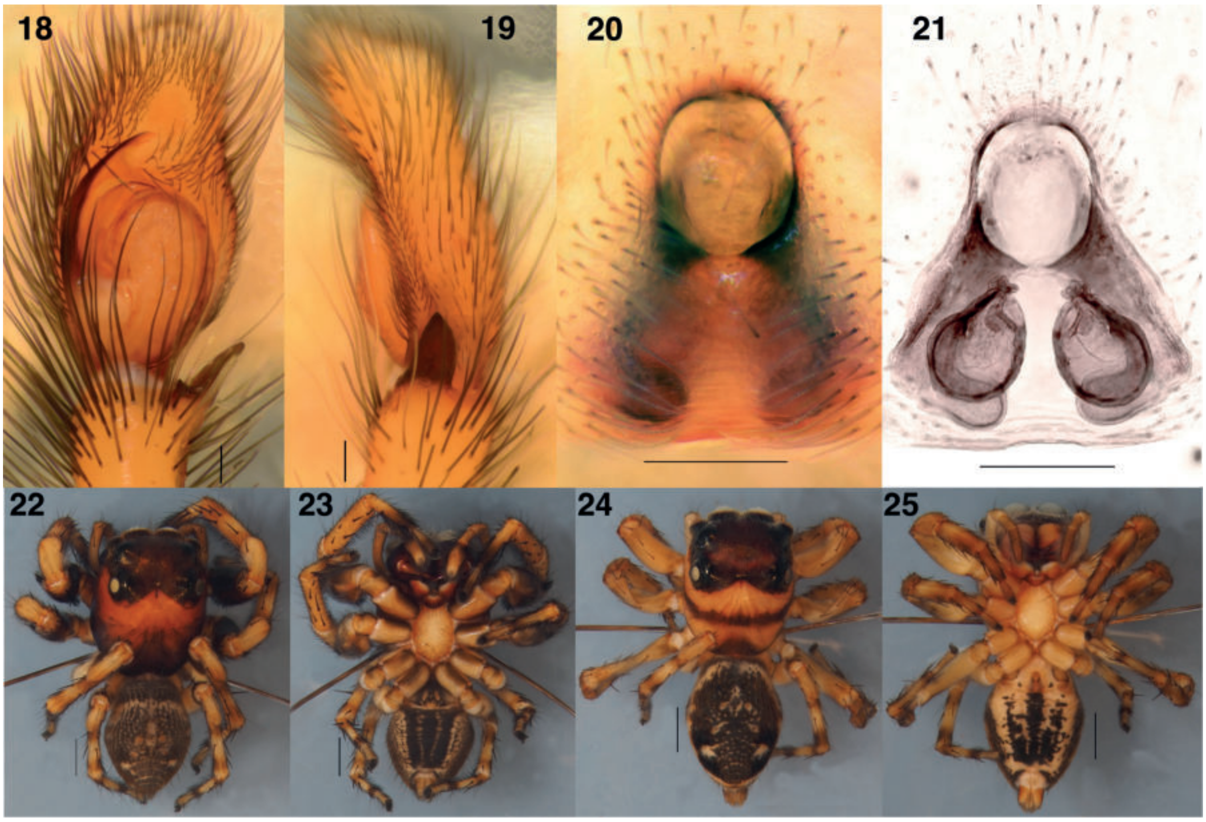
**Figures 8–17.** *Ghatippus paschima* sp. nov. **8** male (paratype IBC-BP819) carapace, dorsal view **9** ditto, side view **10, 11** male endite, ventral and dorsal view respectively (paratype IBC-BP819) **12** male right chelicera, dorsal view (paratype IBC-BP819) **13** female left chelicera, dorsal view (paratype IBC-BP820) **14** male left femur of leg I, prolateral view (paratype IBC-BP819) **15** female left femur of leg I, prolateral view (paratype IBC-BP820) **16** male left femur of leg I, retrolateral view (paratype IBC-BP819) **17** female left femur of leg I, retrolateral view (paratype IBC-BP820). Scale bars: 1.0 mm (**6, 7**); 0.1 mm (**8–15**).

075 • 2 ♂♂ (IBC-BP844 – IBC-BP845), forest & edge, 12.215 to 12.216°N, 75.659 to 75.661°E, 1300 m elev., 25 June 2019, W. Maddison & K. Marathe, WPM#19-077 • 1 ♀ (IBC-BP846), grassland, 12.2145°N, 75.653–75.654°E, 1280–1380 m elev., 26 June 2019, W. Maddison & K. Marathe, WPM#19-080 • 1 ♂ (IBC-BX501), Chingara Falls,12.232°N, 75.653°E, 970 m elev., 27 June 2019, Maddison/ Marathe/ Abhijith/ Pavan, WPM#19-084 • 1 ♂ (IBC-BX502), open woodland,12.216°N, 75.661°E, 1320 m elev., 28 June 2019, K. Marathe & W. Maddison, WPM#19-088.

**Etymology.** The specific epithet *paschima*, a noun in apposition, means “west” in both Sanskrit and Kannada.

**Diagnosis.** As there is only one species in the genus, see the generic diagnosis.

**Description. Male** (focal specimen, holotype, IBC-BP817). ***Measurements***: Carapace 3.9 long, 3.3 wide. Abdomen 4 long, 2.5 wide. ***Leg measurements***: I–9.4 (3.1, 1.9, 2.3, 1.2, 0.9); II–6.9 (2.1, 1.6, 1.3, 1, 0.9); III–7.1 (2.6, 1.5, 1.7, 0.6, 0.7); IV–7.2 (2.2, 1.2, 1.7, 1.3, 0.8). Leg formula I-III-IV-II. ***Carapace*** mostly brown mottled with black. Ocular area dark brown, sparsely covered with lustrous yellowish-golden hairs. Distinct black bulge behind each ALE (Figs 8, 9, 22). Black around PMEs and PLEs. Thorax with steep slope, brown, sparsely



**Figures 18–25.** *Ghatippus paschima* sp. nov. genitalia (top row) and alcohol preserved types habitus (bottom row) **18** male (holotype IBC-BP817) left palp, ventral view **19** ditto, retrolateral view **20** epigyne, ventral view (paratype IBC-BP818) **21** vulva, dorsal view (paratype IBC-BP818) **22** male (holotype IBC-BP817), dorsal view **23** ditto, ventral view **24** female (paratype IBC-BP818), dorsal view **25** ditto, ventral view. Scale bars: 0.1 mm for genitalia; 1.0 mm for bodies.

covered with black hairs. Black along edges. ***Clypeus*** narrow, brown, covered in white hairs appearing like a moustache. ***Chelicerae*** dark brown. Vertical, about as wide as carapace, bulging. Fangs bifid, with second fork near true tip (bearing venom duct) and almost as long as tip (Figs 6, 12). ***Palp*** (Figs 2, 3, 18, 19) yellowish brown. Tibia about as long as patella. Relatively narrow cymbium. Medium-long embolus arising from base at about 7–8 o'clock. Retrolateral edge of embolus extended as firm transparent membrane. Simple kidney-bean-shaped tegulum, gently curved proximally. RTA short and wide blade, simple. ***Legs*** mostly yellowish, brownish near joints, generally robust. Femur I and II distinctively dark brown, robust, and stout, with vertical fringe of short black hairs dorsally and, near patella, posteriolaterally. Metatarsus I with ventral fringe of black hairs, and weaker fringe on metatarsus II. ***Abdomen*** ovoid, medium to dark brown, covered with scales that in life have golden or reddish sheen. Indistinct basal band paler, as are muscle attachment points and posterior medial chevron. Two distinct pale spots in posterior half, one on either side of chevron, and two smaller spots just in front of spinnerets. Spinnerets yellowish, covered with black hairs.

**Female** (focal specimen, paratype, IBC-BP818). ***Measurements*:** Carapace 3.4 long, 2.8 wide. Abdomen 4.2 long, 2.4 wide. ***Leg measurements*:** I–5.4 (1.7, 1.1, 1.2, 0.9, 0.5); II–4.9 (1.7, 0.8, 1.2, 0.8, 0.4); III–6.9 (2, 1.2, 1.5, 1.5, 0.7); IV–6.3 (1.7, 1, 1.5, 1.5, 0.6). Leg formula III-IV-I-II. ***Carapace*** yellow (thorax) to brown (head). Ocular area dark brown, sparsely covered with lustrous white hairs.

**Figures 26–40.** Habitus of *Ghatippus paschima* sp. nov. **26–31** male (IBC-BP828/ AS19.4384) **32–34** male (IBC-BP833/ AS19.3805) **35–38** female, (IBC-BP834/ AS19.3814) **39, 40** (IBC-BP835/ AS19.3821). Scale bar: 1.0 mm.

Distinct black bulge behind each ALE. Black around PMEs and PLEs. Thorax with steep slope, yellowish brown, sparsely covered with black hairs. With origin near front, brown band encircles carapace close to transition between ocular area and thorax. Brown along edges. ***Clypeus*** narrow, brown, covered with white hairs but more sparsely than in male. ***Chelicerae*** yellowish brown. Vertical, narrower than extent of carapace, not bulging as in male, with simple unbifurcated fangs (Figs 7, 13). ***Legs*** mostly yellowish and some brown near joints. ***Abdomen*** ovoid, dark brown but with paler basal band (extended posteriorly to encircle the abdomen), muscle attachment points, and posterior medial chevron. On either of the chevron the brown is especially dark, almost black, and contains distinct pale spot (Fig. 24). ***Epigyne*** (Figs 4, 5, 20, 21): two crescent-shaped anterior copulatory openings share common atrium. No epigynal coupling pocket visible, though there is slight medial indentation of the epigastric furrow. Simple round spermathecae with flattened (lamellar) copulatory ducts ventrally. Fertilizations ducts broad, placed anteriorly on spermathecae.

**Additional materials.** All from India: Kerala: near Thalappuzha, Fringe Ford, and deposited in Biodiversity Lab Research Collections, NCBS. 1 ♂ (IBC-BX503), forest path, 11.888°N, 75.692–75.963°E, 1020 m elev., 1 July 2019, W. Maddison & K. Marathe, WPM#19-095 • 1 ♀ (IBC-BX504), camp area, 11.884°N, 75.965°E, 990 m elev., 1–2 July 2019, W. Maddison & K. Marathe, WPM#19-099 • 3 ♂♂ and 1 ♀ (IBC-BX505 – IBC-BX508), forest, 11.88°N, 75.97°E, 1150 m elev., 2 July 2019, K. Marathe & W. Maddison, WPM#19-102.

**Natural history.** *Ghatippus paschima* sp. nov. was found commonly in both Kodagu and Kerala. Most collecting days in both locations were rainy and overcast. The spiders seemed to be exclusively vegetation dwellers, often found on small to medium-sized trees. Although they were collected from diverse habitats, they were mostly collected in the understorey, edge, and disturbed habitats of the evergreen forests of Honey Valley Estate in Kodagu. In Fringe Ford, Kerala, they were collected from the secondary evergreen growth of an inoperative tea estate.

While male and female salticids typically differ in colour, sexual dimorphism in the fangs is noteworthy. Male fangs are bifid, but female fangs are not (Figs 6, 7, 12, 13). The bifid fangs may possibly be used to hold females during mating, in male-to-male combat, or have a sex-limited ecological function.

**Discussion.** Plexippines account for about ~9% of the total salticid diversity worldwide, with about ~8% of the world's plexippine diversity documented in India (World Spider Catalog 2023). The 45 plexippine species previously known from India, out of 566 species worldwide, belong to 16 genera (Caleb 2019; World Spider Catalog 2023): *Anarrhotus* Simon, 1902 (1 sp. in India, of 2 worldwide), *Burmattus* Prószyński, 1992 (1 in India, of 5 worldwide), *Colopsus* Simon, 1902 (3 of 8), *Dexippus* Thorell, 1891 (3 of 4), *Epeus* G. W. Peckham & E. G. Peckham, 1886 (5 of 19), *Evarcha* Simon, 1902 (3 of 92), *Hyllus* C. L. Koch, 1846 (4 of 67), *Orientattus* Caleb, 2020 (1 of 4), *Pancorius* Simon, 1902 (9 of 45), *Plexippus* C. L. Koch, 1846 (4 of 42), *Pseudamycus* Simon, 1885 (1 of 10), *Ptocasius* Simon, 1885 (1 of 68), *Telamonia* Thorell, 1887 (3 of 40), *Thyene* Simon, 1885 (3 of 55), *Vailimia* Kammerer, 2006 (2 of 6), and *Yaginumaella* Prószyński, 1979 (1 of 14).

While we are beginning to see a steady uptick in the number of new plexippines being described (World Spider Catalog 2023), the unique endemic lineages and their radiations in India are still largely unexplored. With the addition of *Ghatippus paschima* sp. nov., potentially an endemic lineage, the number of plexippines stands at 46 species and 17 genera for India.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

KM and WPM did the field work and managed the specimens. KM did the molecular work. KM and WPM analyzed the molecular data, studied the specimens morphologically, made decisions about new species, and new genus. KM did the drawings, and wrote the first draft of the manuscript. WPM assisted with additions and corrections to the manuscript. KM, WPM, and KK finalized the manuscript.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# Two new species of *Hyalella* (Amphipoda, Dogielinotidae) from the Humid Chaco ecoregion of Paraguay

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## Abstract

The freshwater amphipod genus *Hyalella* Smith, 1874 is widely distributed in the Neotropics, with several biogeographically restricted species and a high cryptic diversity throughout South America. Tens of species of *Hyalella* have been documented from nearby Brazil and Argentina, but no systematic record of the genus exists for Paraguay. Here we describe two new species of *Hyalella*: *H. mboitui* **sp. nov.** and *H. julia* **sp. nov.** from the Ñeembucú wetlands of southwestern Paraguay. *Hyalella mboitui* **sp. nov.** and *H. julia* **sp. nov.** are characterised by a dorsally smooth body, pigmented eyes, uropod 1 endopod with a curved seta, the dorsal margin of uropod 3 ramus without setae, and uropod 3 peduncle longer than wide and with six setae apically. The two species are distinguished by their diagnostic mouthparts, with a median serrated edge on the lacinia mobilis in *H. mboitui* **sp. nov.** and two elongated lateral denticles with a serrated edge in *H. julia* **sp. nov.,** and by the presence of a pronounced cup for the dactylus on gnathopod 2 in *H. mboitui* **sp. nov**. In addition, they show differences in the number of articles on antennae 1 and 2, in the relative length of the pereiopods, and in the numbers and types of setae on their gnathopods and uropods 1–3. *Hyalella mboitui* **sp. nov.** and *H. julia* **sp. nov.** represent the first taxonomically documented occurrence of Paraguayan freshwater amphipods. These new taxa attest to the largely unmapped species richness of freshwater invertebrates in the Humid Chaco of Paraguay. This potential biodiversity hotspot is currently under threat from land conversion, highlighting the need for more systematic studies and effective conservation of the local invertebrate biodiversity.

**Key words:** Amphipoda, conservation, *Hyalella*, new species description, Paraguay, taxonomy

## Introduction

Amphipods are a diverse clade of peracaridan crustaceans inhabiting both marine and freshwater environments, where they represent an ecologically and taxonomically significant component of the planktonic and benthic invertebrate fauna (Thomas 1993; Ishikawa and Urabe 2002). The genus *Hyalella* Smith, 1874 is endemic to the Americas and among the most widely distributed freshwater amphipods in the New World, ranging from southern Canada to Patagonia (Bueno et al. 2014; Damborenea et al. 2020; Reis et al. 2023).

This diverse genus comprises more than 100 described species, and over 80 of them are endemic to South America (Marrón-Becerra and Hermoso-Salazar 2023; Marrón-Becerra et al. 2023; Peralta and Verónica 2023; Reis et al. 2023; Tomikawa et al. 2023). In particular, numerous species of the genus have been reported from Argentina, and southern Brazil, which holds the highest diversity of any single country (González et al. 2006; Talhaferro et al. 2021a, b; Reis et al. 2023). However, occurrences of this genus have not been systematically documented in their neighbouring country, Paraguay. Recent taxonomic and genetic studies of *Hyalella* suggest that the full extent of its diversity and distribution is vastly underestimated (Limberger et al. 2021; Talhaferro et al. 2021a; Waller et al. 2022). Therefore, reported discrepancies in regional taxonomic richness may be largely due to limited sampling (Reis et al. 2020, 2023).

This knowledge gap has potentially broad-ranging repercussions for conservation and habitat management. Amphipods, including *Hyalella*, sustain key links in matter and energy transfers in freshwater ecosystems, where they act as ecologically abundant grazers and detritivores, provide hosts for diverse micro- and macro-parasites, and serve as important prey items for both vertebrate and invertebrate predators (Duffy and Hay 2000; Castiglioni and Bond-Buckup 2008; Giari et al. 2020; Streck-Marx and Castiglioni 2020). Members of *Hyalella* support these critical ecosystem functions across diverse habitats, from hypogean waters to wetlands, from sea level up to above 4000 metres of elevation and inhabit both benthic sediments and a range of aquatic macrophytes (Castiglioni and Bond-Buckup 2008; Limberger et al. 2021; Zapelloni et al. 2021).

Here we describe two new species of *Hyalella* from the Ñeembucú wetlands, part of the Humid Chaco ecoregion of southwestern Paraguay (Mereles et al. 2020). These taxa represent the first scientifically documented occurrence of *Hyalella* in the country and present distinctive limb and mouthpart morphologies not reported for other congeneric species. The taxonomic distinctiveness and ecology of the two species are discussed considering the potential conservation threats to the freshwater habitats of the Ñeembucú region.

## Materials and methods

Freshwater invertebrate specimens were sampled from September 8, 2021 to June 5, 2023, as part of an environmental impact assessment led by Fundación Para La Tierra (PLT) under contract from the Ministry of Public Works and Communications (Ministerio de Obras Públicas y Comunicaciones, MOPC). Five field sites in total were sampled in and near the city of Pilar, Ñeembucú Department (Paraguay): Yegros Paso (26°51'51"S, 58°16'11"W), San Lorenzo (26°52'35"S, 58°18'40"W), Costanera (26°50'52"S, 58°18'51"W), Ring Road (26°52'31"S, 58°14'59"W) and Laguna Gadea (26°50'9"S, 58°18'46"W). Samples were collected using a Seine net in 100 m transects, fragmented into 10 mini-transects of 10 m each. Upon completing the 100 m transect, investigators returned to the beginning, completing as many transects as allowed in a 2-hour period of continuous sampling. There were two 2-hour periods at each site (a total of 4 hours per site), between 7:00 and 9:00, and again between 15:00 and 17:00. This was repeated every three months for 2021–2023. The invertebrate specimens collected were all placed in jars with 70% ethanol and transferred to the PLT laboratory [Centro IDEAL (Investigation, Development, Environmental Education and Leadership), Pilar] for examination and identified to the lowest taxonomic level permitted by the available literature.

Measurements for the two new species were taken under an AmScope Trinocular Stereo Zoom Microscope 3.5×–90× magnification with a millimetric scale. Representative specimens (male paratypes and female allotypes) were dissected using a scalpel, pincers and fine needles, and mounted on permanent slides for storage and drawing under an OMAX 40×–2000× LED Microscope with built-in camera. Our description follows the setal terminology of Zimmer et al. (2009).

Type specimens are stored in the Scientific Collection of PLT (Colección Científica de PLT, CCPLT) at Centro IDEAL in Pilar, Ñeembucú Department (Paraguay).

## Taxonomy

**Order Amphipoda Latreille, 1816**
**Family Dogielinotidae Gurjanova, 1953**
**Subfamily Hyalellinae Bulycheva, 1957**
**Genus *Hyalella* Smith, 1874**

### *Hyalella mboitui* sp. nov.

https://zoobank.org/B7930020-036E-457F-AEDF-26DE31C2B599

**Type material.** ***Holotype*****,** male (Fig. 1A), total body length = 8.29 mm, head length = 0.89 mm (CIPLT-O-38); Allotype female (Fig. 2A), total body length = 7.10 mm, head length = 0.70 mm (CIPLT-O-38). Paraguay, Department of Ñeembucú, Pilar, Ring Road field locality (26°52'31"S, 58°14'59"W), September, 08, 2021. ***Paratypes*****.** 43 males, 54 females, Ring Road (CIPLT-O-37; 26°52'31"S, 58°14'59"W) and San Lorenzo (CIPTL-O-39; 26°52'35"S, 58°18'40"W) field localities.

**Type locality.** Paraguay, Department of Ñeembucú, Pilar, Ring Road field locality (26°52'31"S, 58°14'59"W).

**Diagnosis.** Flagella of antennae 1 and 2 with 13–14 and 16–17 articles, respectively. Left mandible incisor toothed, 5-denticulate; left lacinia mobilis multi-denticulate, with median serrated surface and two prominent elongated denticles laterally. Gnathopod 1 propodus subtriangular, without triangular space between propodus and dactylus, with papposerrate setae on disto-anterior corner. Gnathopod 2 propodus with papposerrate setae on disto-posterior margin, with palm with pronounced cup for dactylus. Pereopod 5 shorter than other pereopods. Uropod 1 endopod with a curved seta. Uropod 3 ramus dorsal margin without setae. Uropod 3 peduncle with two cuspidate setae and four simple setae apically. Uropod 3 peduncle longer than wide (rectangular).

**Description. Male** (Figs 1–5). Mean total body length: 7.98 mm; mean head length: 0.84 mm (*N* = 44). Body surface smooth. Epimeral plates not acuminate. Head smaller than first two thoracic segments, typically gammaridean, rostrum absent. Eyes pigmented, rounded, located between insertion of antennae 1 and 2 (Fig. 2A).

Antenna 1 about 2.2× shorter than body length, 1.4× shorter than antenna 2, 1.8× longer than peduncle of antenna 2; peduncle 1.1× longer than head length; flagellum with 13–14 articles, 1.5× longer than peduncle; aesthetascs occurring distally after article 4 (Fig. 2B).

Antenna 2 about 1.5× shorter than body length; peduncle 1.6× longer than head length; articles 1 to 3 with several simple setae on distal margin; flagellum 1.7× longer than peduncle, with 16–17 articles, with basal article elongated, with several simple setae on distal margins, and with four simple setae apically (Fig. 2C).

Basic amphipodan mandibles (sensu Watling 1993), without palp; left incisor toothed, 5-denticulate; left lacinia mobilis multi-denticulate, with medial surface with multiple small serrated denticles and two prominent elongated denticles laterally, setal row with five papposerrate setae, with setules, molar process large and cylindrical, triturative, with one accessory seta (Fig. 2E). Right mandible incisor 6-denticulate; lacinia 5-denticulate, setal row with six papposerrate setae, with setules.

Upper lip distal margin truncate; distal border covered by setules on ventral and dorsal faces (Fig. 2D). Lower lip outer lobes rounded, not notched, with several setules on dorsal and ventral faces (Fig. 2G).

Maxilla 1 inner plate slender, 1.8× shorter than outer plate, with two apical papposerrate setae and several setules laterally. Outer plate with nine serrate setae and several setules (Fig. 2H). Palp short, uniarticulate, 1.0× longer than wide, with apical and lateral setules, reaching less than half distance between base of palp and base of setae on outer plate.

Maxilla 2 inner and outer plates subequal in length and width. Inner plate with one papposerrate seta and several simple and serrate setae apically, and several setules on inner face; outer plate with several simple setae on apex and margin, longest apically (Fig. 2I).

Maxilliped inner plate 2.0× longer than wide, apically truncated, with two cuspidate setae, several simple setae apically, and several setules on inner margin, comb-scales absent; outer plate approximately 1.3× longer than inner plate, apically rounded, with several apical and lateral simple setae, comb-scales absent; palp approximately 2.1× longer than inner plate, with four articles; article 1 1.1× longer than wide, inner margin with few simple setae; article 2 1.5× longer than wide, inner margin with several simple setae, outer margin with few simple setae; article 3 1.8× longer than wide, inner and outer margins with several long simple setae; article 4 unguiform, 3.0× shorter than third article, 1.6× longer than wide, inner margin with several long simple setae, with distal simple seta, with distal nail and comb-scales absent (Fig. 2J).

Gnathopod 1 subchelate; coxal plate 2.1× wider than long, with several simple setae on anterior and posterior margins; basis with one simple seta on anterior margin and one on disto-posterior corner; ischium with few simple setae on disto-posterior corner; merus with few simple setae on posterior margin; carpus 1.3× longer than wide, 1.1× longer and wider than propodus, posterior lobe produced and forming scoop-like structure, pectinate margin with several serrate setae, comb-scales and polygonal pattern; propodus 1.3× longer than wide, hammer-shaped, with several simple setae on anterior margin, with several papposerrate setae on disto-anterior corner; palm slope oblique, with several simple setae, margin convex, disto-posterior corner with long simple setae, and with a pronounced cup for dactylus; dactylus claw-like, congruent with palm, without comb-scales (Fig. 3A).

Gnathopod 2 subchelate; coxal plate 1.6× wider than long; basis with few simple setae on posterior margin and one serrate seta on disto-anterior margin; ischium and merus with few simple setae on posterior margin; carpus 1.8× wid-

**Figure 1.** *Hyalella mboitui* sp. nov., Department of Ñeembucú, Paraguay **A** holotype, male **B** allotype, female. Scale bars: 1 mm.

er than long, posterior lobe slim, produced between merus and propodus, margin pectinate with several serrate setae; propodus ovate, 1.4× longer than wide, comb-scales absent; palm subequal to posterior margin of propodus, slope oblique, margin convex, slightly irregular, with several simple setae and cuspidate setae with accessory seta; disto-posterior corner with two small cuspidate setae and several papposerrate setae, and with a pronounced cup for dactylus; dactylus claw-like, congruent with palm, without comb-scales (Fig. 3B).

Pereopods 3 to 7 simple. Pereopod 4 (Fig. 4B) with several simple setae on basis posterior margin; pereopods 3 (Fig. 4A) and 4 with several simple setae on merus and carpus posterior margins, with several simple and cuspidate setae on propodus posterior margins; dactylus approximately 3.5× shorter than

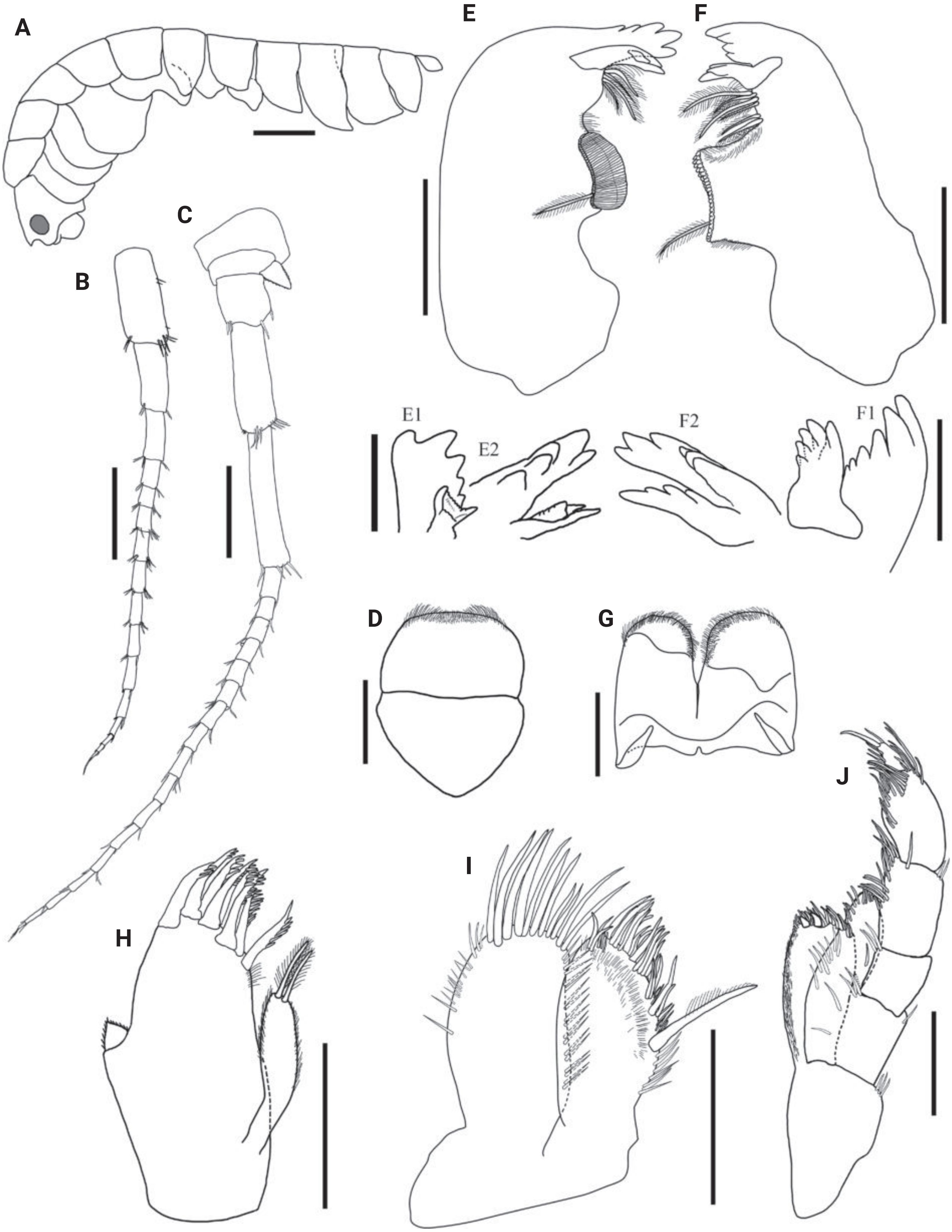

**Figure 2.** *Hyalella mboitui* sp. nov., Department of Ñeembucú, Paraguay. Paratype, male **A** habitus **B** antenna 1 **C** antenna 2 **D** upper lip **E** left mandible, with detail of lacinia and incisor rotated anticlockwise (**E1**) and clockwise (**E2**) **F** right mandible, with detail of lacinia and incisor rotated anticlockwise (**F1**) and clockwise (**F2**) **G** lower lip **H** maxilla 1 **I** maxilla 2 **J** maxilliped. Scale bars: 1 mm (**A**); 0.5 mm (**B, C**); 0.2 mm (**D–J**); 0.1 mm (**E1, E2, F1, F2**).

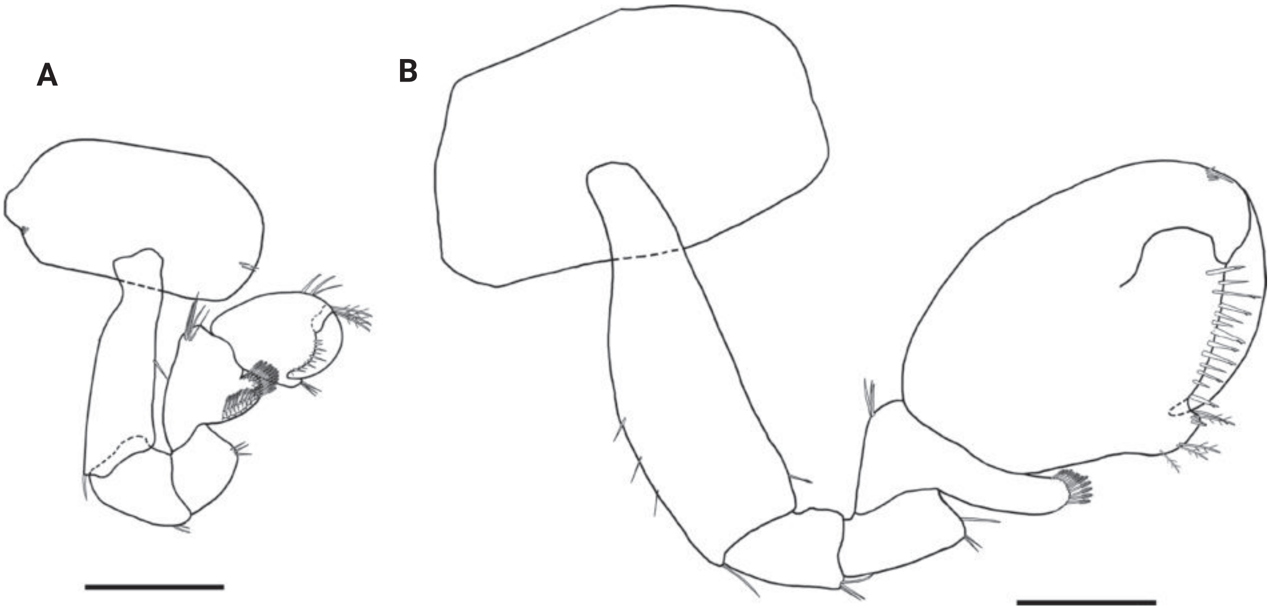

**Figure 3.** *Hyalella mboitui* sp. nov. Paratype, male **A** gnathopod 1 **B** gnathopod 2. Scale bars: 0.5 mm.

propodus, in both. Pereopods 5, 6 and 7 (Fig. 4C–E) with merus, carpus and propodus posterior margins with several cuspidate and simple, dactylus 1.8×, 2.1× and 2.2× shorter than propodus, respectively, unguiform, with plumose seta dorsally on pereopods 6 and 7. Pereopod 3 and 4 of similar sizes; pereopod 5 smaller than others; pereopod 6 slightly shorter than pereopod 7.

Pleopods not modified, biramous, elongated; peduncle 4.0× longer than wide, 1.7× mean size of rami, with coupling spines distally; both rami multi-annulated, longer than peduncle, with articles decreasing in size distally, with several plumose setae (Fig. 5A).

Uropod 1 1.5× longer than uropod 2; peduncle 1.1× longer than longest ramus, with four cuspidate setae; inner ramus 1.4× longer than outer ramus, 4.9× longer than wide, with three dorsal cuspidate setae, with one long curved seta and four cuspidate setae apically; outer ramus with three dorsal cuspidate setae and four cuspidate setae apically (Fig. 5B).

Uropod 2 1.5× shorter than uropod 1; peduncle rectangular, subequal in length to outer ramus and 1.2× shorter than inner ramus, 2.0× wider than outer ramus and 1.5× than inner ramus, with two cuspidate setae; inner ramus slightly longer than outer ramus, with four cuspidate setae dorsally and three cuspidate setae apically; outer ramus with three cuspidate setae dorsally and four cuspidate setae apically (Fig. 5C).

Uropod 3 (Fig. 5D) 2.2× shorter than peduncle of uropod 1 and 1.1× than peduncle of uropod 2; peduncle 1.5× longer than wide, 3.7× wider than ramus, with six apical long cuspidate setae; inner ramus absent; outer ramus uniarticulate, 1.2× longer than peduncle, with two cuspidate and four simple setae apically.

Telson entire, 1.1× longer than wide, apically rounded, without setae laterally, with five apical cuspidate setae (Fig. 5E).

Coxal gills sac-like present on pereonites 3 to 6; sternal gills tubular and present on pereonites 3 to 7.

**Female** (Figs 1B, 5E, 6). Mean total body length: 6.23 mm; mean head length: 0.62 mm (*N* = 55).

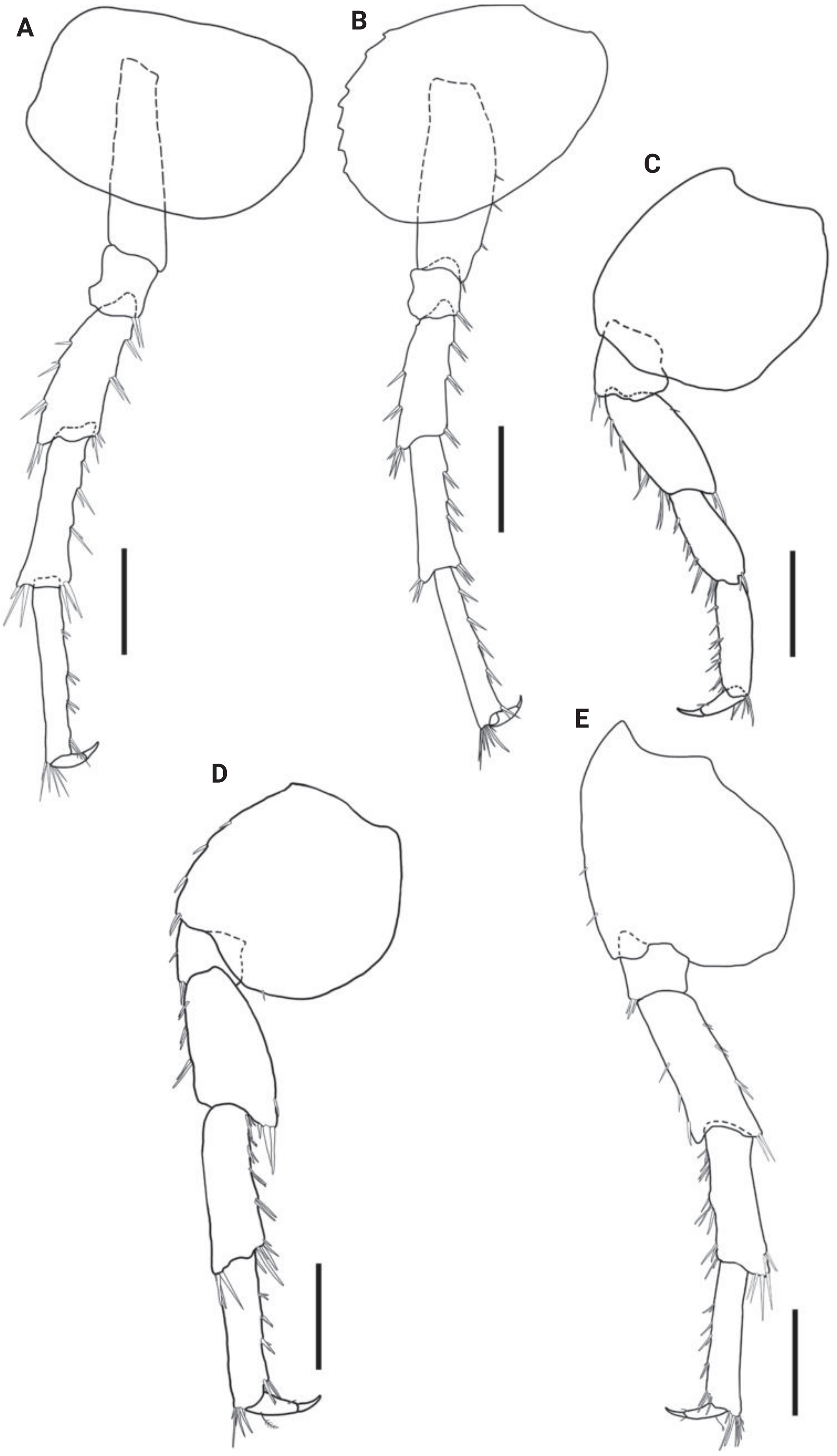

**Figure 4.** *Hyalella mboitui* sp. nov. Paratype, male **A** pereopod 3 **B** pereopod 4 **C** pereopod 5 **D** pereopod 6 **E** pereopod 7. Scale bars: 0.5 mm.

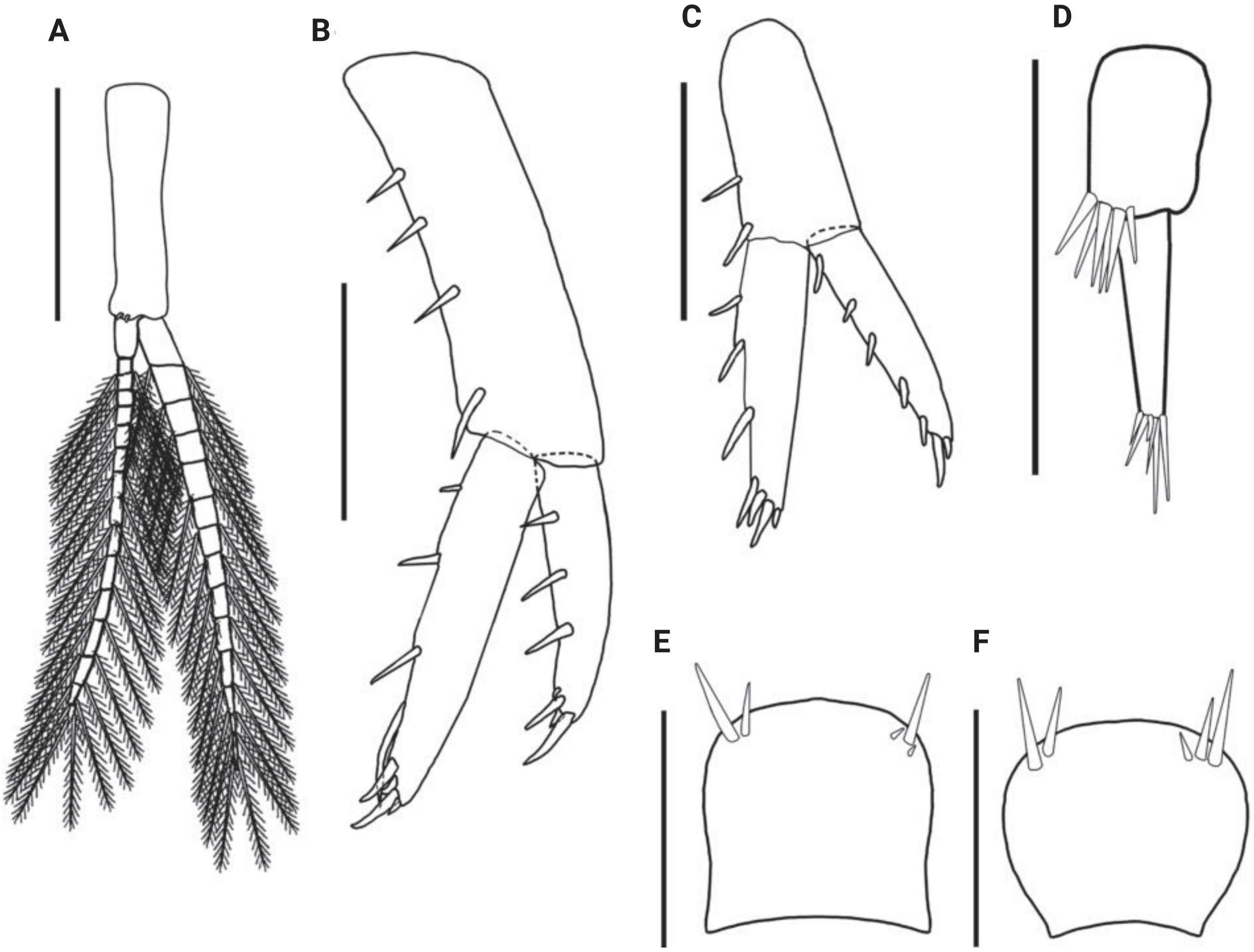

**Figure 5.** *Hyalella mboitui* sp. nov. Paratype, male. **A** pleopod **B** uropod 1 **C** uropod 2 **D** uropod 3 **E** male telson **F** paratype, female telson. Scale bars: 0.5 mm (**A–D**); 0.2 mm (**E, F**).

Antennae similar in shape to male. Antenna 1 flagellum with 10–11 articles. Antenna 2 flagellum with 16–17 articles.

Gnathopod 1 (Fig. 6A) similar to male gnathopod 1 in size but different in shape; basis with few simple setae on disto-anterior and disto-posterior margins; ischium with few simple setae on disto-posterior margin; merus with several simple setae and comb-scales on posterior margin; carpus 1.7× longer than wide, 1.3× longer and 1.2× wider than propodus, with several simple setae on disto-anterior corner, posterior lobe produced and forming scoop-like structure, with pectinate margin, with comb-scales, with several serrate setae and polygonal pattern, and with three serrate setae on inner margin; propodus 1.6× longer than wide, hammer-shaped, inner margin with six simple setae with accessory setae, dorsal margin with two simple setae, disto-anterior corner with several simple setae; palm 1.4× shorter than posterior margin of propodus, slope transverse, margin slightly irregular, with several simple setae, with few simple setae and two cuspidate setae on disto-posterior corner; dactylus claw-like, with one plumose seta dorsally.

Gnathopod 2 (Fig. 6B) similar in size and shape to gnathopod 1; basis with one simple seta on posterior margin, with few simple setae on disto-anterior corner, and two pappose setae on disto-posterior corner; ischium with several simple setae on disto-posterior corner; merus with several simple setae on posterior margin; carpus 1.5× longer than wide, 1.0× longer and 1.3× wider than propodus, with several simple setae on disto-anterior corner, posterior lobe produced and forming scoop-like structure with pectinate margin, with comb-scales, with several serrate setae and polygonal pattern, inner margin with few simple setae; propodus longer than wide, hammer-shaped, with comb-scales and several simple setae on disto-posterior margin, and several simple setae on disto-anterior corner; inner face with several simple setae; palm 1.9× shorter than posterior margin of propodus, slope oblique, margin slightly concave, with several simple setae, disto-posterior corner with two cuspidate setae; dactylus claw-like, with one plumose seta dorsally.

Telson approximately as long as wide, with more convex lateral margins than in male, and with five cuspidate setae apically (Fig. 5F).

Uropod 1 similar in size and shape to male uropod 1, except for absence of curved seta.

**Habitat.** Freshwater, epigean.

**Distribution.** Paraguay, Department of Ñeembucú, Pilar. Field localities of Ring Road (26°52'31"S, 58°14'59"W) and San Lorenzo (26°52'35"S, 58°18'40"W).

**Etymology.** In reference to Mbói Tu'i, one of the seven legendary monsters of Guaraní mythology and protector of wetlands and aquatic life. The species is named in Guaraní in honour of it being an endemic Paraguayan species.

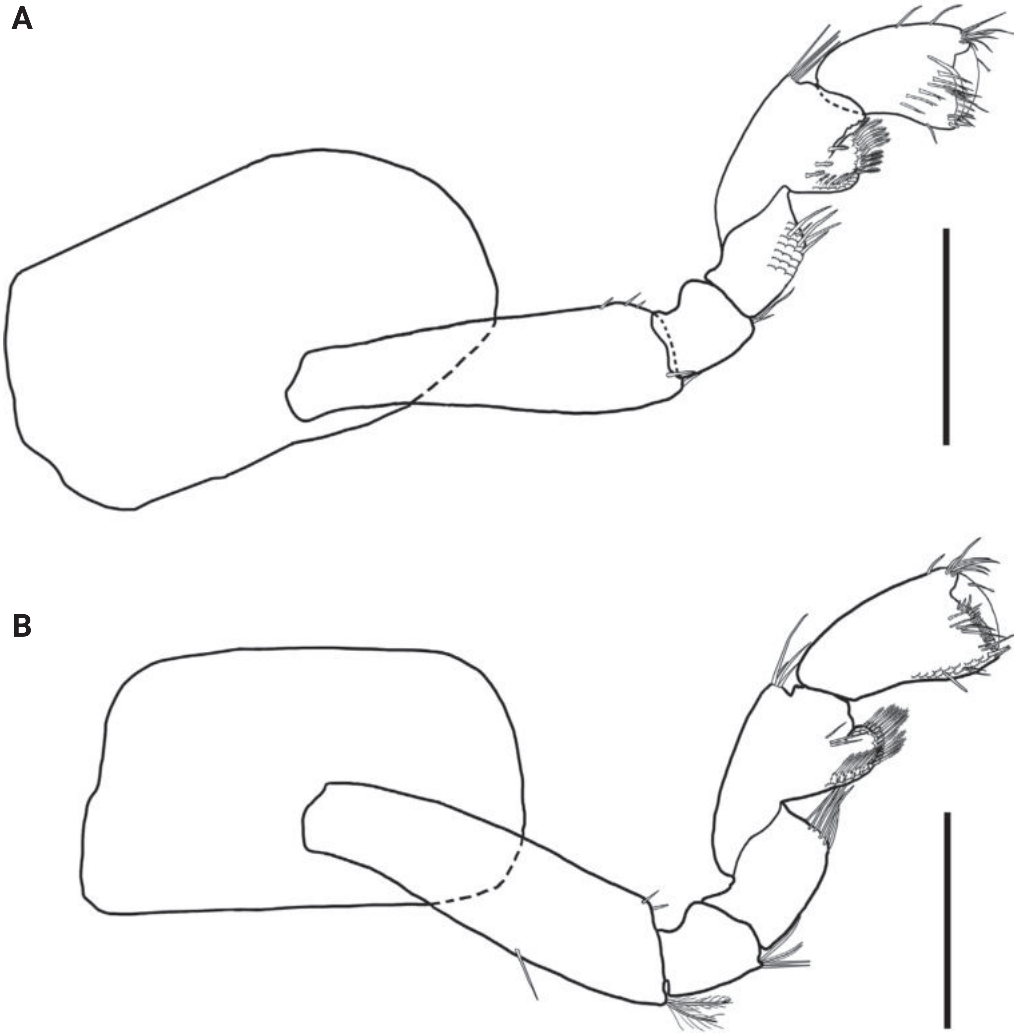

**Figure 6.** *Hyalella mboitui* sp. nov. Paratype, female. **A** gnathopod 1 **B** gnathopod 2. Scale bars: 0.5 mm.

### ***Hyalella julia* sp. nov.**

https://zoobank.org/4F2CE36F-B2A1-47AB-A812-ED4CC0D6D4A7

**Type material.** ***Holotype*,** male (Fig. 7A), total body length = 8.81 mm, head length = 0.78 mm (CIPLT-O-40); Allotype female (Fig. 7B), total body length = 5.44 mm, head length = 0.42 mm (CIPLT-O-40). Paraguay, Department of Ñeembucú, Pilar, Yegros Paso field locality (26°51'51"S, 58°16'11"W), September, 06, 2021. ***Paratypes*.** 9 males, 20 females (CIPLT-O-40), Yegros Paso field locality (26°51'51"S, 58°16'11"W).

**Type locality.** Paraguay, Department of Ñeembucú, Pilar, Yegros Paso field locality (26°51'51"S, 58°16'11"W).

**Diagnosis.** Flagella of antennae 1 and 2 with 10–11 and 13–14 articles, respectively. Left mandible incisor toothed, 4-denticulate; left lacinia mobilis 3-denticulate, with short median denticle and two prominent elongated denticles with serrated margin laterally. Gnathopod 2 propodus with palm lacking pronounced cup for dactylus, without papposerrate setae, with cuspidate setae with accessory setae on disto-posterior corner. Pereopod 5 slightly longer than other pereopods. Uropod 1 endopod with a curved seta. Uropod 3 ramus dorsal margin without setae. Uropod 3 peduncle with six simple setae apically. Uropod 3 peduncle longer than wide (rectangular).

**Description. Male** (Figs 7–11). Mean total body length: 7.24 mm; mean head length: 0.76 mm (*N* = 10). Body surface smooth. Epimeral plates not acuminate. Head smaller than first two thoracic segments, typically gammaridean, rostrum absent. Eyes pigmented, ovoid, located between insertion of antennae 1 and 2 (Fig. 8A).

Antenna 1 about 3.2× shorter than body length, 1.3× shorter than antenna 2, 2.2× longer than peduncle of antenna 2; peduncle not surpassing head length; flagellum with 10–11 articles, 2.1× longer than peduncle; aesthetascs occurring distally after article 4 (Fig. 8B).

Antenna 2 about half of body length; peduncle 1.1× longer than head; articles 1 to 3 with several simple setae on distal margin, article 3 with several simple setae on lateral margin; flagellum 2.4× longer than peduncle, with 13–14 articles, with basal article elongated; articles with several simple setae on distal margins; four simple setae apically (Fig. 8C).

Basic amphipodan mandibles (sensu Watling 1993), without palp; left incisor toothed, 4-denticulate; left lacinia mobilis 3-denticulate, with short median denticle, with two prominent elongated denticles with serrated upper margin laterally. Setal row with four papposerrate setae, molar process large and cylindrical, triturative, with one accessory seta (Fig. 8E). Right mandible incisor 7-denticulate; lacinia 4-denticulate, setal row with six papposerrate setae (Fig. 8F).

Upper lip distal margin rounded, covered by several setules on dorsal and ventral faces (Fig. 8D). Lower lip outer lobes rounded and distally notched, covered distally by several setules on dorsal and ventral faces (Fig. 8G).

Maxilla 1 inner plate slender, 1.4× shorter than outer plate, with two apical papposerrate setae and several setules laterally; outer plate with nine serrate setae (Fig. 8H). Palp short, uniarticulate, 1.2× longer than wide, with a distal setule, reaching less than half of distance between base of palp and base of setae on outer plate.

Maxilla 2 inner plate 1.1× longer than outer plate; inner plate with one papposerrate seta and several simple and serrate setae apically, with several setules laterally; outer plate with several simple setae, longest apically, with several setules laterally (Fig. 8I).

Maxilliped inner plate 1.7× longer than wide, apically truncated, with three apical cuspidate setae and several simple setae, without comb-scales; outer plate 1.3× longer than inner plate, apically rounded, with several apical and lateral simple setae; palp 2.3× longer than inner plate, 1.7× longer than outer plate, with four articles; article 1 1.3× longer than wide, with strongly concave distal margin; article 2 1.0× longer than wide, with inner, outer, and distal margins with several long simple setae; article 3 1.2× longer than wide, with inner and outer margins with several simple setae; article 4 unguiform, 1.5× longer than wide, 2.0× shorter than third article, with distal simple setae, with distal nail and comb-scales absent (Fig. 8J).

Gnathopod 1 subchelate; coxal plate 1.9× wider than long; basis with one simple seta on inner margin and one on disto-posterior corner, ischium with few simple setae on disto-posterior corner; merus with several simple setae on posterior margin; carpus 1.5× longer than wide, 1.2× longer and 1.2× wider than propodus, with several simple setae on disto-anterior corner, some with accessory seta, with few simple setae on inner margin, with posterior lobe folded to form scoop-like structure, with pectinate margin with comb-scales, several serrate setae and polygonal pattern; propodus 1.6× longer than wide, hammer-shaped, with simple seta with accessory seta on anterior margin, with inner margin with several simple setae, with several long simple setae on disto-anterior corner; palm slope transverse, margin slightly concave, with many simple setae, with disto-posterior corner with cuspidate seta with accessory seta; dactylus claw-like, congruent with palm, without comb-scales (Fig. 9A). Microtrichs present on propodus.

Gnathopod 2 subchelate; coxal plate 1.8× wider than long; basis with one simple seta on anterior margin and several simple setae on disto-posterior margin; merus with several simple setae on posterior margin; carpus 2.0× wider than long, with one simple seta on inner margin and two on disto-anterior, with posterior lobe slim produced between merus and propodus, with posterior margin pectinate, with several serrate setae and comb-scales; propodus ovate, 1.4× longer than wide, with two simple setae on anterior margin; palm subequal to posterior margin of propodus, slope oblique, margin convex, with several long and short simple setae with accessory setae; disto-posterior corner with two cuspidate setae with accessory setae; very shallow cup for dactylus; dactylus claw-like, congruent with palm, without comb-scales (Fig. 9B).

Pereopods 3 to 7 simple. Pereopods 3 and 4 (Fig. 10A, B) with posterior margins of merus and carpus with several simple and cuspidate setae; propodus posterior margin with several simple and cuspidate setae; dactylus 2.6× and 1.9× shorter than propodus in pereopods 3 and 4, respectively, unguiform. Pereopods 5 to 7 (Fig. 10C–E) with posterior margins of merus, carpus and propodus with several cuspidate and simple setae; dactylus 2.7×, 2.6×, and 3.0× shorter than propodus, respectively, unguiform, with a plumose seta dorsally. Pereopod 3 and 4 of similar sizes, shorter than pereopods 5–7; pereopods 6 and 7 of similar length, pereopod 5 slightly longer than other pereopods.

Pleopods not modified, biramous, elongated; peduncle 4.0× longer than wide, 1.5× shorter than mean size of rami, with coupling spines distally; both rami multi-annulated, longer than peduncle; articles decreasing in size distally in both rami; both rami with several plumose setae (Fig. 11A).

**Figure 7.** *Hyalella julia* sp. nov., Department of Ñeembucú, Paraguay **A** holotype, male **B** allotype, female. Scale bars: 1 mm.

Uropod 1 1.3× longer than uropod 2; peduncle 1.1× shorter than outer ramus and 1.2× shorter than inner ramus, with three cuspidate setae; inner ramus 1.1× longer than outer ramus, with four cuspidate setae dorsally, and one long curved seta and five cuspidate setae apically; outer ramus with four cuspidate setae dorsally and five cuspidate setae apically (Fig. 11B).

Uropod 2 1.3× shorter than uropod 1; peduncle rectangular, 1.0× shorter than outer ramus and 1.3× than inner ramus, 2.4× wider than outer ramus and 1.3× than inner ramus, with one cuspidate seta dorsally; inner ramus 1.3× longer than outer ramus, with three cuspidate setae dorsally and three cuspidate se-

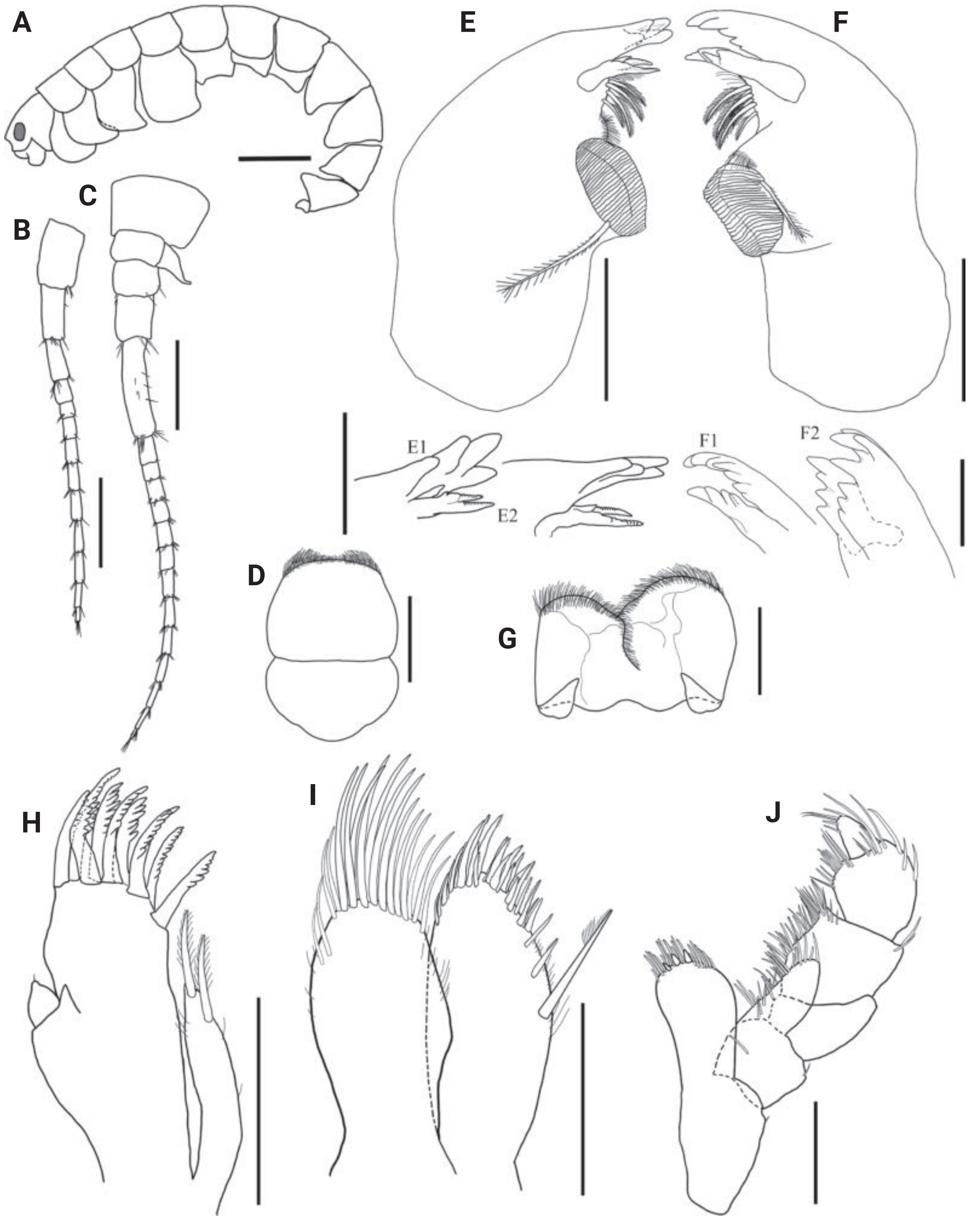

**Figure 8.** *Hyalella julia* sp. nov., Department of Ñeembucú, Paraguay. Paratype, male **A** habitus **B** antenna 1 **C** antenna 2 **D** upper lip **E** left mandible with detail of lacinia and incisor rotated anticlockwise (**E1**) and clockwise (**E2**) **F** right mandible, with detail of lacinia and incisor rotated anticlockwise (**F1**) and clockwise (**F2**) **G** lower lip **H** maxilla 1 **I** maxilla 2 **J** maxilliped. Scale bars: 1 mm (**A**); 0.5 mm (**B, C**); 0.2 mm (**D–J**); 0.1 mm (**E1, E2, F1, F2**).

tae apically; outer ramus with four cuspidate setae dorsally and four cuspidate setae apically (Fig. 11C).

Uropod 3 (Fig. 11D) 1.6× shorter than peduncle of uropod 1 and 1.1× than peduncle of uropod 2; peduncle 1.9× longer than wide, 2.0× wider than ramus, with six cuspidate setae apically; inner ramus absent; outer ramus uniarticulate, subequal in length to peduncle, with six simple setae apically.

Telson entire, 1.1× longer than wide, with convex margins, and rounded apically, without setae laterally, and with five cuspidate setae apically (Fig. 2D).

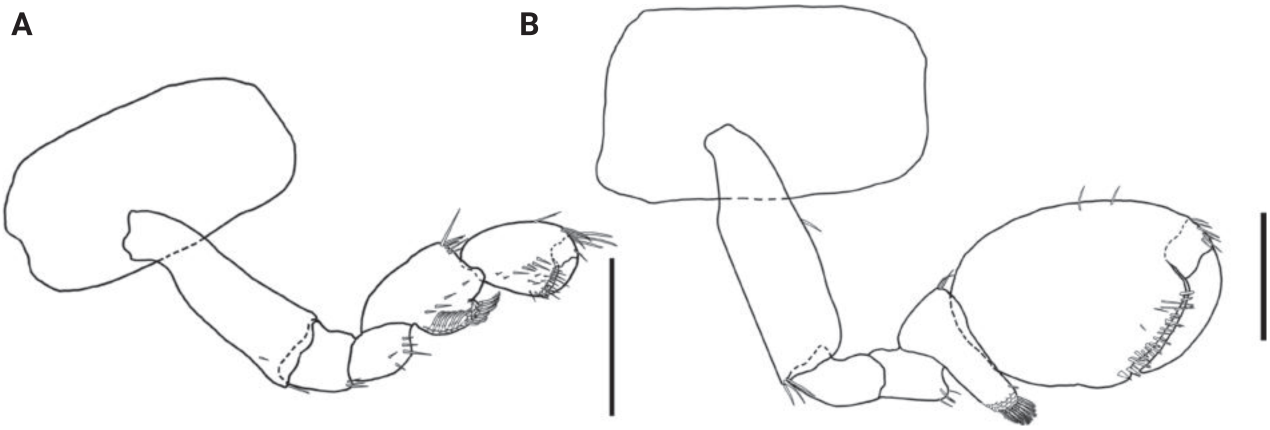

**Figure 9.** *Hyalella julia* sp. nov. Paratype, male **A** gnathopod 1 **B** gnathopod 2. Scale bars: 0.5 mm.

Coxal gills sac-like present on pereonites 3 to 6; sternal gills tubular and present on pereonites 3 to 7.

**Female** (Figs 7B, 11E, 12). Mean total body length: 5.23 mm; mean head length: 0.46 mm (*N* = 21).

Antennae similar in shape to male. Antenna 1 flagellum with 10–11 articles. Antenna 2 flagellum with 11–12 articles.

Gnathopod 1 (Fig. 12A) slightly larger than male gnathopod 1 different from male gnathopod 1 in shape; basis with few simple setae on disto-anterior and posterior margins; ischium with several simple setae on disto-posterior margin; merus with several simple setae on posterior margin; carpus 1.6× longer than wide, with several serrate setae on disto-anterior corner, posterior lobe with pectinate margin, with comb-scales and one row of serrate setae; propodus 1.8× longer than wide, hammer-shaped; anterior margin with two simple setae, disto-anterior corner with several simple setae, posterior margin with several simple setae and comb-scales, inner margin with four simple setae; palm slope transverse, margin slightly irregular, slightly concave, with several simple setae, with few simple setae and two long cuspidate setae on disto-posterior corner; dactylus claw-like, with one plumose seta dorsally.

Gnathopod 2 (Fig. 12B) similar in size and shape to gnathopod 1; basis and ischium with several simple setae on disto-posterior corner; merus with several simple setae on posterior margin; carpus 1.3× longer than wide, with several simple setae on disto-anterior corner, posterior lobe produced and forming scoop-like structure, pectinate margin with comb-scales, several serrate setae and polygonal pattern; propodus 1.6× longer than wide, hammer-shaped, with comb-scales on disto-posterior margin, with few simple setae on anterior and posterior margins, with several long simple setae on disto-anterior corner, inner face with several simple setae; palm slope oblique, margin slightly irregular, with several simple setae, disto-posterior corner with two simple and two cuspidate setae; dactylus claw-like, with one plumose seta dorsally.

Telson subequal in length and width, with more convex lateral margins than in male, and with five cuspidate setae, one with accessory seta.

Uropod 1 similar in size and shape to male uropod 1, except for absence of curved seta.

**Habitat.** Freshwater, epigean.

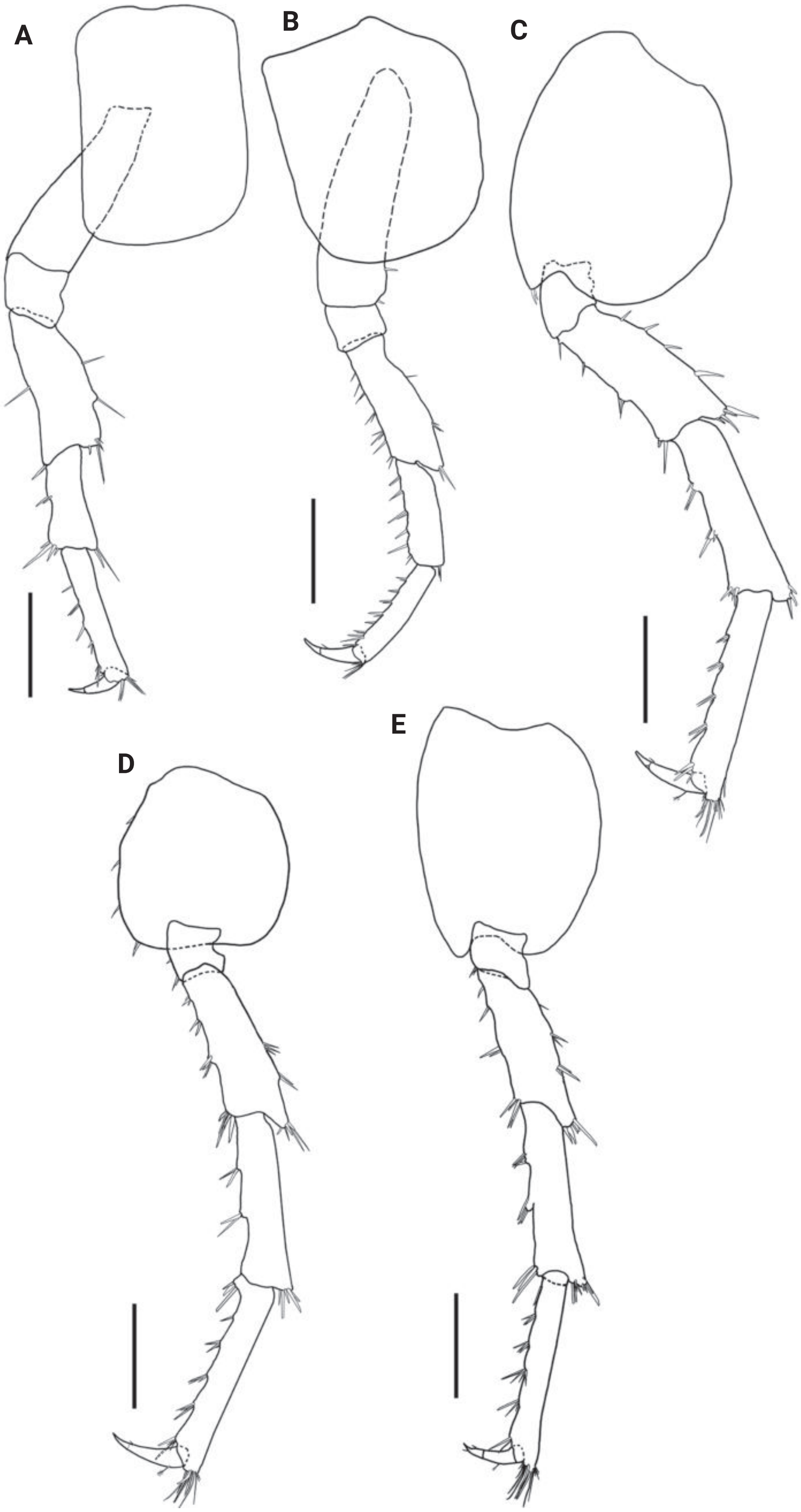

**Figure 10.** *Hyalella julia* sp. nov. Paratype, male **A** pereopod 3 **B** pereopod 4 **C** pereopod 5 **D** pereopod 6 **E** pereopod 7. Scale bars: 0.5 mm.

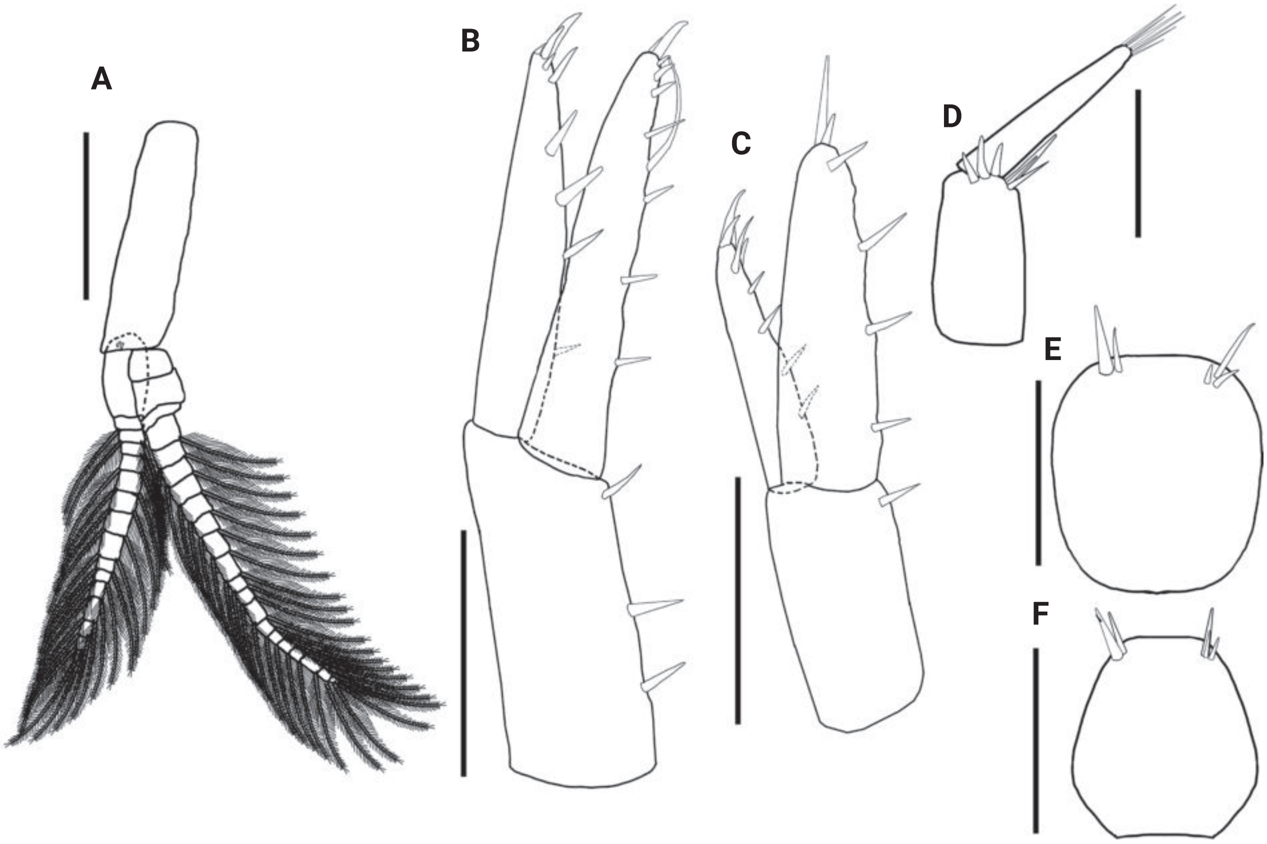

**Figure 11.** *Hyalella julia* sp. nov. Paratype, male **A** pleopod **B** uropod 1 **C** uropod 2 **D** uropod 3 **E** male telson **F** paratype, female telson. Scale bars: 0.5 mm (**A–C**); 0.2 mm (**D–F**).

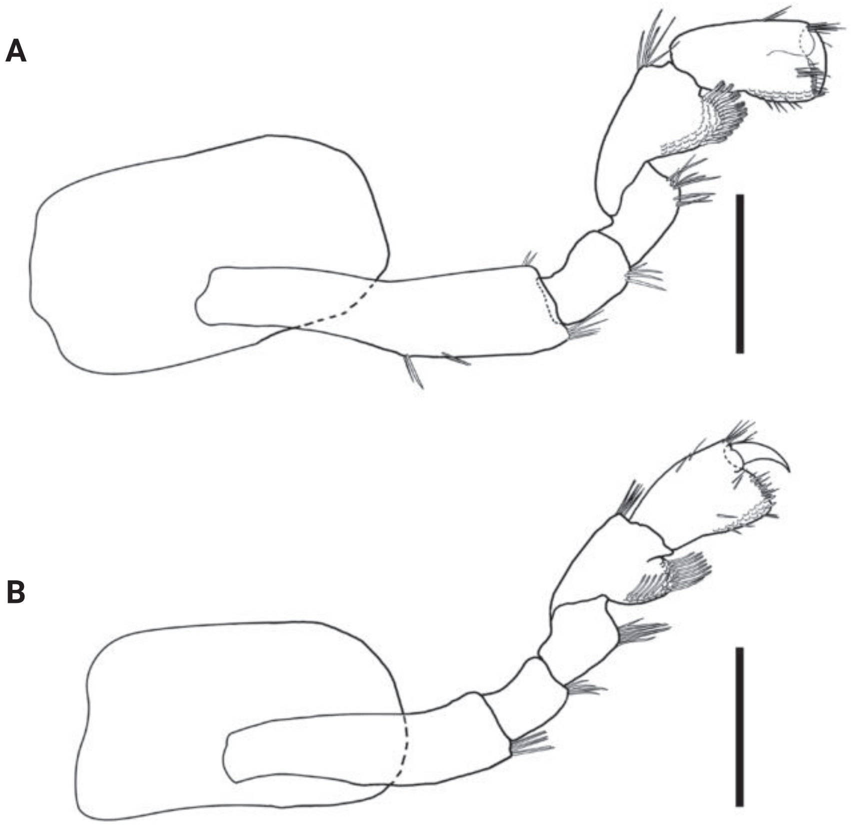

**Figure 12.** *Hyalella julia* sp. nov. Paratype, female **A** gnathopod 1 **B** gnathopod 2. Scale bars: 0.5 mm.

**Distribution.** Paraguay, Department of Ñeembucú, Pilar. Field locality of Yegros Paso (26°51'51"S, 58°16'11"W).

**Etymology.** In honour of the late Don Julio Rafael Contreras, for his seminal studies of Paraguayan biodiversity and generous support of Fundación Para La Tierra.

## Taxonomic remarks

*Hyalella mboitui* sp. nov. and *H. julia* sp. nov. can be recognised as distinct species based on the taxonomic keys by Damborenea et al. (2020) and morphological differences from other recently described South American species (Reis et al. 2020; Jaume et al. 2021; Limberger et al. 2021; Rocha Penoni et al. 2021; Talhaferro et al. 2021a, b; Vernica et al. 2022; Waller et al. 2022; Peralta and Verónica 2023; Reis et al. 2023). Both *H. mboitui* and *H. julia* show a smooth body without dorsal or lateral processes or mucronations, have pigmented eyes, and lack setae on the dorsal margin of uropod 3. The presence of a curved seta on the ramus of male uropod 1 links both new taxa to a large cluster of South American species spanning Venezuela, Brazil, Chile, Argentina and Uruguay (Bastos-Pereira and Bueno 2012; Rodrigues et al. 2014; Damborenea et al. 2020; Talhaferro et al. 2021a).

Like *H. brasiliensis* Bousfield, 1996 from Paraná State (Brazil), both *H. mboitui* and *H. julia* lack plumose setae on their telson, but can be readily distinguished from this species by the number of setae on uropods 1 and 2 (Bousfield 1996; Talhaferro et al. 2021a, b). The presence of six apical setae on the rectangular peduncle of uropod 3 and its rectangular (longer than wide) shape in *H. mboitui* and *H. julia* are shared with the Argentinian taxa *H. pampeana* Cavalieri, 1968 and *H. bonariensis* Dos Santos, Bond-Buckup & Araujo, 2008, and with *H. gauchensis* Streck et al., 2017 from Rio Grande do Sul, Brazil (Damborenea et al. 2020). However, the two Paraguayan species lack the space between the dactylus and the margin of the propodus of male gnathopod 2 characteristics of *H. pampeana* (Dos Santos et al. 2008) and differ markedly from *H. bonariensis* in the pattern and distribution of setae and comb-scales on their limbs and telson, as well as in the numbers of denticles on the mandibular incisor and lacinia mobilis (Dos Santos et al. 2008). In addition, they differ from *H. gauchensis* in their mandibular morphology and setal cover of the telson and uropods (cf. Streck et al. 2017).

The two new Paraguayan taxa are also readily distinguishable from recently described *Hyalella* species from nearby Argentina (Peralta and Miranda 2019; Vernica and Alejandra 2022) and southern Brazil (Reis et al. 2020; Limberger et al. 2021; Rocha Penoni et al. 2021;Talhaferro et al. 2021a, b) by the number and type of setae on the telson and uropods 1 and 3 (Figs 5B, D, 11B, D). Their level of morphological differentiation also indicates that the new Paraguayan species cannot be subsumed under the South American *H. curvispina* Shoemaker, 1942 species complex, which appears to comprise significant cryptic diversity based on recent molecular marker analyses (Waller et al. 2022). Despite similarities in telson shape and the morphology and setal cover of maxillae and maxillipeds (Figs 2H–J, 8H–J; Shoemaker 1942; Grosso and Peralta 1999), *H. mboitui* and *H. julia* are distinguished from *H. curvispina* by their diagnostic mandibular dentition, the absence of a plumose seta on the dactyli of male gnathopods, the number of setae on the telson, and the shape and number of setae of the uropod 3 peduncle, which is wider than long in *H. curvispina* (Shoemaker 1942; Grosso and Peralta 1999; Damborenea et al. 2020) but not in *H. mboitui* and *H. julia* (Figs 5D, 11C).

Despite the geographical vicinity of their type locations, *H. mboitui* and *H. julia* are separated by clear morphological differences at the level of the gnathopods, uropods and mandibles, as well as by minor differences in the morphology and setal covers of their antennae, maxillae and maxillipeds. Antennae 1 and 2 have fewer articles in their flagellum in *H. julia* than in *H. mboitui*: *H. julia* has minimally 13 articles in antenna 1 and 16 in antenna 2, whereas *H. mboitui* has minimally 10 in antenna 1 and 13 in antenna 2. The mandibles of the two taxa differ in the number of incisor teeth, with 5 and 6 teeth present in the left mandibles of *H. mboitui* and *H. julia*, respectively, and 4 and 7 in their right mandibles. In addition, the left lacinia mobilis of *H. julia* lacks the distinctive median serrated surface of *H. mboitui*, and sports instead two prominent, elongated denticles with a serrated edge laterally. The maxillipeds of the two species differ in the number of cuspidate setae on the outer plate and in the shape of palp articles (Figs 2J, 8J). The male gnathopods of *H. julia* and *H. mboitui* differ in the number and type of setae: notably, papposerrate setae are absent in the disto-posterior corner of the gnathopod 2 propodues in *H. julia*, which shows instead two stout cuspidate setae with accessory setae (Fig. 9B, cf. Fig. 3B). Papposerrate setae are also present on gnathopod 1 in *H. mboitui*, but not *H. julia* (Fig. 9A, cf. Fig. 3A). In addition, *H. julia* lacks papposerrate setae on the disto-anterior margin of the gnathopod 1 propodus (Fig. 9A, cf. Fig. 3A). The propodi of female gnathopods are also more elongated and less subtriangular in *H. julia*, and differ in the presence and extent of their cover of comb-scales (Fig. 6, cf. Fig. 12). Pereopod 5 is the shortest pereopod in *H. mboitui*, but the longest in *H. julia*. Moreover, uropods 1, 2 and 3 in the two species differ in the number of cuspidate setae on their rami and peduncle (Figs 5B, C, 11B, C).

## Habitat and conservation

The geographical vicinity of the two new species and their distinct mandibular morphologies suggest that their differences may stem at least in part from trophic partitioning (Limberger et al. 2021). Distinct feeding habits may be tied to the different environments characterising the type localities of the two species (Fig. 13). Yegros Paso, the type locality of *H. julia* (Fig. 13B), falls within a complex of seasonal ponds with relatively stagnant waters bordering on a stream. Locally, water bodies expand and contract in cyclic dry and wet phases depending on rainfall levels (Hordijk et al. 2023). In contrast, the bodies of water in the type localities of *H. mboitui* (Ring Road and San Lorenzo; Fig. 13C, D) are characterised by somewhat stronger riverine influence, with more active flow regimes, and higher availability of macrophytes near the banks. Some distinctions in the morphology of their pleopod setae may suggest corresponding differences in locomotion. *Hyalella julia* has denser, more strongly developed plumose setae on the pleopods that suggest a higher natatory capacity than in *H. mboitui*, and may make *H. julia* better adapted to swimming in lentic habitats (Streck et al. 2017). In contrast, *H. mboitui* may predominantly inhabit substrates in its lotic environment or remain near the river bank macrophytes.

The type locality of *H. julia* is managed for ongoing conservation and research projects on the endangered Pilar tuco-tuco (*Ctenomys pilarensis*). In contrast, major developments are scheduled or currently taking place at the type localities of *H. mboitui*, San Lorenzo and Ring Road, for the planned construction of flood defences. The connections between the bodies of water inhabited by

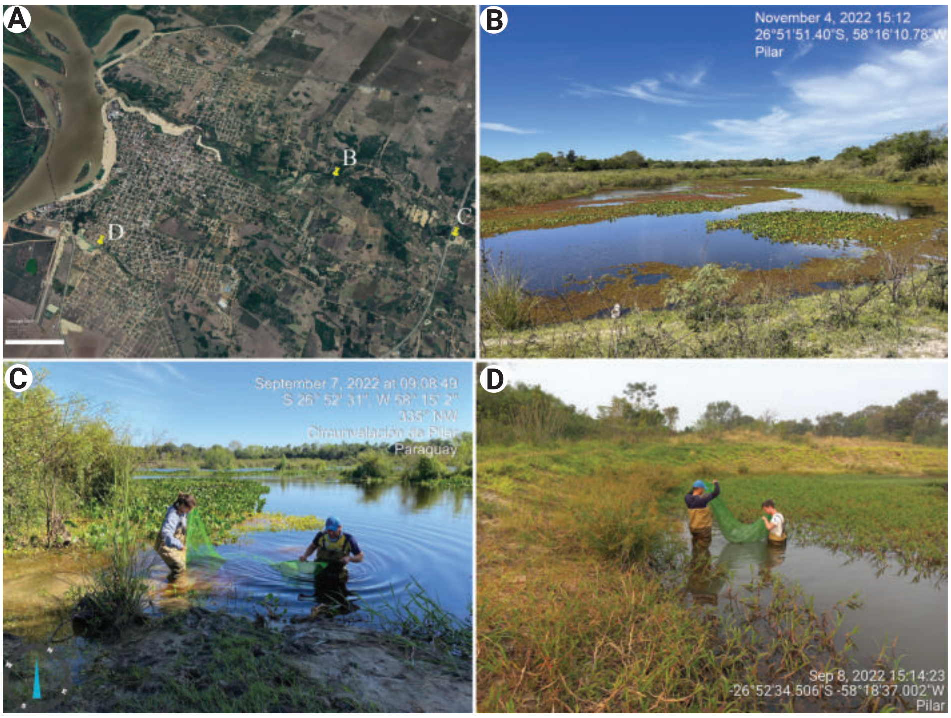

**Figure 13.** Localities of occurrence for *Hyalella mboitui* sp. nov. and *Hyalella julia* sp. nov. in Pilar, southwestern Paraguay **A** map showing the position of the type localities **B–D** with scale: 900 m **B** Yegros Paso **C** Ring Road **D** San Lorenzo.

*H. mboitui* and *H. julia*, and their seasonal continuity with the Ñeembucú River, preliminarily suggest that their area extends beyond the type localities. However, *Hyalella* is known for its high degree of endemism across South America, and the geographic range of different species in the genus is highly variable (Grosso and Peralta 1999; Streck et al. 2017). To map the ranges of *H. mboitui* and *H. julia*, and the degree to which ongoing developments may threaten the species survival, we recommend a wider sampling of freshwater invertebrates in the wetland complex around Pilar and more broadly in the Ñeembucú region.

The discovery of two new crustacean species, collected in a non-targeted impact assessment survey near an urban area, highlights the untapped potential of the Ñeembucú wetlands for biodiversity and conservation research. This ecologically important patchwork of rivers, streams, and flooded grasslands is severely understudied, and its invertebrate fauna remains virtually unexplored amid escalating anthropic impacts (Dickens et al. 2020; Mereles et al. 2020). More broadly, despite still comprising unfragmented areas of natural habitat, the Humid Chaco ecoregion in Paraguay is under increasing pressure from land use changes, resulting in high and rapid ongoing biodiversity losses (Mereles et al. 2020). Therefore, taxonomic studies are urgently needed to address the large remaining gaps in the scientific understanding of the region's biodiversity. Our findings of two undescribed species provide supporting evidence of the potential presence of a significant number of undocumented taxa in the Ñeembucú wetlands, which are likely to benefit from habitat protection measures.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

G.M. made specimen photographs and drawings and wrote the first draft of the manuscript. G.V. and N.D.S. provided field site photographs and assisted with manuscript drafting, editing, and specimens storage and cataloguing.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# The ants of the genus *Rhopalothrix* Mayr, 1870 (Hymenoptera, Formicidae, Myrmicinae) in Colombia

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## Abstract

The ants of the genus *Rhopalothrix* are diverse in the Neotropical region, with 14 of the 16 described species. Based on museum material and recent fieldwork, *Rhopalothrix* ants in Colombia were reviewed. Morphological analysis of the workers allowed delimitation of six species, including two new species, *Rhopalothrix mandibularis* Guerrero & Grajales, **sp. nov.** and *Rhopalothrix mariaemirae* Tocora, Fiorentino & Fernández, **sp. nov.** A new combination *Rhopalothrix amati* **comb. nov.** is proposed for *Eurhopalothrix amati*. A worker-based taxonomic key, high-definition images of the workers, and a distribution map of all *Rhopalothrix* species present in Colombia are provided.

**Key words:** *Basiceros* genus group, identification key, *isthmica* clade, new species, South America, taxonomy

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## Introduction

Ants are a dominant and ecologically key component of the highly diverse fauna of mostly exceedingly small arthropods that live in the litter layer that accumulates on the forest floor. Habitat type, as well as leaf-litter quality and heterogeneity, can influence the ant community (Silva et al. 2011), allowing some genera of ants to become more conspicuous (e.g., *Pheidole* Westwood, 1839 or *Strumigenys* Smith, 1860), while others are cryptic and poorly represented, such as *Rhopalothrix* Mayr, 1870.

The *Basiceros* genus group contains the genera *Basiceros* Schulz, 1906, *Eurhopalothrix* Brown & Kempf, 1961, *Octostruma* Forel, 1912, *Protalaridris* Brown, 1980, *Rhopalothrix*, and *Talaridris* Weber, 1941. The ants of the genus *Rhopalothrix* are small and with a distinctive combination of features. The worker mandible is an arched shaft with an apical fork; most other members of the *Basiceros* genus group have triangular mandibles. The genus *Protalaridris* has elongate mandibles, similar to *Rhopalothrix*, but can be distinguished by their antennae with 9 segments, instead of 7 in *Rhopalothrix*. *Rhopalothrix* workers also have squamiform setae varying in number and size on the head, mesosoma or gaster.

Currently, sixteen species are recognized within *Rhopalothrix* (Bolton 2023), but at least a dozen species await description (AntWeb 2023). The genus *Rhopalothrix* is distributed in Australia (1 species), New Guinea (1 species) and the Neotropical region (14 species) (Longino and Boudinot 2013). Longino and Boudinot (2013) studied *Rhopalothrix*, mainly the Mesoamerican forest fauna. These authors proposed the *Rhopalothrix isthmica* clade, defined by two synapomorphies: absence of squamiform setae on the face and development of shallow arcuate grooves and ridges on the face. This clade contains 13 of the 14 described Neotropical species. Several additional Neotropical species of uncertain phylogenetic position are now known, with characters that place them outside the *isthmica* clade (see images on AntWeb 2023).

We describe two new species, one that fits in the *isthmica* clade and another with scale-like setae on the face, similar to those present in *Rhopalothrix ciliata* Mayr, 1870. We also propose a new combination for one species previously described in the genus *Eurhopalothrix*. We provide a key to the six Colombian species, new occurrence records, and results on the distribution of the species in the country.

## Materials and methods

### Specimen processing

We used the worker-based key to species of *Rhopalothrix* proposed by Longino and Boudinot (2013) for identification of the studied specimens. To integrate our data into a review of the genus *Rhopalothrix* from the Brazilian Atlantic and Amazonian rainforest (J. Chaul, personal communication) and better characterize the species described here, we implemented several complementary measurements (for definitions see below; Fig. 1) to the one used by Longino and Boudinot (2013). The latter only used the maximum width of the head capsule in full-face view (HW) as a surrogate measure of ant size. Although HW is useful for the separation of known species of *Rhopalothrix*, the morphological diversity within the genus requires the exploration of other measures to support the delimitation of new taxa.

Specimens were observed using a Nikon SMZ 745 stereomicroscope. Measurements were made with a dual-axis micrometer stage with output in increments of 0.001 mm. However, variation in specimen orientation, alignment of crosshairs with edges of structures, and interpretation of structure boundaries resulted in measurement accuracy to the nearest 0.01 mm. All measurements (Fig. 1) are presented in mm:

| | |
|---|---|
| **ClyL** | in full-face view, maximum width of the clypeal plate including the lateral expansions above the insertion of the mandibles. |
| **ClyW** | in full-face view, maximum length of the clypeal plate from the most anteroclypeal projection to the most posterior clypeal margin. |
| **GL** | in lateral view, the straight-line length of the gaster measured from the most anterior margin of the first tergite to the posterior margin of the fourth tergite. |

| | |
|---|---|
| **HL** | in full-face view, maximum length of the head measured from the most anterior projection of the clypeus to the most posterior projection of the cephalic capsule. |
| **MdL** | in full-face view, the straight-line length of the mandible from the basal-most mandibular external margin to the apex of the subapical tooth. |
| **MdbW** | in full-face view, shortest diagonal line connecting the most basal point of the masticatory margin with the mandibular external margin. |
| **PetL** | in profile view, the distance from the inflection point marking the juncture of the cylindrical posterior portion of the segment to the anterior inflection point where the petiole is obscured by the posteroventral lobes of the propodeum. |
| **PpetL** | in lateral view, the distance from anterior to posterior inflections of postpetiole node. |
| **PetW** | maximum width of the petiolar node in dorsal view. |
| **PpetW** | maximum width of the postpetiolar node in dorsal view. |
| **PrnW** | maximum width of the pronotum in dorsal view. |
| **T4L** | in lateral view, length of the fourth abdominal tergite (= first gastral tergite) measured with the anterior and posterior margins in the same plane. |
| **WL** | the diagonal length of the mesosoma in profile from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron. |

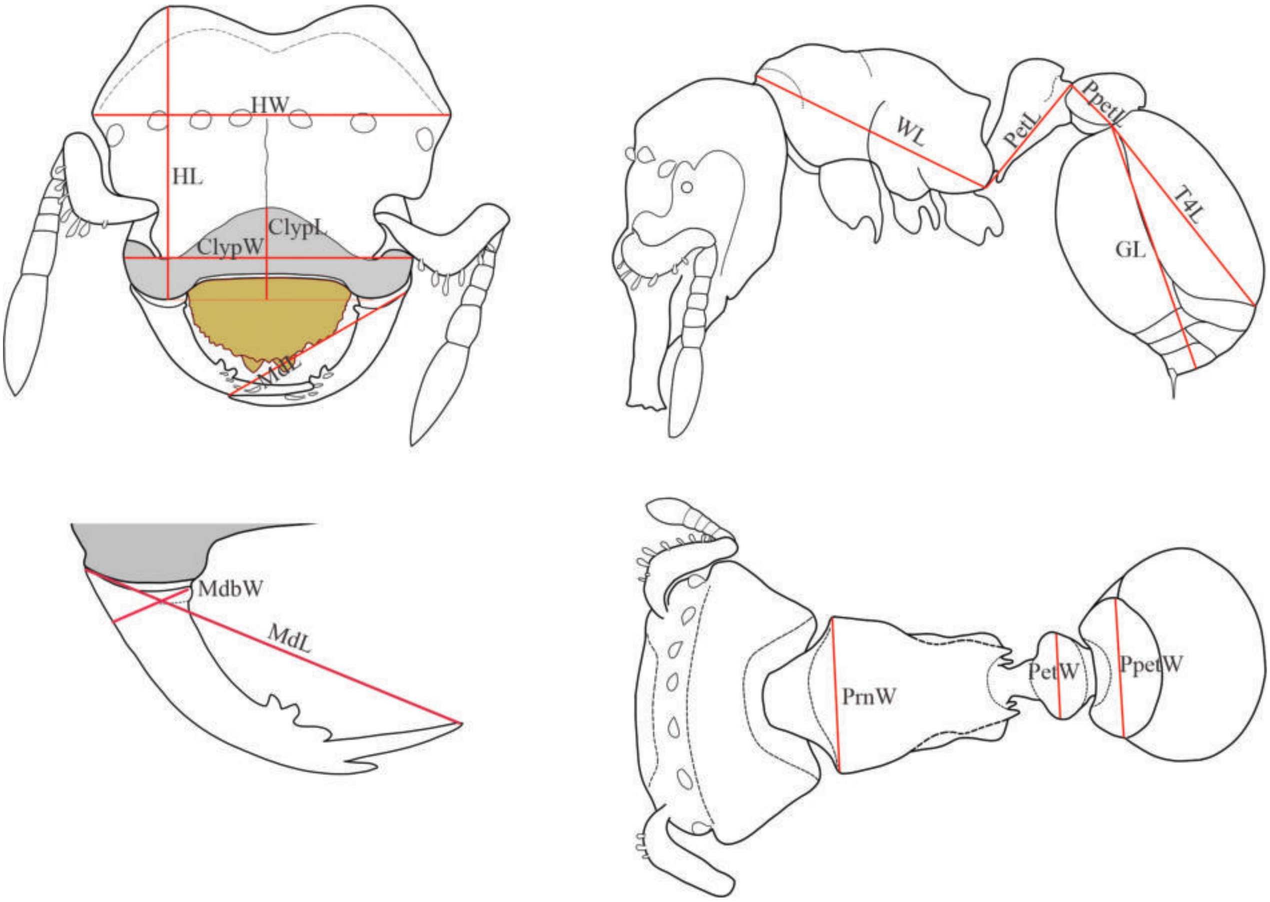

**Figure 1.** Measurements recorded in the habitus of *Rhopalothrix* worker. Definitions of the acronyms are described in Material and methods.

The taxonomic key provided here includes the relationship between labral width (LabW) and labral length (LabL) (see also couplet 4 in Longino and Boudinot (2013)). In full-face view, we measured the width (LabW) and the length of the labrum (LabL) in those specimens corresponding to *Rhopalothrix isthmica* (Weber, 1941), *R. mandibularis* sp. nov. and *R. weberi* Brown & Kempf, 1960. The values are expressed as a percentage, (LabW/LabL)*100. When preparing specimens of both species it is recommended to carefully open the mandibles so that the labrum is completely exposed.

High-resolution images of *Rhopalothrix ciliata* Mayr, 1870 lectotype (CASENT0915695) and *Rhopalothrix mariaemirae* sp. nov. (= *Rhopalothrix* jtl021: ANTWEB1038216, UFV-LABECOL-001953 and USNMENT01127994) workers were downloaded from http://www.antweb.org. For each image, we record all the measurements indicated above using Image J software (NIH, Bethesda, MD, USA). For the *R. ciliata* lectotype, only those measurements of the head, mandible, and mesosomal and petiolar/postpetiolar dorsum were recorded; those measurements taken in lateral view could not be recorded due to the position of the specimen on the pin.

The global distribution of *Rhopalothrix* was obtained from AntMaps (Janicki et al. 2016). The distribution map for all species of *Rhopalothrix* in Colombia was made with R software (R Core Team 2020), using information from specimen collection labels. The shapefiles were extracted from the *rnaturalearth library World Map Data* from Natural Earth v. 0.3.3 (Massicotte 2024). The digital elevation model was developed using the geodata library. The final map presented here was obtained using the graphical tool “ggplot2”.

For comparative purposes, type, and non-type specimens of different *Rhopalothrix* species were studied from high-quality images downloaded from www.antweb.org (AntWeb 2023); unique specimen numbers are provided in all cases.

## Specimen drawing, imaging, Micro-CT scanning and 3D-reconstruction

Drawings of the general habitus of *Rhopalothrix* with measurements, and the mandibular apical fork of each species recorded here were created using Adobe Sketchbook v. 9.0.

Color montage images of the species were created using an Auto-Montage Leica M205A and the images were combined using the program LAS v. 4.6. The images were edited (Corel Photo–Paint X3 v. 13.0) to enhance brightness and contrast details. Finally, all figures were arranged using CorelDRAW Graphics Suite X3.

Micro-CT scans of a specimen of *Rhopalothrix mariaemirae* sp. nov. were generated with a Zeiss Xradia 510 Versa 3D X-ray microscope operated with the Zeiss Scout-and-Scan Control System software (v. 14.0.14829.38124). The scan was carried out at the Okinawa Institute of Science and Technology Graduate University, Japan. Scans were conducted with a 40 kV (75 μA) / 3 W beam using the 4x magnification objective. The scan was performed at an exposure time of 25 s and a voxel size of 0.645545 μm.

## Repositories

We examined specimens deposited in the following collections:

| | |
|---|---|
| **CBUMAG** | Colecciones Biológicas de la Universidad del Magdalena, Santa Marta, Magdalena, Colombia. |
| **CELC** | Coleção Entomológica do Laboratório de Sistemática e Biologia de Coleoptera, Universidade Federal de Viçosa, Viçosa, Brazil. |
| **CPDC** | Centro de Pesquisas del Cacao, Comissão do Plano de Lavoura, Itabuna, Bahia, Brazil. |
| **CTNI** | Colección Taxonómica Nacional de Insectos Luis María Murillo, Corporación Colombiana de Investigación Agropecuaria – AGROSAVIA, Tibaitatá, Mosquera, Cundinamarca, Colombia. |
| **DZUP** | Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil |
| **JTLC** | John T. Longino, personal collection, University of Utah, Salt Lake City, UT, USA. |
| **IAvH** | Instituto de investigaciones en recursos biológicos Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia. |
| **ICN** | Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia. |
| **INPA** | Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil |
| **MEFLG** | Museo Entomológico Francisco Luis Gallego, Universidad Nacional de Colombia, Medellín, Colombia. |
| **MPEG** | Museo Paraense Emilio Goeldi, Belem, Pará, Brazil. |
| **MUSENUV** | Museo de Entomología de la Universidad del Valle, Valle del Cauca, Santiago de Cali, Colombia. |
| **MZSP** | Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil |
| **NHMW** | Naturhistorisches Museum, Wien, Austria. |
| **USNM** | National Museum of Natural History, Washington, DC, USA. |

# Results

## Taxonomic list of *Rhopalothrix* in Colombia

*Rhopalothrix amati* (Fiorentino, Tocora & Fernández, 2022), comb. nov.
*Rhopalothrix ciliata* Mayr, 1870
*Rhopalothrix isthmica* (Weber, 1941)
*Rhopalothrix mandibularis* Guerrero & Grajales, sp. nov.
*Rhopalothrix mariaemirae* Tocora, Fiorentino & Fernández, sp. nov.
*Rhopalothrix weberi* Brown & Kempf, 1960

## Key to Colombian *Rhopalothrix* species based on workers

1 Face with conspicuous squamiform setae (Fig. 3A) .................................**2**
– Face lacking large squamiform setae (Fig. 6A) (*R. isthmica* clade) ..........**4**

2 Head elongate in full-face view, wider posterad than anterad. Lateral cephalic margin above antennal insertion straight and continuous, curved inwards posteriorly (Fig. 4A). Rounded occipital corner (Fig. 5A) .................................................................................................................. ***R. ciliata*** **Mayr**

– Head subquadrate in full-face view, almost as wide posterad as anterad. Lateral cephalic margin above the antennal insertion discontinuous, projecting outward over half of its length. Angled occipital corner (Figs 3A, 8A)... **3**

3 Mandible triangular, with curved external margin and straight masticatory margin. Masticatory margin of mandible with a row of teeth (Fig. 3C). Face with 12 specialized spatulate setae (6 in the anterior row, 6 in the posterior row, Fig. 3A) ............................. ***R. amati*** **(Fiorentino, Tocora & Fernández)**

– Mandible elongated and arched, with the external and masticatory margins subparallel to each other (Figs 8A, 9). Masticatory margin of the mandible with only two teeth near the subapical tooth (Fig. 9). Face with single posterior row of 8 specialized spatulate setae (Figs 8A, 9)...***R. mariaemirae*** **sp. nov.**

4 In lateral view, mandible dorsally inclined in relation to head plane (Fig. 7B). Mandible elongated (MdL > 0.5) with five teeth on masticatory margin (Fig. 7A). Labrum about as long as broad (LabW/LabL < 100%), medial notch deep. Petiole with well-developed peduncle (Fig. 7A)........................ ................................................................................... ***R. mandibularis*** **sp. nov**.

– In lateral view, mandible oriented in the same plane as the head (Figs 6B, 10B). Mandible short (MdL < 0.3), subtriangular (Figs 6A, 10A), and wide at base, with 2–3 teeth on masticatory margin. Labrum distinctly broader than long (LabW/LabL > 110%), medial notch shallow (Figs 6A, 10A). Petiole with short peduncle (Figs 6B, 10B) ......................................................**5**

5 Head broader than long, with slightly rounded cephalic lateral margins at the level of the crest on the face (Fig. 6A). Posterior cephalic margin strongly concave. Mandible with three teeth on masticatory margin, middle tooth largest (Fig. 6A). Subapical tooth longer than width of mandible at base, about twice as long as apical tooth ................***R. isthmica*** **(Weber)**

– Head as broad as it is long, with cephalic lateral margins projecting at an angle at the level of the crest on the face (Fig. 10A). Posterior cephalic margin slightly concave. Mandible with only two small teeth at the base of the masticatory margin (Fig. 10A). Subapical tooth shorter than width of mandible at base, only slightly longer than apical tooth....... ***R. weberi*** **Brown & Kempf**

## Species accounts

### *Rhopalothrix amati* (Fiorentino, Tocora & Fernández, 2022), comb. nov.

Figs 2, 3

*Eurhopalothrix amati* Fiorentino, Tocora & Fernández, 2022: 3, figs 2, 3, 4 A, C. Holotype worker. IAvH-E-55017. Examined.

**Worker measurements (*N* = 5).** MdL 0.16–0.2, MdbW 0.06–0.07, ClyL 0.12–0.15, ClyW 0.26–0.29, HL 0.38–0.42, HW 0.39–0.43, WL 0.4–0.46, PrnW 0.24–0.3, PetL 0.18–0.23, PpetL 0.09–0.11, PetW 0.13–0.15, PpetW 0.2–0.24, T4L 0.33–0.39, GL 0.42–0.48.

**Geographic range.** Colombia.

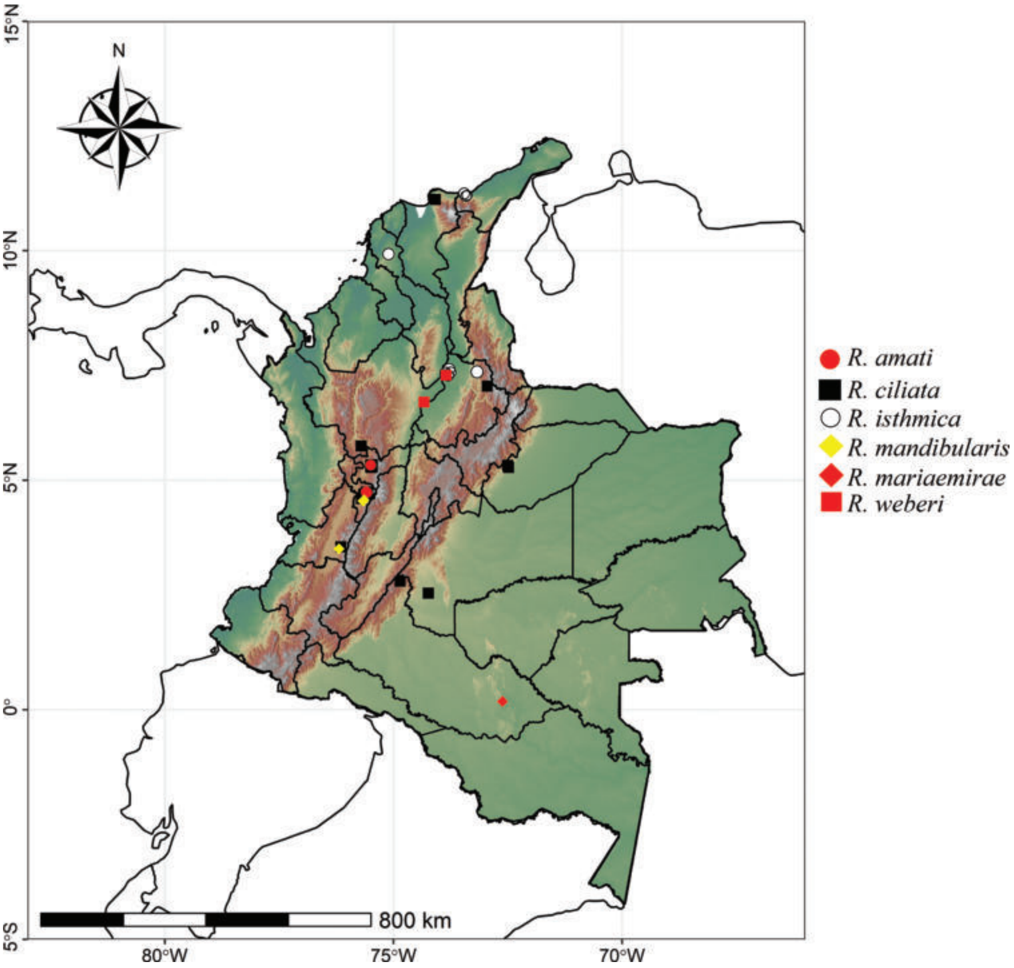

Figure 2. Distribution map of *Rhopalothrix* species in Colombia.

**Examined type material. *Holotype*.** Colombia • 1 worker; Risaralda, Pereira, SFF El Otún Quimbaya, Vda. La Suiza, Plantación Urapán 7; 4.7321972°N, 75.578869°W; 1870 m a.s.l.; M.F. Reina & L.E. Franco legs.; sifted litter; IAvH-E-55017. ***Paratype*.** Colombia • 1 worker; Risaralda, Pereira, vda. La Suiza, Finca el Amparo de Niños; 4.7466278°N, 75.596939°W; 1810 m a.s.l.; 28–30 Nov. 2002; L.E. Franco leg.; secondary growth forest, ex sifted leaf litter; IAvH-55018.

**Additional examined material.** Colombia • 1 worker; Antioquia, Támesis, vda. Alacena, Finca Villa Fátima; 5.2829167°N, 75.474139°W; 1940 m a.s.l.; 2 Oct. 2003; R. García leg.; IAvH-25326. • 3 workers; Caldas, Aranzazú, Vda. La Guaira, Finca Chambery; 5.7130556°N, 75.721833°W; 1900 m a.s.l.; 1–3 Jul. 2003; L.E. Franco & J. Cruz legs; ex sifted leaf litter, secondary growth forest; IAvH-55012.

**Comments.** Holotype and paratype workers (IAvH-55017 and IAvH-55018) and three non-type specimens were analyzed and measured (HW 0.39–0.43) showing a mandibular dentition different from either of the two states described for *Eurhopalothrix* (Longino 2013). Fiorentino et al. (2022) indicate that the workers of this species have “masticatory margin with a single row of ~13 long needle shaped teeth…”, but this dentition does not match the simple row of 11 similar, low, triangular teeth mentioned for *Eurhopalothrix* by Longino (2013). Reanalyzing the mandible dentition of the workers, they present a row of between seven (IAvH55005 in AntWeb 2023) to ten teeth (holotype). The shape of the mandible of the workers of this species also does not match those of *Eurhopalothrix*, being more like the man-

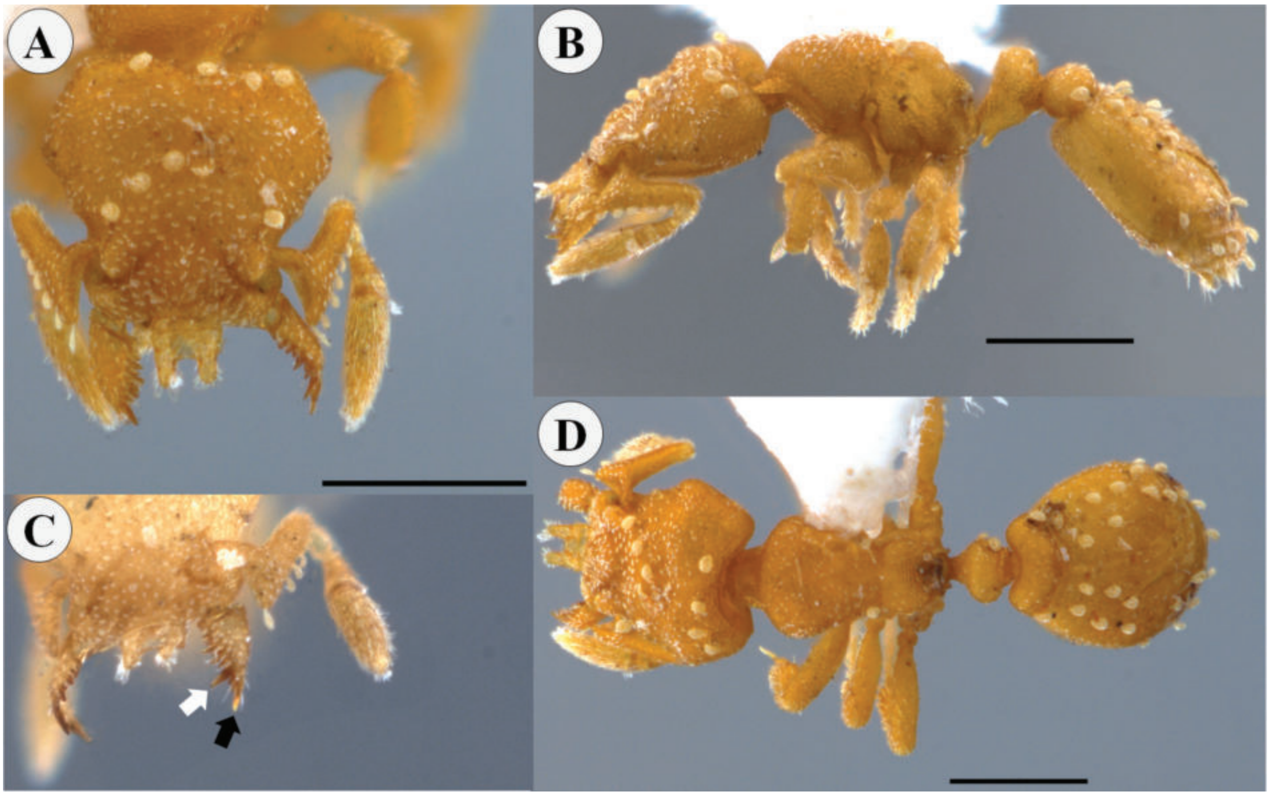

**Figure 3.** *Rhopalothrix amati* paratype worker (IAvH-55018) **A** full-face view **B** lateral view **C** dorsal view **D** portion of the head viewed obliquely showing the mandibles and the apical fork of the left mandible; the black arrow points to the subapical tooth while the white one points to the apical tooth of the apical fork of the mandible. Scale bars: 0.2 mm.

dible of some undescribed *Rhopalothrix* (e.g., CASENT0639185 *Rhopalothrix* jtl014 or CASENT0646264 *Rhopalothrix* jtl023). It is possible that the triangular shape of the mandible of *Rhopalothrix amati* has generated the misclassification of this species in the genus *Eurhopalothrix*. All the workers studied, however, have the subapical tooth larger than the apical one (Fig. 3C), the latter being below the subapical tooth, a combination of traits present in *Rhopalothrix*. Based on all morphological evidence, we transfer this species to the genus *Rhopalothrix* generating the following new combination *Rhopalothrix amati* (Fiorentino, Tocora & Fernández, 2022).

### ***Rhopalothrix ciliata* Mayr, 1870**
Figs 2, 4, 5

**Type material. *Lectotype*.** Colombia • 1 worker; Santa Fe de Bogota; G. Mayr, leg.; AntWeb image examined, CASENT0915695; NHMW.

**Worker measurements (*N* = 13).** MdL 0.3–0.36, MdbW 0.05–0.09, ClyL 0.15–0.22, ClyW 0.32–0.47, HL 0.43–0.81, HW 0.49–0.72, WL 0.49–0.8, PrnW 0.29–0.45, PetL 0.28–0.35, PpetL 0.1–0.16, PetW 0.14–0.21, PpetW 0.23–0.37, T4L 0.43–0.68, GL 0.52–0.86.

**Geographic range.** Colombia, Ecuador, Venezuela. In Colombia, this species is known from Antioquia, Cundinamarca, Huila, Magdalena (Sierra Nevada de Santa Marta), Quindío and Valle del Cauca (Fernández and Serna 2019). New records in Colombia come from Caldas, Risaralda, and Santander.

**Examined material.** Colombia • 4 workers; Antioquia, Támesis, Vda. LaVirgen Fca La Cumbre; 5.74531°N, 75.70542°W; 1610 m a.s.l.; 18 Aug. 2003; E. Patiño, leg.; winkler, low vegetation (stubble); IAvH 25286 to IAvH 25289. • 3 workers; Caldas, Aranzazu, Vda. Buenavista, Fca. La Palma; 5.27956°N, 75.49238°W; 2025 m a.s.l.; 29–31 Jul. 2003; L.E. Franco & J. Cruz legs.; winkler, living fence; IAvH 25010. • 1 worker; Caldas, Aranzazu, Vda. Chamberry, Fca. Las Garzas; 5.301939°N, 75.50144°W; 1940 m a.s.l.; 31 Jul.-4 Aug. 2003; L.E. Franco & J. Cruz legs.; winkler, mature forest fragment; IAvH 248793. • 1 worker; Caldas, Aranzazu, Vda. El Edén, Fca. El Gibarito; 5.29681°N, 74.8867°W; 1930 m a.s.l.; 5–7 Aug. 2003; L.E. Franco & J. Cruz legs.; winkler, riparian vegetation; IAvH 56368. • 2 workers; Caldas, Aranzazu, Vda. Guiaira, Fca. Villa Ofelia; 5.28549°N, 75.46419°W; 1965 m a.s.l.; 1–3 Aug. 2003; L.E. Franco & J. Cruz legs.; winkler, riparian vegetation; IAvH 54998. • 1 worker; Caldas, Aranzazu, Vda. La Guaira, Fca. Alto Bonito; 5.27883°N, 72.48461°W; 2056 m a.s.l.; 25–26 Jul. 2003; L.E. Franco & J. Cruz legs.; winkler; IAvH 56374. • 1 worker; Caldas, Aranzazu, Vda. La Pradera, Fca. Mina Manzanillo; 5.32169°N, 75.50144°W; 2080 m a.s.l.; 2–4 Aug. 2003; L.E. Franco & J. Cruz legs.; winkler, mature forest fragment; IAvH 55000. • 1 worker; Caldas, Aranzazu, Vda. San José, Fca. El Montier; 5.32694°N, 72.99028°W; 1960 m a.s.l.; 2–4 Jul. 2003; L.E. Franco & J. Cruz legs.; winkler, secondary forest fragment; IAvH 25012. • 1 worker; Caldas, Aranzazu, Vda. San José, Fca. Santa Teresa; 5.32475°N, 75.49786°W; 2005 m a.s.l.; 2–4 Aug. 2003; L.E. Franco & J. Cruz legs.; winkler; IAvH 56356. • 1 worker; Caquetá, PNN Picachos; 2.7975°N, 74.8549°W; 1775 m a.s.l.; Nov. 1997; F. Escobar leg.; ICN-MHN 080314. • 1 worker; Quindío, Armenia, Parque de la Vida; 4.5461398°N, 75.65933°W; 151 m a.s.l.; 8 Oct. 2020; A.F. Grajales-Andica & D.R. García-Cárdena legs.; winkler, bamboo forest; CBUMAG:ENT:35948.• 1 worker; Quindío, Circasia, Fca. Calamar; 5.9778°N, 75.7°W; 1450 m a.s.l.; 12 Oct. 1999; E. González leg.; winkler; IAvH 110900. • 1 worker; same data as for preceding; IAvH 80377. • 3 workers; Quindío, Filandia, Vda. Cruces, Fca. Agua Bonita; 4.68581°N, 75.62822°W; 1830 m a.s.l.; 20–22 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, riparian vegetation; IAvH 56350; • 1 worker; Quindío, Filandia, Vda. Cruces, Fca. Agua Bonita; 4.68778°N, 75.62729°W; 1870 m a.s.l.; 21–23 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, riparian vegetation; IAvH 56343. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca Brasil; 4.68817°N, 75.64245°W; 1850 m a.s.l.; 24–26 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, forest fragment; IAvH 56355. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca. El Palacio; 4.69325°N, 75.63291°W; 1810 m a.s.l.; 18–20 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, forest edge; IAvH 56358. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca El Roble; 4.68239°N, 75.65247°W; 1990 m a.s.l.; 3–5 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler; IAvH 56365. • 3 workers; Quindío, Filandia, Vda. Cruces, Fca. La Cha; 4.70468°N, 75.62649°W; 1920 m a.s.l.; 28–30 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, forest; IAvH 56359. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca La Tunja; 4.68475°N, 75.65247°W; 2000 m a.s.l.; 17–19 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, forest fragment; IAvH 56372. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca Paraiso; 4.695°N, 75.62278°W; 1870 m a.s.l.; 4–6 Jun. 2002; E. Jiménez & M.F. Reina, legs.; winkler, forest; IAvH 25870. • 3 workers; Quindío, Filandia, Vda. Cruces, Fca Paraiso; 4.69767°N, 75.62582°W; 1910 m a.s.l.; 27–29 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, forest; IAvH 56348. • 1 worker; same data as for preceding; IAvH-E-112817. • 1 worker; same data as for pre-

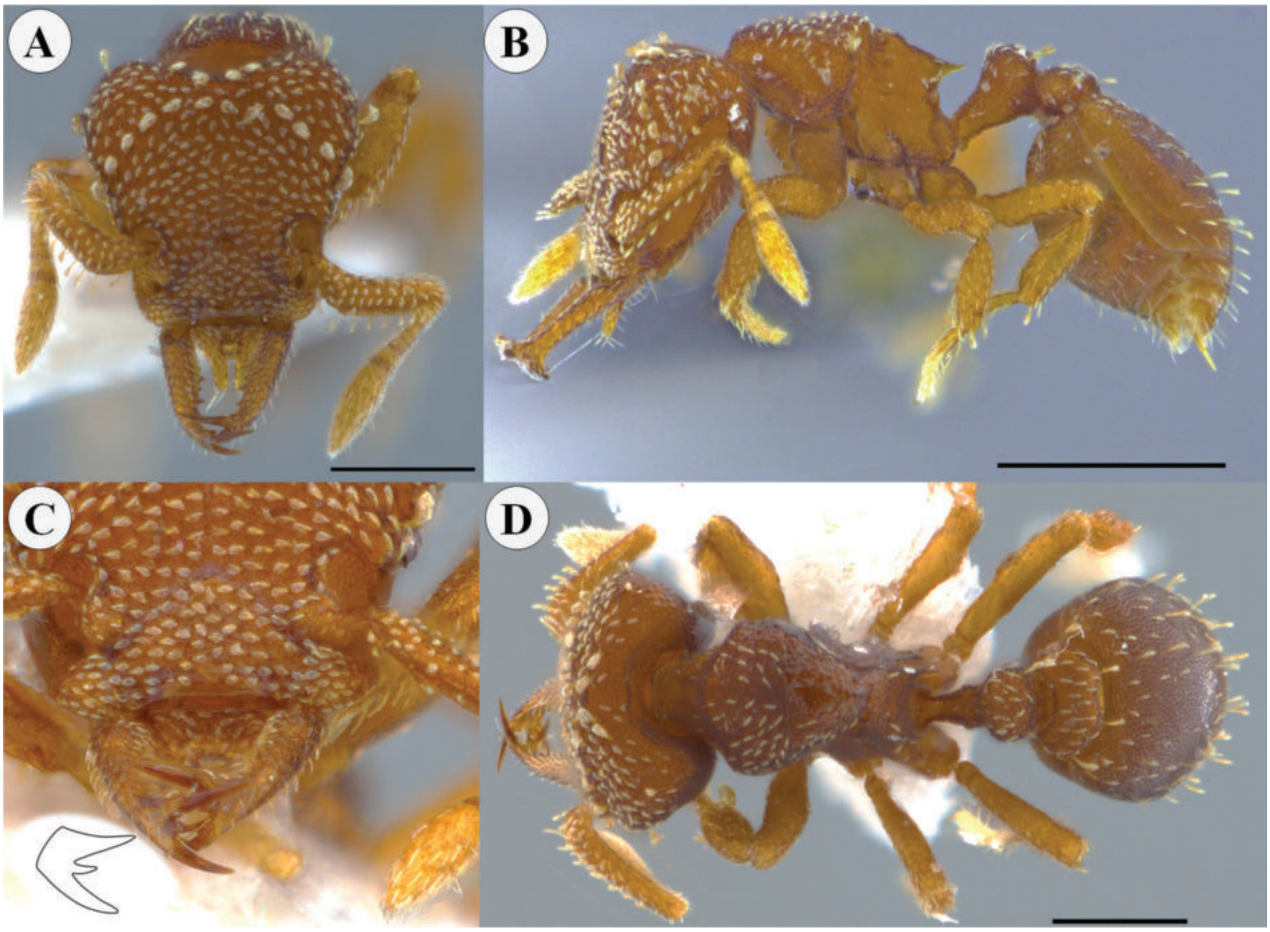

**Figure 4.** *Rhopalothrix ciliata* worker (CBUMAG:ENT:35948) **A** full-face view **B** lateral view **C** mandible distinguishing the teeth of the apical fork; drawing inserted showing the arrangement of the teeth of the apical fork of the mandible **D** dorsal view. Scale bars: 0.3 mm (**A, D**); 0.5 mm (**B**).

ceding; IAvH-E-112817. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca Paraiso; 4.69278°N, 75.62009°W; 1910 m a.s.l.; 7–9 Jul. 2002; E. Jiménez & M.F. Reina, legs.; winkler, riparian vegetation; IAvH 56361. • 1 worker; same data as for preceding; IAvH-E-248916. • 1 worker; same data as for preceding; IAvH 56342. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca Paraiso; 4.69302°N, 75.62009°W; 1910 m a.s.l.; 7–9 Jul. 2002; E. Jiménez & M.F. Reina, legs.; winkler, riparian vegetation; IAvH 56357. • 3 workers; same data as for preceding; IAvH 56362. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca Paraiso; 4.69302°N, 75.62009°W; 1910 m a.s.l.; 12–14 Jul. 2002; E. Jiménez & L.E. Franco legs.; winkler, riparian vegetation; IAvH 56349. • 3 workers; Quindío, Filandia, Vda. Cruces, Fca Veracruz; 4.695°N, 75.60217°W; 28–30 Jul. 2002; 2010 m a.s.l.; E. Jiménez & L.E. Franco legs.; winkler, forest fragment; IAvH 56354. • 1 worker; Quindío, Filandia, Vda. Cruces, Fca Veracruz; 4.70317°N, 75.62945°W; 2010; 5–7 Jul. 2002; E. Jiménez & M.F. Reina, legs.; winkler, plantation; IAvH 56351. • 3 workers; Risaralda, Pereira, Vda. La Aurora, Fca. Los Balcones; 5.32714°N, 75.46688°W; 1957 m a.s.l.; 30 Jul-1 Aug. 2003; L.E. Franco & E. Londoño legs.; winkler, secondary forest fragment; IAvH 25007. • 1 worker; Risaralda, Pereira, Vda. La Suiza Fca. Cartón Colombia; 4.72544°N, 75.60016°W; 2100 m a.s.l.; 21–23 Nov. 2003; M.F. Reina & L.E. Franco legs.; winkler, Eucalyptus plantation; IAvH 25001. • 2 workers; Risaralda, Pereira, Vda. La Suiza, Fca. El Amparo de Niños; 4.7455°N, 75.59672°W;

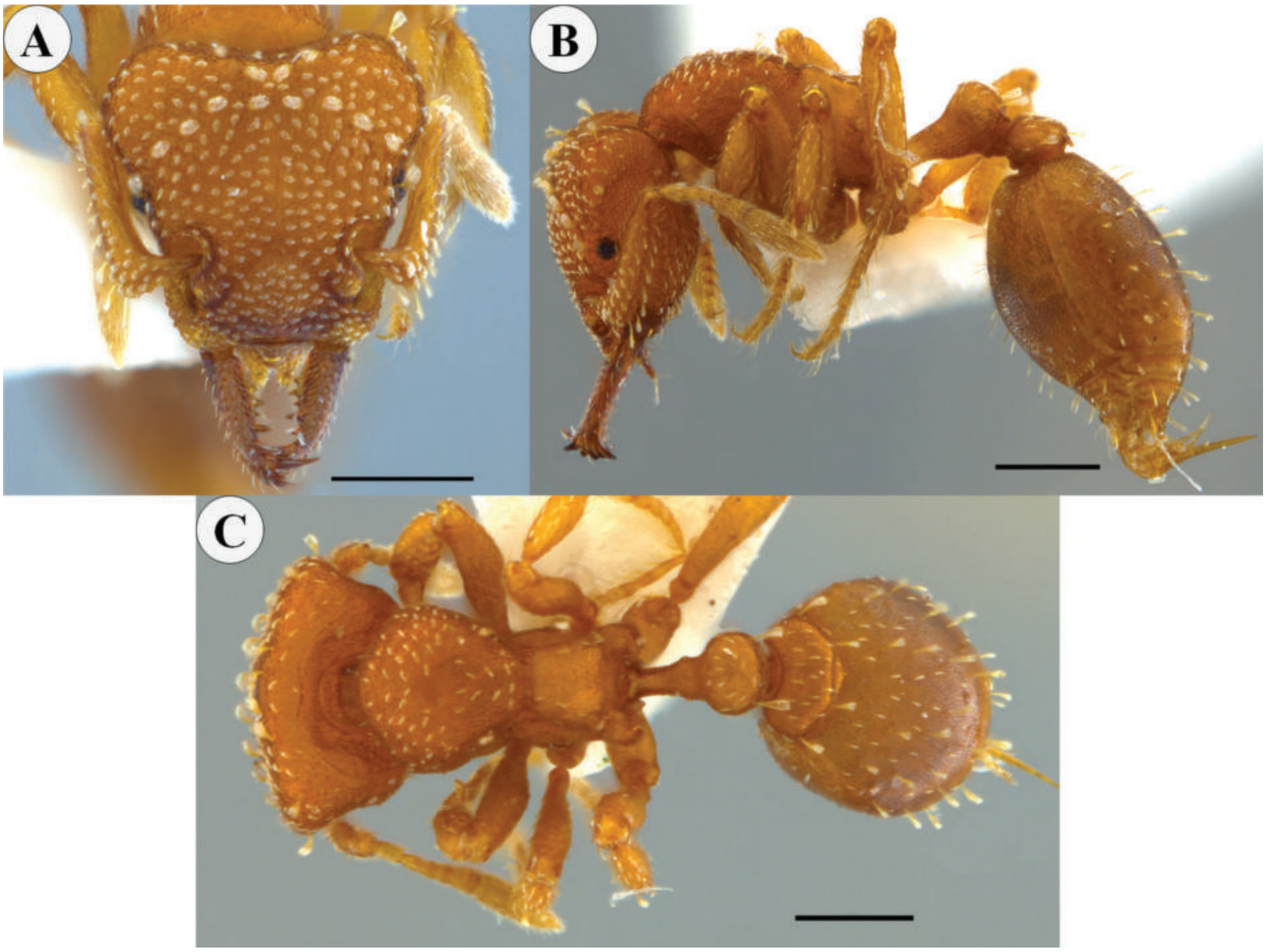

**Figure 5.** *Rhopalothrix ciliata* worker (ICN80314) **A** full-face view **B** lateral view **C** dorsal view. Scale bars: 0.2 mm.

1840 m a.s.l.; 28–30 Nov. 2003; L.E. Franco & E. Londoño legs.; winkler, mature forest; IAvH 24995. • 3 workers; Risaralda, Pereira, Vda. La Suiza, Fca. Lisdrand; 4.74293°N, 75.58028°W; 1930 m a.s.l.; 4–6 Dec. 2003; L.E. Franco & E. Londoño legs.; winkler, mature forest; IAvH 56360. • 1 worker; Risaralda, Pereira, Vda. La Suiza, Fca. Tesorito; 4.72236°N, 75.560108°W; 2050 m a.s.l.; 27–29 Nov. 2003; L.E. Franco & E. Londoño legs.; winkler, mature forest; IAvH 56366. • 1 worker; Risaralda, Pereira, Vda. La Suiza, SFF Otún Quimbaya; 4.71962°N, 75.58028°W; 1910 m a.s.l.; 26 Feb. 2003; L.E. Franco & E. Londoño legs.; winkler, urapán plantation; IAvH 56371. • 2 workers; Risaralda, Pereira, Vda. La Suiza, SFF Otún Quimbaya; 4.71962°N, 75.580423°W; 1910 m a.s.l.; 11–13 Jan. 2003; L.E. Franco & E. Londoño legs.; winkler, urapán plantation; IAvH 24999. • 1 worker; Risaralda, Salamina, Vda. En Medio de Rio, Fca. Villa Belmira; 5.33563°N, 75.48236°W; 1740 m a.s.l.; 29–31 Jul. 2003; L.E. Franco & J. Cruz, legs.; winkler, shade-grown coffee; IAvH 25003. • 1 worker; Santander, Piedecuesta, Cgto. Sevilla Vda. Cristales, reserva experimental demostrativa El Rasgón; 7.05°N, 72.95°W; 2150 m a.s.l.; 21–23 Sep. 2004; I. Quintero & E. González legs.; winkler, high Andean forest; IAvH 71848. • 1 queen; Valle del Cauca, vda. La Quisiquina, Finca Casa Blanca; 3.55°N, 76.15°W; 1914 m a.s.l.; Aug. 2006; Grupo hormigas UV., legs.; ex sifted leaf litter, forest fragment; MUSENUV HOR 006. • 1 worker; same data as for preceding; MUSENUV HOR 007. • 1 worker; same data as for preceding; IAvH-E-248789. • 1 worker; same data as for preceding; IAvH-E-248886.

**Natural history.** In Colombia, this species is known from forests at altitudes above 1500 m, with populations in the Sierra Nevada de Santa Marta and in regions of the central and western cordilleras. It is a very abundant species in modified environments and in agroecosystems such as coffee crops that include native trees.

**Comments.** The specimen from Caquetá (ICN-MHN 080314) is the largest worker (HW 0.72, WL = 0.8; Fig. 5) known so far compared to the other workers (HW 0.49–0.63, *N* = 12) studied here and the lectotype (HW 0.66, WL = 0.75; from Brown and Kempf 1960). A worker (IAvH 110900) from Quindío is the smallest (HW 0.49).

### ***Rhopalothrix isthmica*** **(Weber, 1941)**

Figs 2, 6

**Worker measurements (*N* = 8).** MdL 0.28–0.3, MdbW 0.08–0.09, ClyL 0.14–0.19, ClyW 0.4–0.43, HL 0.51–0.53, HW 0.54–0.59, WL 0.51–0.56, PrnW 0.29–0.32, PetL 0.23–0.3, PpetL 0.12–0.15, PetW 0.16–0.17, PpetW 0.28–0.31, T4L 0.49–0.55, GL 0.55–0.58.

**Geographic range.** Colombia, Honduras, Guatemala, Panama. In Colombia, this species is known from Antioquia, Bolívar, Santander and Sucre.

**Examined material.** COLOMBIA • 1 worker; Antioquia, Amalfi, cañon del Porce, La Cancana; 6.76667°N, 74.91667°W; 1000 m a.s.l.; 30 Jul. 1997; F. Serna leg.; ex sifted leaf litter mini-Winkler, low vegetation (stubble); MEFLG 11112. • 1 worker; Bolívar, SFF Los Colorados, La Yaya; 9.92611°N, 75.10583°W; 280 m a.s.l.; 3–5 Jul. 2001; ex sifted leaf litter, dry forest; IAvH-E-263435. • 3 workers; La Guajira, Dibulla, Bello Horizonte, río Cañas; 11.25687°N, 73.44852°W; 6 m a.s.l.; 12 Oct. 2015; ex sifted leaf litter, dry forest; IAvH-E-172164. • 3 workers; La Guajira, Dibulla, Alto San Jorge, río Cañas; 11.218°N, 73.428°W; 73 m a.s.l; 12 Oct. 2015; ex sifted leaf litter, dry forest; IAvH-E-172162, IAvH-E-172163, IAvH-E-172165. • 1 worker; Santander, Rionegro, Vereda Galapagos, Km 32 vía al mar, C.I. La Zuiza; 7.370278°N, 73.17762°W, 537 m a.s.l.; 2020; J.M. Montes leg.; CTNI 8304. • 2 workers; Santander, Puerto Wilches, Platero; 7.3483°N, 73.8960°W; 28 m a.s.l.; 10–15 Nov. 2021; ex sifted leaf litter Winkler No. 4; L. Perez leg.; CBUMAG:ENT:35949. • 1 worker; Santander: Puerto Wilches, Vereda Puente Sogamoso; 7.30537°N, 73.82779°W; 87 m a.s.l.; 22 Jul. 2022; L. Velázquez leg.; IAvH-E-226990. • 14 workers; Santander, Puerto Wilches, Vereda Centro, 7.32972°N, 73.84256°W; 88 m a.s.l.; 8 Jul. 2022; L. Arcila leg; ex sifted leaf litter, riparian forest; IAvH-E-226992, IAvH-E-226993, IAvH-E-226994, IAvH-E-226995, IAvH-E-226996, IAvH-E-232292, IAvH-E-233744, IAvH-E-238973, IAvH-E-238974, IAvH-E-238975, IAvH-E-238976, IAvH-E-243661, IAvH-E-243688. • 1 worker; Santander: Puerto Wilches, Vereda San Claver; 7.34831°N, 73.76817°W; 93 m a.s.l.; 8 Jul. 2022; C. Quevedo-Vega leg.; ex sifted leaf litter, riparian forest; IAvH-E-226997. • 1 worker; Santander: Puerto Wilches, Vereda San Claver; 7.34792°N, 73.76817°W; 77 m a.sl.; 8 Jul. 2022; C. Quevedo-Vega leg.; ex sifted leaf litter, riparian forest; IAvH-E-226998.

**Natural history.** *Rhopalothrix isthmica* workers inhabit dry forest in northern Colombia and both in open grassland and riparian forest in eastern Colombia. In the latter it is a relatively abundant species, being found in 8 of 20 MiniWin-

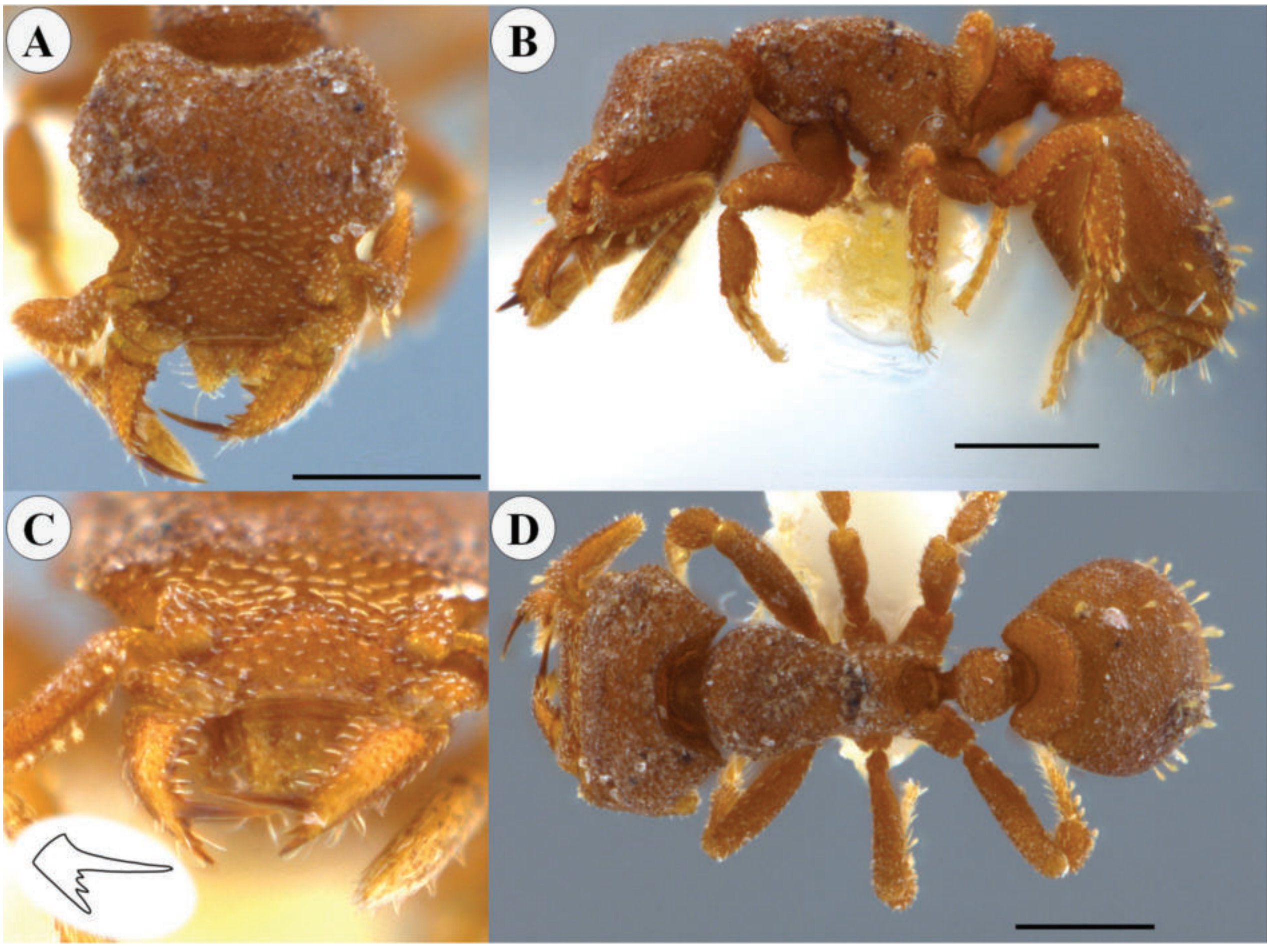

**Figure 6.** *Rhopalothrix isthmica* worker (IAvH-E-172166) **A** full-face view **B** lateral view **C** mandible distinguishing the teeth of the apical fork; drawing inserted showing the arrangement of the teeth of the apical fork of the mandible **D** dorsal view. Scale bars: 0.3 mm.

kler litter samples. *Rhopalothrix isthmica* populations have an elevational distribution from near sea level to 1000 m.

**Comments.** The morphology of the workers matches the diagnostic characters of *R. isthmica*, including HW 0.57–0.61 (*N* = 6) recorded by Longino and Boudinot (2013). In the workers of populations from La Guajira (northern Colombia), the portion of the lamella ventral to the propodeal tooth (infradental lamella) is relatively straighter on the outer margin than described by Longino and Boudinot (2013).

### ***Rhopalothrix mandibularis*** **Guerrero & Grajales, sp. nov.**

https://zoobank.org/F063C899-9938-4D48-B1B1-BAA604287043

Figs 2, 7

**Type material.** ***Holotype.*** Colombia • 1 worker; Quindío, Armenia, Sena; 4.56931°N, 75.64347°W; 1565 m a.s.l.; 18 Feb. 2020; A.F. Grajales-Andica & D.R. García-Cárdenas legs.; ex sifted leaf litter, gallery forest; CBUMAG:ENT:35947. ***Paratypes*** (*N* = 4). Colombia • 1 worker; same data as for holotype; CIUQ-025287. • 1 worker; Quindío, Armenia, Parque de la Vida; 4.54614°N, 75.65933°W; 1515 m a.s.l.; 8 Oct. 2020; A.F. Grajales-Andica & D.R. García-Cárdenas legs.;

ex sifted leaf litter, gallery forest; CIUQ-025288. • 1 worker; Quindío, Armenia, Yulima; 4.5515°N, 75.671°W; 1485 m a.s.l.; 8 Feb. 2020; A.F. Grajales-Andica & D.R. García-Cárdenas legs.; ex sifted leaf litter, gallery forest; CIUQ-025289. • 1 worker; Valle del Cauca, Vda. El Tenjo, Finca La Alejandría; 3.51667°N, 76.16667°W; 1703 m a.s.l.; Aug. 2006; Grupos Hormigas U. V. legs.; ex sifted leaf litter; MUSENUV HOR 008.

**Holotype worker measurements.** MdL 0.48, MdbW 0.08, ClyL 0.2, ClyW 0.44, HL 0.67, HW 0.76, WL 0.65, PrnW 0.43, PetL 0.36, PpetL 0.13, PetW 0.19, PpetW 0.31, T4L 0.6, GL 0.68.

**Paratype workers measurements (*N* = 3).** MdL 0.48–0.52, MdbW 0.08–0.09, ClyL 0.19–0.21, ClyW 0.44–0.47, HL 0.65–0.69, HW 0.76–0.78, WL 0.65–0.69, PrnW 0.43–0.45, PetL 0.36–0.38, PpetL 0.13–0.17, PetW 0.19–0.22, PpetW 0.3–0.31, T4L 0.6–0.73, GL 0.67–0.73.

**Geographic range.** Colombia.

**Diagnosis.** Mandible elongated, much longer (MdL > 0.48) than those of other species in the *isthmica* clade, mandibles with outer and masticatory margins subparallel to each other and curving inward at tip; labrum with two slender subrectangular lobes, notch deep; propodeal tooth large, acute, right angled to declivitous face of propodeum, infradental lamella poorly developed, forming a thin rim.

**Description. Worker.** Head in full-face view broader than long, diamond-shaped, with straight cephalic lateral margins strongly diverging posteriorly, extending below the level of the dorsal crest of the head, at the level of the latter a rounded widening that continues on lateral margins converging towards the rounded posterolateral cephalic corners; wide and concave posterior cephalic margin; front visibly protruding in dorsal view, with an arched transverse carina (= crest), and depression impressed behind the crest. In lateral view, mandible dorsally inclined in relation to head plane (Fig. 7B); mandible with four to five teeth on masticatory margin as follow: three large equidistant teeth located medially on masticatory margin, basalmost (first) large tooth with a small tooth (sometimes undeveloped) above its base, a middle tooth almost half as long as the previous one, third tooth as long as first, a small fourth tooth as long as 1/3 of first; subapical tooth about twice as long as apical tooth, with denticles at base of both subapical and apical tooth. Trapezoidal labrum as long as broad, with slightly concave sides, subparallel anteriorly, and straight-sided base, labrum with two long blunt subrectangular lobes, with parallel inner faces and deep notch between, length of lobe equal to about 1 /3 of the distance from the base of the notch to the transverse carina at the base of the labrum, Clypeus almost twice as wide as long, with anteroclypeal lobes projecting anterad. Scape just reaching maximum width of head; pedicel and second flagellomere conical towards the base as long as wide, third and fourth flagellomere rectangular wider than long, fifth flagellomere subsquare, last flagellomere finger-shaped tapering apically, as long as the previous four funiculus.

In lateral view, pronotum and mesonotum at the same level, divided by arcuate promesonotal groove and metanotal groove moderately impressed; propodeal dorsum sloping in lateral view. In dorsal view, pronotum with slightly concave anterior margins, narrowing anteriorly to form a distinguishable neck, pronotum with rounded corners at maximum width; in dorsal view, mesonotum wider than long, narrowing posteriorly. Petiole with well-developed peduncle; in lateral view, with straight dorsal face and posteriorly convex ventral face, the

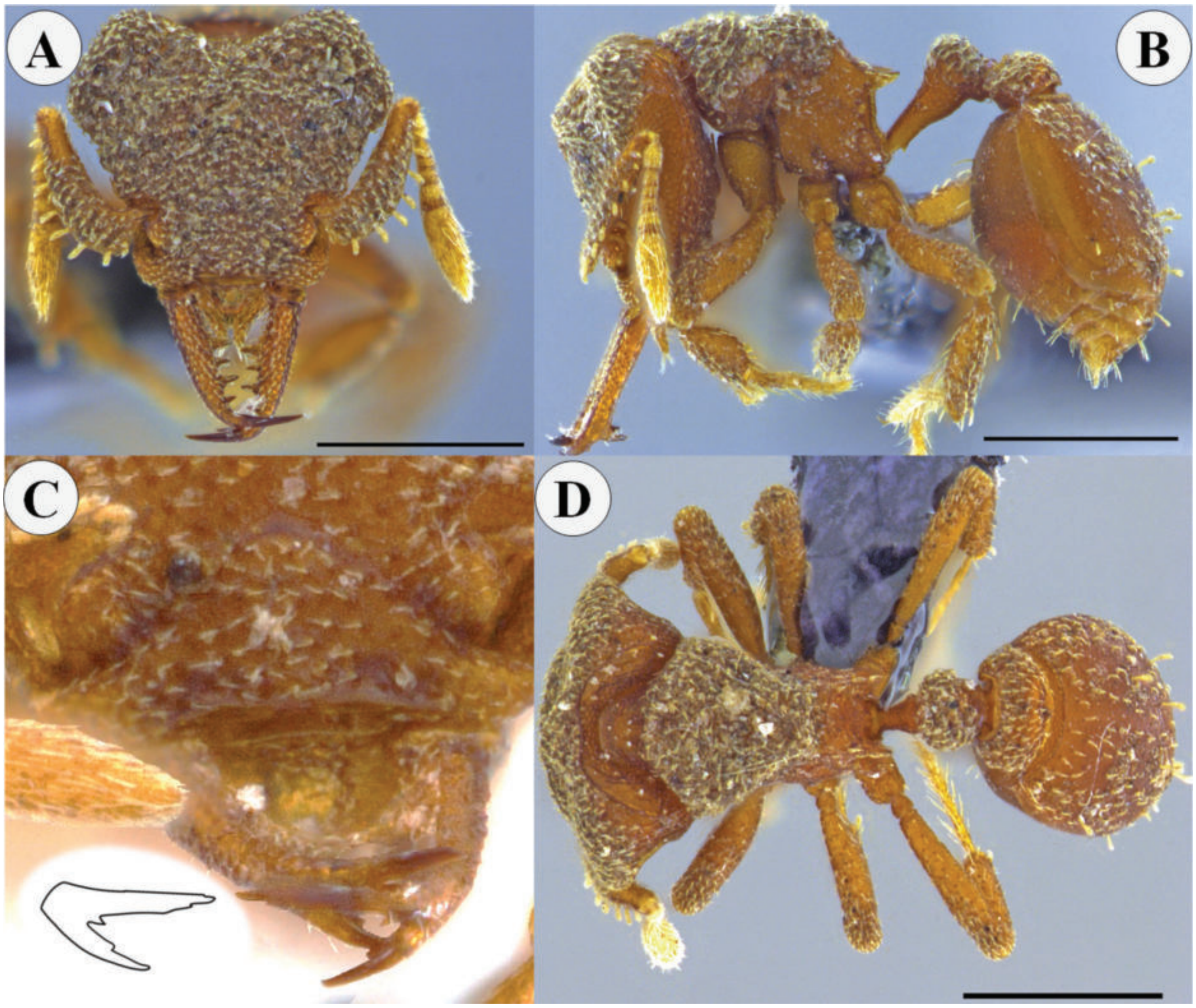

**Figure 7.** *Rhopalothrix mandibularis* sp. nov. Holotype worker (CBUMAG:ENT:35947) **A** full-face view **B** lateral view **C** mandible distinguishing the teeth of the apical fork; drawing inserted showing the arrangement of the teeth of the apical fork of the mandible **D** dorsal view. Scale bars: 0.5 mm.

latter with a small subpetiolar process projecting anterad as a blunt tooth; petiolar scale rounded in lateral view; postpetiole twice as wide as long (Fig. 7C).

Short decumbent hairs on surface of head and mesosoma; dorsum of clypeal plate and above posteroclypeal margin with small squamiform hairs. External margin of scape with about 7–9 squamiform hairs similar in size; apex of scape with erect hairs shorter than squamiform ones; funicles with simple subdecumbent hairs. Legs with coxa and femur with few short decumbent hairs; tibia with abundant long, thick semi-erect hairs, and a pair of long flattened hairs located apically on the external surface of each one. About 4–8 squamiform setae on posterior half of first gastral tergite, unspecialized curved hairs scattered over the disc of the first gastral tergite.

Head, mesosoma, petiole and postpetiole shagreened, legs shiny with granular surface, except all tibiae with smooth surface; surface of first gastral tergite finely shagreened. Color reddish brown to ferruginous brown, with yellowish brown distal antennal flagellomeres.

**Natural history.** This species inhabits humid forests between 1400 and 1700 m above sea level. The holotype and several paratypes were collected in fragments of humid gallery forest and Guadua (bamboo) forest in the city of Armenia. All known specimens are from Winkler samples of sifted leaf litter.

**Etymology.** The name refers to the long mandibles of the worker, a trait not found in any other species in the *isthmica* clade.

**Comments.** This species is placed in the diverse *isthmica* clade because it shares the two synapomorphies proposed by Longino and Boudinot (2013). This new species, however, has been widely confused in some Colombian collections with *R. ciliata* due to its similarity in mandibular shape, the shape of the two lobes of the labrum and the depth of the sinus. *Rhopalothrix mandibularis* can be differentiated from *R. ciliata* by the absence of squamiform setae on the rostrum, the latter with specialized setae and a flattened surface on the rostrum. Also, mandibles are longer and thinner along their length in *R. mandibularis* while in *R. ciliata* they are short and broad; in *R. ciliata* the tip of the labral lobes can reach up to half the length of the mandible, but in *R. mandibularis* the anterior margin of the labrum barely reaches the first tooth of the mandible.

Habitus of the worker of *Rhopalothrix mandibularis* is similar to that of *R. stannardi* Brown & Kempf, 1960, but the mandible length is remarkably different between the two, as well as the mandible dentition; *R. mandibularis* has three teeth located towards the middle of the masticatory margin (the most basal tooth is far from the base), while in *R. stannardi* the three teeth are equidistant, with the most basal tooth starting at the base of the masticatory margin. Another different feature is the infradental lamella, which is very poorly developed in *R. mandibularis*, while in *R. stannardi* the lamella is broad and descends almost perpendicularly from the tooth.

### ***Rhopalothrix mariaemirae* Tocora, Fiorentino & Fernández, sp. nov.**

https://zoobank.org/5EB90D5A-42C0-4D0F-815C-EDB577DD2782
Figs 1, 8, 9

**Type material. *Holotype*.** Colombia • 1 worker; Guaviare, Solano, PNN Serranía de Chiribiquete; 0.18189°N 72.61589°W; 250 m a.s.l.; 30 Nov. 2000; F. Acevedo leg.; ICNC: 099809. ***Paratypes*** (*N* = 7). • 1 worker; same data as holotype; CBUMAG:ENT:35950. BRAZIL • 1 worker; Amazonas, Manaus, 2.40262°S, 59.86655°W; 12 Aug. 2016; B. Boudinot, I. Fernandes I & J. Chaul; winkler; ANTWEB1038216; INPA. • 1 worker; same data as for preceding; UFV-LABECOL-001942; MZSP. • 1 worker; same data as for preceding; UFV-LABECOL-001945; MPEG. • 1 worker; same data as for preceding; UFV-LABECOL-001953; CELC. • 1 worker; same data as for preceding; UFV-LABECOL-007266; JTLC. • 1 worker; Amazonas, Manaus, 2.40372°S, 59.86573°W; 12 Aug. 2016; B. Boudinot, I. Fernandes I & J. Chaul; winkler; UFV-LABECOL-001944; DZUP.

**Other examined material.** Colombia • 1 worker; Amazonas, Parque Nacional Natural Amacayacu; 3.81028°S, 70.2662°W; 88 m a.s.l.; 07 Oct. 2007; J. Sosa-Calvo & J. Rodriguez legs.; winkler, leaf litter, forest; USNMENT01127995; USNMENT01127995; USNM. Brazil • 1 worker; Amazonas, Manaus; 2.93333°S, 59.95°W; 6 Oct. 2006; J.L.P. Souza & J.S. Araújo legs.; ANTWEB1038211; INPA. • 1 worker; same data as for preceding; J.L.P. Souza & P.Y. Oliveira legs.; ANTWEB1038212; INPA. • 1 worker; Amazonas; 2.56669°S, 60.09999°W; 9 Sep. 1990; M.O. de A Ribeiro leg.; ANTWEB1038213; INPA. • 1 worker; Rondônia: Jaci

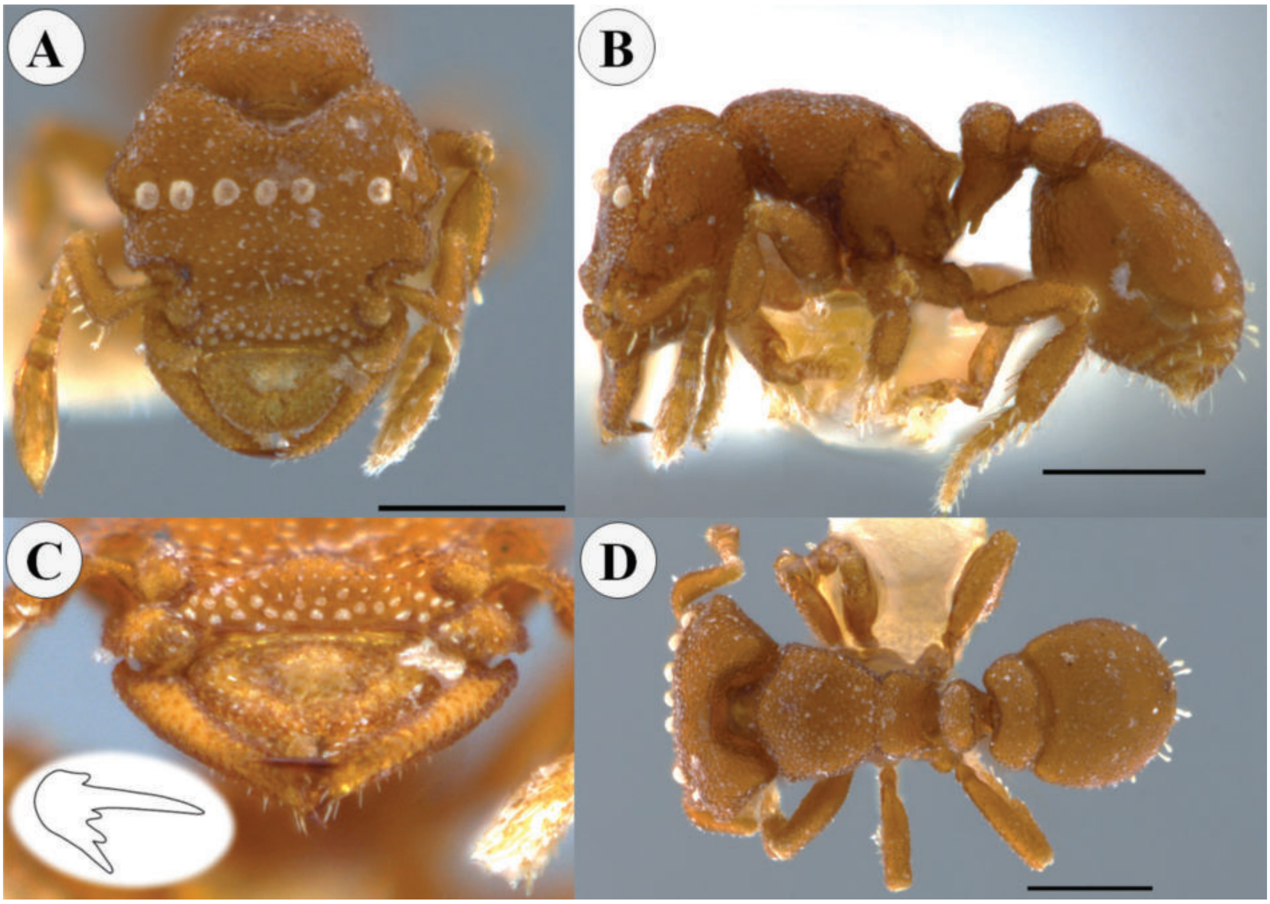

**Figure 8.** *Rhopalothrix mariaemirae* sp. nov. paratype worker (CBUMAG:ENT:35950) **A** full-face view **B** lateral view **C** mandible distinguishing the teeth of the apical fork; drawing inserted showing the arrangement of the teeth of the apical fork of the mandible **D** dorsal view. Scale bars: 0.3 mm.

Novo; 22 Oct. 2013; ANTWEB1038214; INPA. • 1 worker; Pará, Melgaço, Estação Científica Ferreira Penna; 1.71668°S, 51.41668°W; J.L.P. Souza & C. Moura; 26 Oct. 2003; ANTWEB1038215; INPA. • 1 worker; Rondônia, Porto Velho, área Mutum (M5P2); 9.591389°S, 65.04917°W; 17–27 Jul. 2013; G.R. Mazão & R.S. Probst legs.; CPDC. • 1 worker; Pará, Marituba; 1.36667°S, 48.33333°W; 20 m a.s.l.; 22 Oct. 2004; J.R.M. Santos leg.; winkler, mata; CPDC. GUYANA • 1 worker; Rupununi, nr. Kamoa River, nr Kamoa R. Camp; 1.55077°N, 58.83832°W; 535 m a.s.l.; 24 Oct. 2006; R. Williams & P. Suse legs.; winkler, leaf litter; USNMENT01127994; USNM.

**Geographic range.** Colombia, Guyana, Brazil.

**Holotype worker measurements.** MdL 0.3, MdbW 0.06, ClyL 0.16, ClyW 0.43, HL 0.48, HW 0.55, WL 0.52, PrnW 0.35, PetL 0.3, PpetL 0.12, PetW 0.19, PpetW 0.28, T4L 0.42, GL 0.56.

**Paratype workers measurements (*N* = 7).** MdL 0.25–0.33, MdbW 0.06–0.08, ClyL 0.12–0.17, ClyW 0.38–0.44, HL0.39–0.49, HW 0.48–0.55, WL 0.43–0.52, PrnW 0.29–0.35, PetL 0.21–0.30, PpetL 0.09–0.13, PetW 0.16–0.19, PpetW 0.24–0.29, T4L 0.35–0.42, GL 0.42–0.56.

**Diagnosis.** Masticatory margin of mandible with two small teeth near the base of the subapical tooth; labrum rounded, about as long as broad, with two poorly produced, bluntly, rounded anterior lobes; promesonotal and metanotal groove continuously concave; larger specialized hairs on face are shaped like inverted bowls of broad flat spoons lying close to and paralleling the integu-

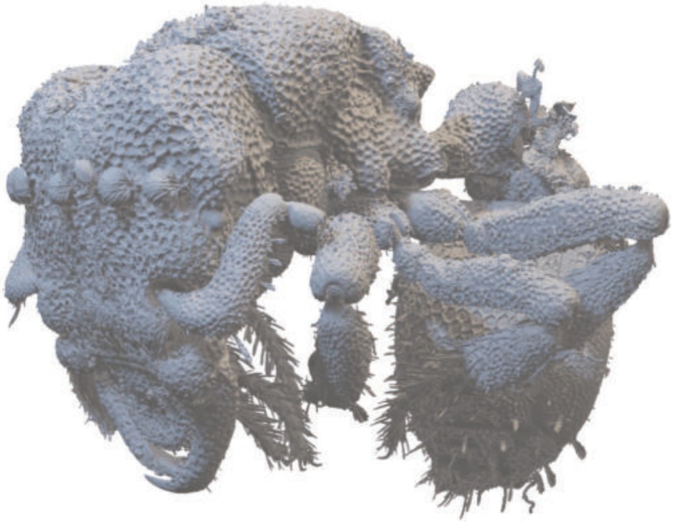

**Figure 9.** Volume render of *Rhopalothrix mariaemirae* sp. nov. worker.

mental surface, in perpendicular view they look like eight large, rounded white scales on head.

**Description. Worker.** Head in full-face view wider than long, with cephalic lateral margins subparallel to each other, profile interrupted by a deeply impressed notch at the level of the antennal insertions and a triangular notch shallower than the previous one below the level of the diadem of circular/squamiform hairs, at the level of the latter, widened profile projecting rounded angulations continuing on slightly convergent lateral margins towards the angled posterolateral cephalic corners; wide and strongly concave posterior cephalic margin. In lateral view, mandible in the same plane of the head; subapical tooth with prominent recurved acute tooth, directed posteriorly, subapical tooth shorter than width of mandible at base, about twice as long as apical tooth. In full-face view, anterior margin of labrum with shallow median notch, posteromedial portion of labrum translucid. Clypeus about 2.5 times wider than long, with rounded anteroclypeal lobes projecting anterad. Scape just beyond the most posterior notch of the lateral cephalic margin; Pedicel subsquare, second to fourth flagellomere conical towards the base, fifth flagellomere rectangular longer than wide, last flagellomere finger-shaped tapering towards the apex, almost as long as almost as long as the five flagellomeres combined.

In lateral view, promesonotum convex continuing with the profile of the dorsum of the propodeum, promesonotal depression and metanotal groove slightly impressed; propodeal dorsum falling on a slight slope in lateral view; propodeal tooth developed, distinctly in top half of declivitous face of propodeum in lateral view; infradental lamella very narrow. In dorsal view, pronotum with straight lateral and convex anterior margin, pronotum with angled corners at their maximum width that continue towards slightly convex lateral margins; mesonotum trapezoid-shaped, wider than long, narrowing posteriorly. Petiole with poor-developed peduncle; in lateral view, with the dorsal face short, strongly inclined to connect with the anterior face of the rounded petiole scale, ventral surface straight with a small elongated subpetiolar process projecting anterad; in dorsal view, postpetiole 1.5 times wider than width of petiole (Fig. 8C).

Head with short decumbent squamiform hairs, notably dispersed and arranged transversely; anterodorsal portion of clypeus with small squamiform hairs broadened apicad. External margin of the scape with about 6–7 squamiform hairs similar in size; apex of scape with few shorter and thicker erect hairs, widely scattered; flagellomeres with simple subdecumbent hairs. Coxa and femur with few very short hairs; tibiae with long, thick semi-erect squamiform hairs on the inner surface, external face of the tibiae devoid of erect hairs, with only a few long, flattened hairs located apically. First gastral tergite largely devoid of setae, with 2–3 squamiform setae at posterolateral margins.

Head, mesosoma, petiole and postpetiole shagreened, with the surface strongly areolate (Fig. 9); surface of first gastral tergite areolate. Color ocher to orange, concolorous.

**Queen and male.** Unknown.

**Etymology.** This species is named after María Emir Sánchez (1953–2023), as a tribute to María C. Tocora's beloved and inspiring *abuela*, who recently passed away.

**Comments.** This species is easily recognized by the anterior labral convexity condition, the two small blunt lobes of the labrum, and the large squamate hairs, 8 in total, on the frons like those of *R. diadema* (Longino and Boudinot 2013).

The workers of *Rhopalothrix* jtl021 (ANTWEB1038216, UFV-LABECOL-001953, and USNMENT01127994) match to *R. mariaemirae*. Those specimens coincide in the strongly convex labrum, distal margin of labrum slightly notched, and the two poorly-developed lobes. In *Rhopalothrix* jtl021 the posteromedial portion of labrum is translucid. Also, all specimens share eight strongly convex rounded scales located below the maximum width of the head.

### ***Rhopalothrix weberi*** **Brown & Kempf, 1960**

Figs 2, 10

**Worker measurements (*N* = 1).** MdL 0.16, MdbW 0.07, ClyL 0.12, ClyW 0.25, HL 0.36, HW 0.37, WL 0.38, PrnW 0.24, PetL 0.17, PpetL 0.09, PetW 0.14, PpetW 0.2, T4L 0.33, GL 0.41.

**Geographic range.** Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Cuba, Colombia, Guyana, Suriname.

**Examined material.** Colombia • 1 worker; Santander, Puerto Wilches, Vereda Centro; 7.32972°N, 73.84256°W; 87 m a.s.l.; 13 Jul. 2021; G. Mercado leg.; ex sifted leaf litter riparian forest; IAvH-E-233235.

**Natural history.** The only specimen studied here was extracted from the low-density litter of a riparian forest with shrubby vegetation.

**Comments.** This species is recorded by Achury and Suarez (2018) from the Colombian inter-Andean valley, but we were not able to study those specimens to corroborate the identity. Ants recently collected in Puerto Wilches (Santander) in eastern Colombia included one specimen that matches the taxonomic definition of *R. weberi*, thus corroborating the presence of this species in Colombia.

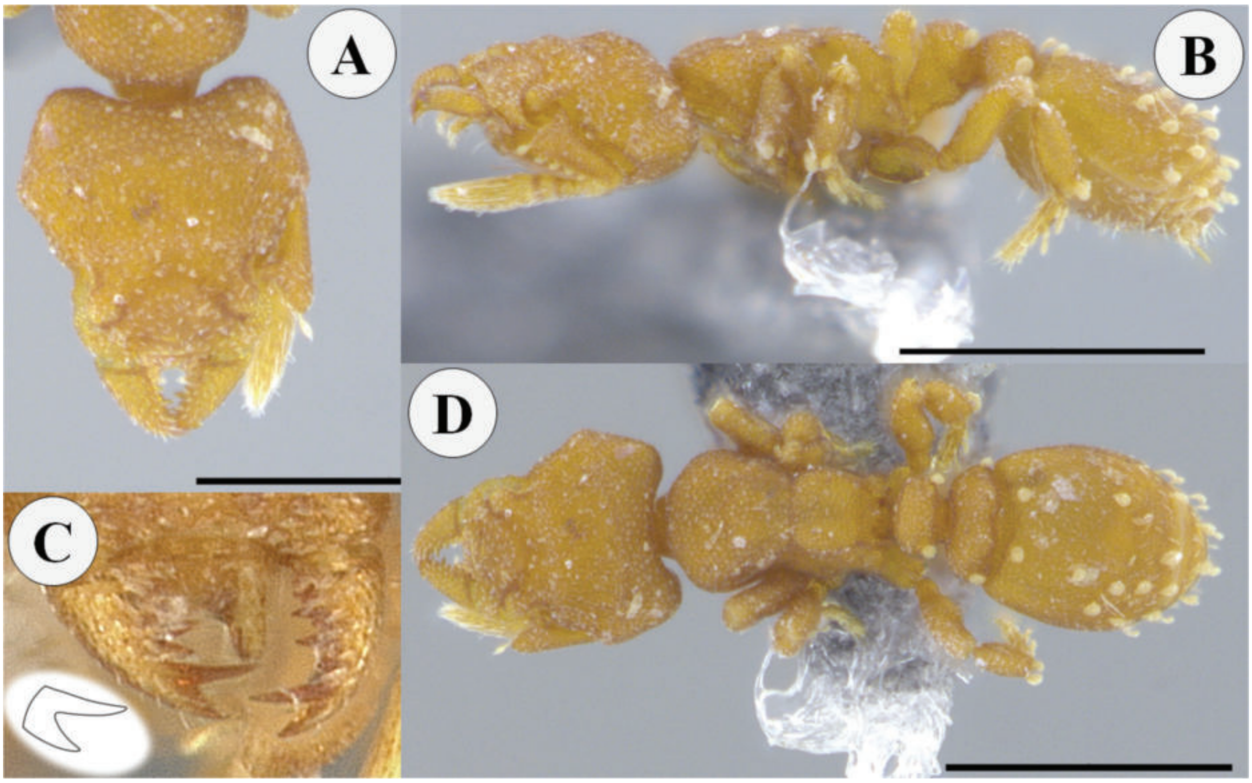

**Figure 10.** *Rhopalothrix weberi* worker (IAvH-E-233235). **A** full-face view **B** lateral view **C** mandible distinguishing the teeth of the apical fork; drawing inserted showing the arrangement of the teeth of the apical fork of the mandible **D** dorsal view. Scale bars: 0.3 mm.

## General comments

The ant genus *Rhopalothrix* is reviewed for the first time for Colombia. Previously only three species were known: *R. ciliata*, *R. isthmica* and *R. weberi* (Janicki et al. 2016); the last with an uncertain record for Antioquia (Achury and Suarez 2018). Our study increases the number of species to six, with the description of two new species, *R. mandibularis* and *R. mariaemirae*.

*Rhopalotrhix ciliata* and *R. isthmica* are the most widely distributed species in Colombia, the first species with populations mainly in the Andean region and the Sierra Nevada de Santa Marta (northern Colombia), while *R. isthmica* has populations in dry forests of the Colombian Caribbean, in cleared open areas and in remnants of riparian forest in Santander in the valley of the eastern Cordillera of Colombia. Interestingly, *Rhopalotrhix ciliata* overlaps its distribution with both *R. amati* and *R. mandibularis* in the coffee-producing region of central Colombia and in Valle del Cauca; in the latter, however, a disjunct altitudinal distribution is evident, as *R. ciliata* can be found above 2000 m while *R. mandibularis* is at 1700 m. Another example of sympatric distribution is recorded for *R. isthmica* and *R. weberi* in riparian forests in northeastern Colombia, where both species were found coexisting in leaf litter.

## Acknowledgments

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

RJG studied and described most of the species, except for Rhopalothrix mariaemirae. MCT, GP and FF described R. mariaemirae. RJG drafted this manuscript, supervised the generation and editing of the photographs, as well as the generation of the distribution map. RJG, AFGA, MCT, FF, GF, and DRG read, proofread, and edited the different versions of the manuscript.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Research Article

# The ants of the Galápagos Islands (Hymenoptera, Formicidae): a historical overview, checklist, and identification key

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## Abstract

The Galápagos ant fauna has long been understudied, with the last taxonomic summary being published almost a century ago. Here, a comprehensive and updated overview of the known ant species of the Galápagos Islands is provided with updated species distributions. The list is based on an extensive review of literature, the identification of more than 382,000 specimens deposited in different entomological collections, and recent expeditions to the islands. The ant fauna is composed of five subfamilies (Dolichoderinae, Dorylinae, Formicinae, Myrmicinae, and Ponerinae), 22 genera, 50 species, and 25 subspecies, although three species (*Crematogaster crinosa* Mayr, 1862, *Camponotus senex* (Smith, 1858), and *Solenopsis saevissima* (Smith, 1855)) are considered dubious records. Finally, an illustrated identification key of the species found in the archipelago is presented.

**Key words:** Checklist, distribution, Galápagos ants, taxonomy

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## Introduction

Until recently, the ant fauna of the Galápagos Islands was poorly studied. Early expeditions to the Galápagos collected only a few specimens at specific sites, primarily in the arid zones, which were more accessible (Smith 1877; Emery 1893; Wheeler 1919, 1924, 1933). This resulted in the first lists of Galápagos ant species published by Wheeler (1919, 1924, 1933) and Stitz (1932). Linsley and Usinger (1966) updated these lists by compiling all known reports of ants in the Galápagos archipelago, reporting 19 species and 34 subspecies. Only after Silberglied (1972) reported *Wasmannia auropunctata* (Roger, 1863), the invasive little fire ant, in the Galápagos, did the interest in ants increase. At that time, studies were mainly focused on understanding the impact of *W. auropunctata* on native species (Clark et al. 1982; Lubin 1984). These studies led to several new records though they were limited to certain localities on a few major islands. Later studies by Pezzatti et al. (1998) and Snelling and Longino (1992) provided some important additions to the Galápagos ant fauna, but a systematic sampling of all islands was still needed (Brandão and Paiva 1994). In 2005, we initiated a project to study material deposited in collections worldwide and sampled all major islands in the archipelago, which resulted in many new ant records (Fig. 1) (among others: Longino 2003; Pacheco et al. 2007; Herrera and Longino 2008; Herrera and Causton 2010; Lattke 2011; Herrera et al. 2013, 2014). Here, we list all known species records (past and present) from the Galápagos Islands and provide an illustrated identification key for the established 47 taxa known to date, we do not include dubious records in the key. Also, this checklist does not include species intercepted in quarantine inspection activities in the Galápagos as these have not been confirmed as established in the islands. These intercepted species include: *Acromyrmex octospinosus* (Reich, 1793), *Brachymyrmex patagonicus* Mayr, 1868, *Camponotus brettesi* Forel, 1899, *Crematogaster curvispinosa* Mayr, 1862, *Eciton vagans angustatum* Roger, 1863, *Ectatomma ruidum* (Roger, 1860), *Linepithema humile* (Mayr, 1868), and *Notoncus ectatommoides* (Forel, 1892).

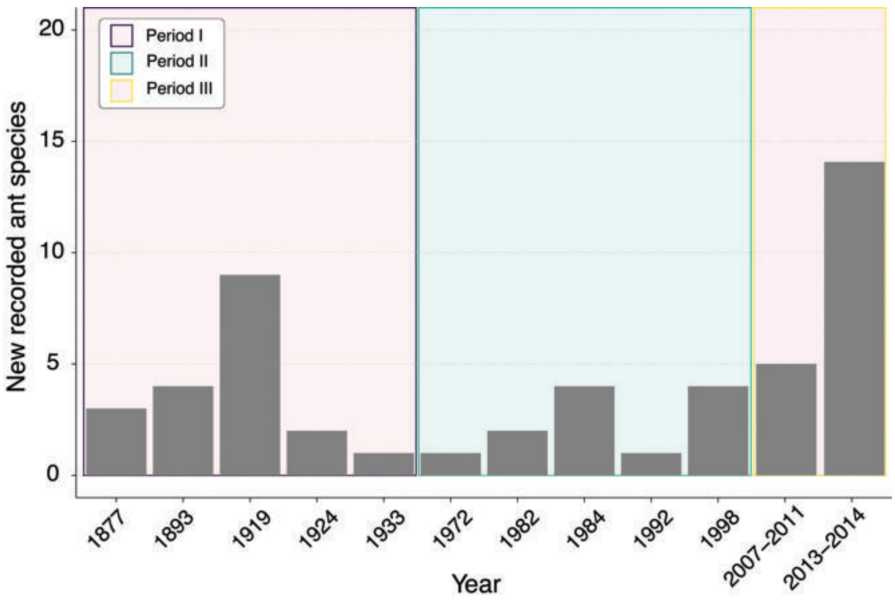

**Figure 1.** Delimitation of the three periods in the study of Galápagos ants. Period I: 1877–1933; Period II: 1933 until the end of the 1990's; Period III: 2000 onwards. The following references correspond to the years listed in the figure: 1877 = Smith (1877); 1893 = Emery (1893); 1919 = Wheeler (1919); 1924 = Wheeler (1924); 1933 = Wheeler (1933); 1972 = Silberglied (1972); 1982 = Clark et al. (1982); 1984 = Lubin (1984); 1992 = (Snelling and Longino 1992); 1998 = Pezzatti et al. (1998); 2007 – 2011 = Pacheco et al. (2007), Herrera and Longino (2008), Herrera and Causton (2010), Lattke (2011); 2013 – 2014 = Herrera et al. (2013, 2014).

## Materials and methods

This paper is based on literature reviews and the study of 382,023 specimens deposited mostly in the Terrestrial Invertebrates Collection of the Charles Darwin Research Station (**ICCDRS**) as well as the collections of John T. Longino (**JTLC**), California Academy of Sciences (**CAS**), Quito Catholic Zoology Museum (**QCAZ**), the University of Texas Insect Collection (**UTIC**) and the Royal Belgian Institute of Natural Sciences (**RBINS**). We mapped the geographical distribution of the sampling events using the Free and Open Source QGIS. We revised and updated information on samples used for previous publications and indicated where this material is deposited. The list of subfamilies and species is ordered alphabetically. Specimens from the genus *Nylanderia* are currently under revision and are merged into *Nylanderia* spp. Accordingly, only previous literature records of *Nylanderia* species are included in the checklist. We implemented a similar approach for the only known from Galápagos subspecies of *Camponotus macilentus* Smith, 1877 and *Camponotus planus* Smith, 1877, for which the taxonomic key is only at species level. Neither the material examined, nor the vague descriptions found in old literature allowed us to morphologically discriminate between the proposed subspecies. The genus *Nylanderia* in Galápagos and the *Camponotus* (sub)species complexes will be addressed in future studies. Scanning images at high resolution were obtained using Scanning Electron Microscope (SEM) (Todokoro and Ezumi 1999) and z-stacked images available in AntWeb (Herrera 2019) were used to illustrate the key. Morphological terms referred to in the key (Fig. 2A–D), followed Eady (1968), Harris (1979), Bolton (1994), and Bolton et al. (2003). Locality terminology referring to

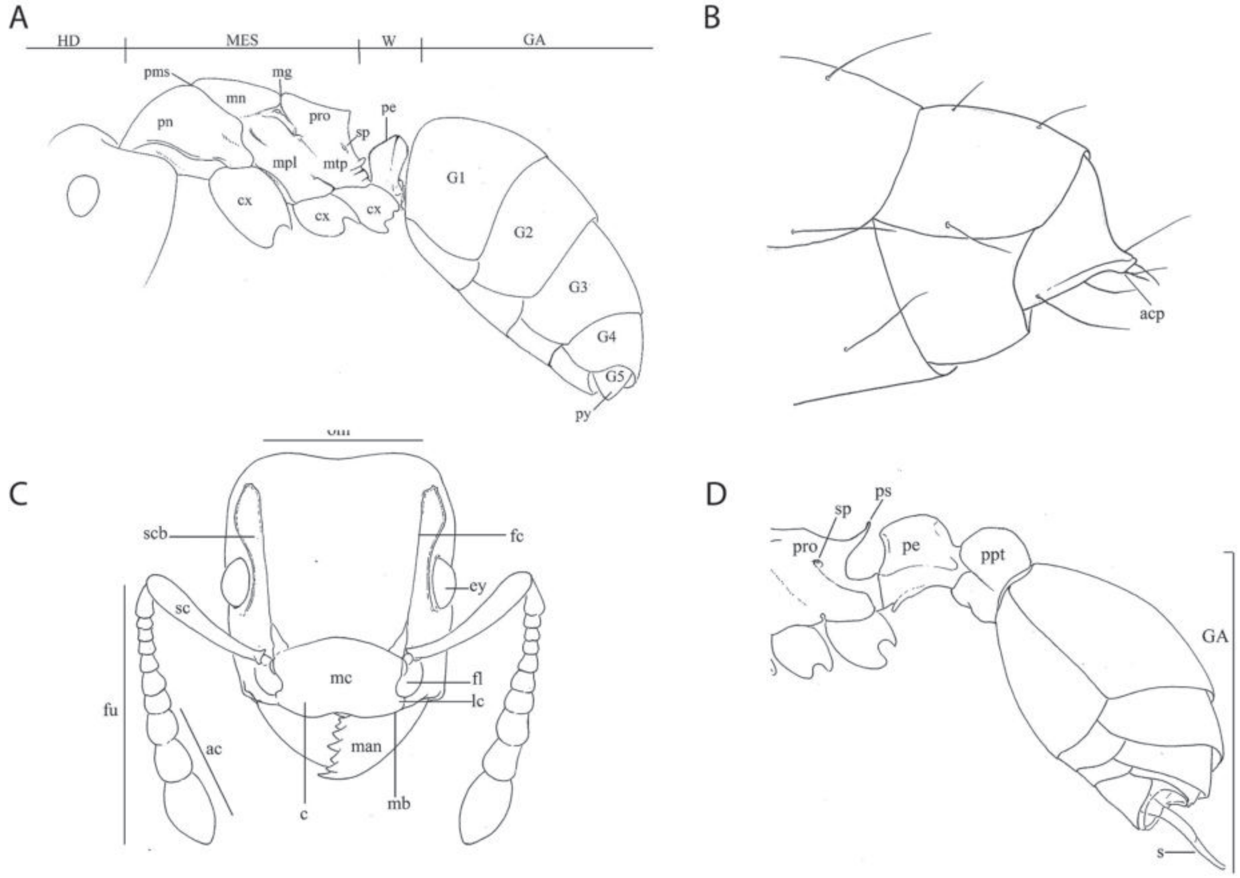

**Figure 2.** Glossary of terminology labeled from left to right **A** lateral view of a major worker of *Camponotus planus* **B** profile view of terminal portion of gaster of *Paratrechina longicornis* (Latreille, 1802) **C** frontal view of *Tetramorium bicarinatum* (Nylander, 1846) **D** lateral view of *Tetramorium bicarinatum*. Abbreviations: ac = antenna club; acp = acidopore; c = clypeus; cx = coxa; ey = eye; fc = frontal carina; fl = frontal lobe; fu = funiculus; GA = gaster; G1, 2, 3, 4, 5 = gastral segments 1–5; HD = head; lc = lateral portion of clypeus; man = mandible; mb = basal margin of mandible; mc = median portion of clypeus; MES = mesosoma; mg = metanotal groove; mn = mesonotum; mpl = mesopleuron; mtp = metapleuron; om = occipital margin; pe = petiole; pms = promesonotal; pn = pronotum; pro = propodeum; ppt = post-petiole; ps = propodeal spine; py = pygidium; s = sting; sc = scape scb = scrobe; sp = spiracle.

the different volcanoes on Isabela Island is as follows: Alcedo Crater (**CA**), Volcano Alcedo (**VA**), Volcano Ecuador (**VE**), Volcano Darwin (**VD**), Volcano Sierra Negra (**SN**), and Volcano Wolf (**VW**).

## Results

Five subfamilies of Formicidae can be found in the Galápagos: Dolichoderinae, Dorylinae, Formicinae, Myrmicinae, and Ponerinae, representing 22 genera, 50 species and 25 subspecies. The subfamily Myrmicinae is the largest with 32 species, while only one species on the islands represents Dorylinae, *Cylindromyrmex whymperi* (Cameron, 1891). The introduced species *Solenopsis globularia* (Smith, 1858) (on 35 islands, islets, and/or rocks), *Tetramorium bicarinatum* (Nylander, 1846) (on 33), *Cardiocondyla emeryi* Forel, 1881 (on 30), *Monomorium floricola* (Jerdon, 1851) (on 27), *Camponotus zonatus* Emery, 1894 (on 24), *Tetramorium lanuginosum* Mayr, 1870 (on 24), *Wasmannia auropunctata* (on 21), *Solenopsis geminata* (Fabricius, 1804) (on 20), and

*Tapinoma melanocephalum* (Fabricius, 1793) (on 18), are the most widely distributed species in the archipelago. Among the putative endemic species (8, Herrera et al. 2020), *Leptogenys santacruzi* Lattke, 2011 is most rare, with only a few records from the islands of Santa Cruz and Santiago.

## Discussion

We report 50 species and 25 subspecies of ants from 22 genera from the Galápagos Islands. The number of new species and locality records in the last 15 years combined with the fact that many islands are still highly understudied demonstrates that considerable work still needs to be done to identify and understand the islands' ant diversity.

Of the species recorded in this checklist, there are still dubious records. This is the case for *Camponotus senex*, *Crematogaster crinosa*, and *Solenopsis saevissima* (Wheeler 1924; Crocker 1933; Peck et al. 1998). Recent fieldwork, extensive studies and revision of old collections could not confirm their presence in the archipelago. Wheeler (1924) defined *C. senex* as a species that is unlikely to be present in the Galápagos, while Trager (1991) and Pacheco et al. (2007) did not mention *S. saevissima* as part of the fauna of the archipelago. Regarding *C. crinosa*, this species could have been sampled from locations outside the archipelago by Mr. Maurice Willows during the Templeton Crocker Expedition (Crocker 1933). Wheeler (1924) cataloged this record as unexpected in the Galápagos. These three species are not included in the taxonomic keys in this work. Furthermore, the records of *Anoplolepis gracilipes* (Smith, 1857), *Camponotus planatus* Roger, 1863, *Strumigenys godeffroyi* Mayr, 1866, *Tetramorium pacificum* Mayr, 1870, and *Pseudoponera stigma* (Fabricius, 1804) in the Galápagos (McGlynn 1999) are considered doubtful due to potential misidentification of these species. It is also possible that these species were collected on recently arriving in Galápagos and that they did not establish. As such, these species are not included in this species checklist.

Regarding the genus *Camponotus*, our studies suggest that the identification of the introduced ant *Camponotus zonatus* may have been confused with that of the only known from Galápagos species *C. macilentus*. This confusion is of particular interest regarding ecological studies that have cited the abundance of *C. macilentus*, which is typically more cryptic (McMullen 2011). Material examined retrospectively by the first author, collected by Pezzatti et al. (1998), von Aesch and Cherix (2005), and von Aesch (2006), showed that *C. zonatus* was collected during these field trips, nevertheless, this ant is not mentioned in any of these papers. Some of the records for the subspecies of *Camponotus* are also questioned for putative subspecies of *C. macilentus* and *C. planus* in the archipelago, and for now, we have only cited the records of Wheeler (1919, 1924, 1933) and Stitz (1932). Lastly, for the genus *Nylanderia*, future taxonomic and genetic studies are necessary to understand the number of species present and their status in Galápagos.

Although efforts in the last two decades have substantially increased our knowledge of the ant fauna of the Galápagos Islands, a good portion of the material studied during the last 15 years came from surveys that were not focused on ants. Ants remain poorly studied, and systematic sampling of the archipelago is necessary. Apart from Santa Cruz (in 1982, 1984) and Floreana (in 1997 and 2005) (Clark et al. 1982; Lubin 1984; Pezzatti et al. 1998; von Aesch 2006; HWH unpublished data), none of the other islands have been sampled extensively

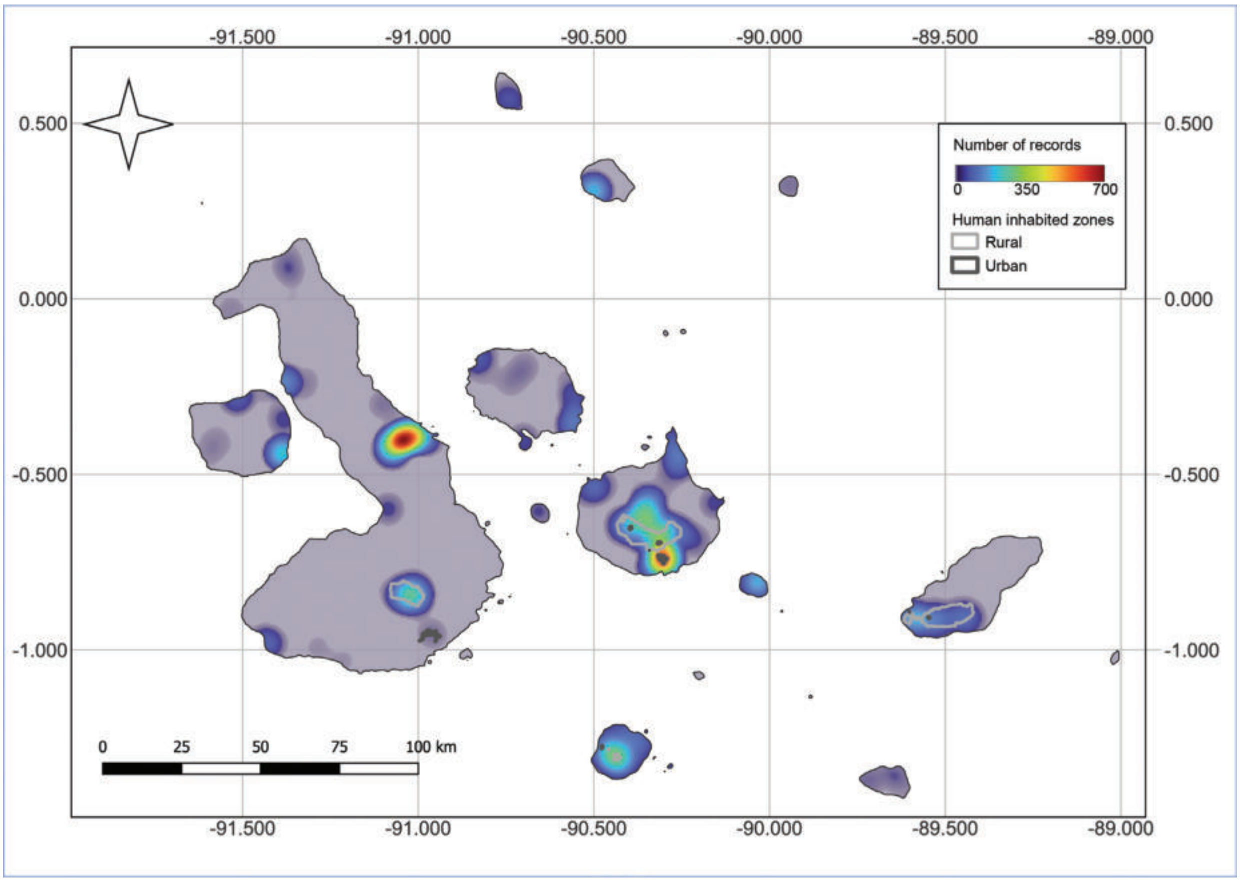

**Figure 3.** Heatmap highlighting the distribution of ant samples taken from 1963 to 2022. Regions indicated in pale purple have not yet been sampled for ants.

(Fig. 3). As a result, a multi-institutional project was initiated in 2020 to remedy this by surveying all islands. In addition, revision of taxonomic material in yet unexplored collections is underway. Revisions of these collections and systematic field surveys will provide the much-needed information to understand the role of ant species in ecosystem processes in the Galápagos as well as for prioritizing the management of introduced and invasive species and protecting endemic species.

## Checklist and identification keys

### Key to the subfamilies of the Galápagos Islands

1 Mesosoma attached to the gaster by a single intermediate segment, the petiole (Fig. 44C) ........................................ **2**

– Mesosoma attached to the gaster by two intermediate segments, the petiole, and post-petiole (Fig. 36C) ........................................ **Myrmicinae**

2 Gaster with a slight to remarkable constriction between its first and second segments (Fig. 45C); in the first case mandibles elongated (Fig. 48C); last segment of the gaster with sting, sometimes visible ........................................ **3**

– Gaster without constriction between its first and second segments (Fig. 8D); never with long and slender mandibles; last segment of the gaster without sting ........................................ **4**

3 Pygidium with small spines or denticles (Fig. 7C); antennal scape short and robust, never surpassing the middle of the eyes; funiculus robust, with segments increasing progressively in size toward the apex; head in frontal view with frontal carinae very well marked, and with thick longitudinal ridges running from occipital margin towards the clypeus (Fig. 7D).......... ........................................................ (**Dorylinae**) ***Cylindromyrmex whymperi***

– Pygidium without spines or denticles (Fig. 44D); antennal scape surpassing the middle of the eyes (long and slender); head in frontal view without ridges ..............................................................................................**Ponerinae**

4 Apex of abdomen with a circular orifice surrounded by a fringe of short setae, the acidopore, formed from the hypopygium (Fig. 8E) ... **Formicinae**

– Apex of abdomen without acidopore (Fig. 4D) .................. **Dolichoderinae**

## Key to species and subspecies of the subfamily Dolichoderinae

1 In lateral and dorsal views, petiole visible (Fig. 4B, D); cluster of long hairs located in the ventral surface of the head, the psammophore (Fig. 4E); dorsopropodeum with cone (Fig. 4D); head and mesosoma reddish brown, gaster, funiculus of antenna, petiole, and legs brownish black (Fig. 5B) *Dorymyrmex*)...................................***Dorymyrmex pyramicus albemarlensis***

– Petiole squamiform and notably reduced, in lateral and dorsal view, hidden under the first segment of the gaster (Fig. 5B, E); psammophore lacking on the ventral surface of the head; propodeum without cone on the dorsum (Fig. 5D) (*Tapinoma*)........................................................................**2**

2 Small (~ 1.5 mm), head mesosoma and antennae pale brown, legs and gaster pale yellow (Fig. 5A, B); anterior margin of clypeus relatively straight (Fig. 5C).............................................................***Tapinoma melanocephalum***

– Ants measuring ~ 2 mm with body and legs brown-gray (Fig. 6A, B); anterior base of clypeus slightly concave in the middle (Fig. 6C)...................... ..........................................................................................***Tapinoma* sp. hh07**

### Genus *Dorymyrmex* Mayr, 1866

### *Dorymyrmex pyramicus albemarlensis* Wheeler, 1919

Fig. 4

**Remarks.** In Wheeler (1924) [CAS], Wheeler (1933). Cited as *Conomyrma pyramica albemarlensis* (Linsley and Usinger 1966), *Conomyrma* sp. (Clark et al. 1982) [ICCDRS], *C. pyramica* (Lubin 1983), *C. albemarlensis*, *C. pyramica* (Lubin 1984), *C. albemarlensis* (Lubin 1985), *Conomyrma* sp. (Meier 1994), *Dorymyrmex pyramicus* (Abedrabbo 1994) [ICCDRS] and *C. albemarlensis* (de la Vega 1994). Registered also in Roque-Albelo et al. (2000) [ICCDRS], Herrera and Causton (2010) [ICCDRS], Herrera (2015), Herrera (2019) and Herrera et al. (2020) [ICCDRS, RBINS].

**Taxonomic history**. Kempf (1972), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution**. Possibly endemic: Baltra, Bartolomé, Daphne Mayor, Edén, Española, Fernandina, Genovesa, Isabela (VA, VD, VW), Marchena, Pinta, Rábida, Santa Cruz, Santa Fé, Santiago (Herrera et al. 2020).

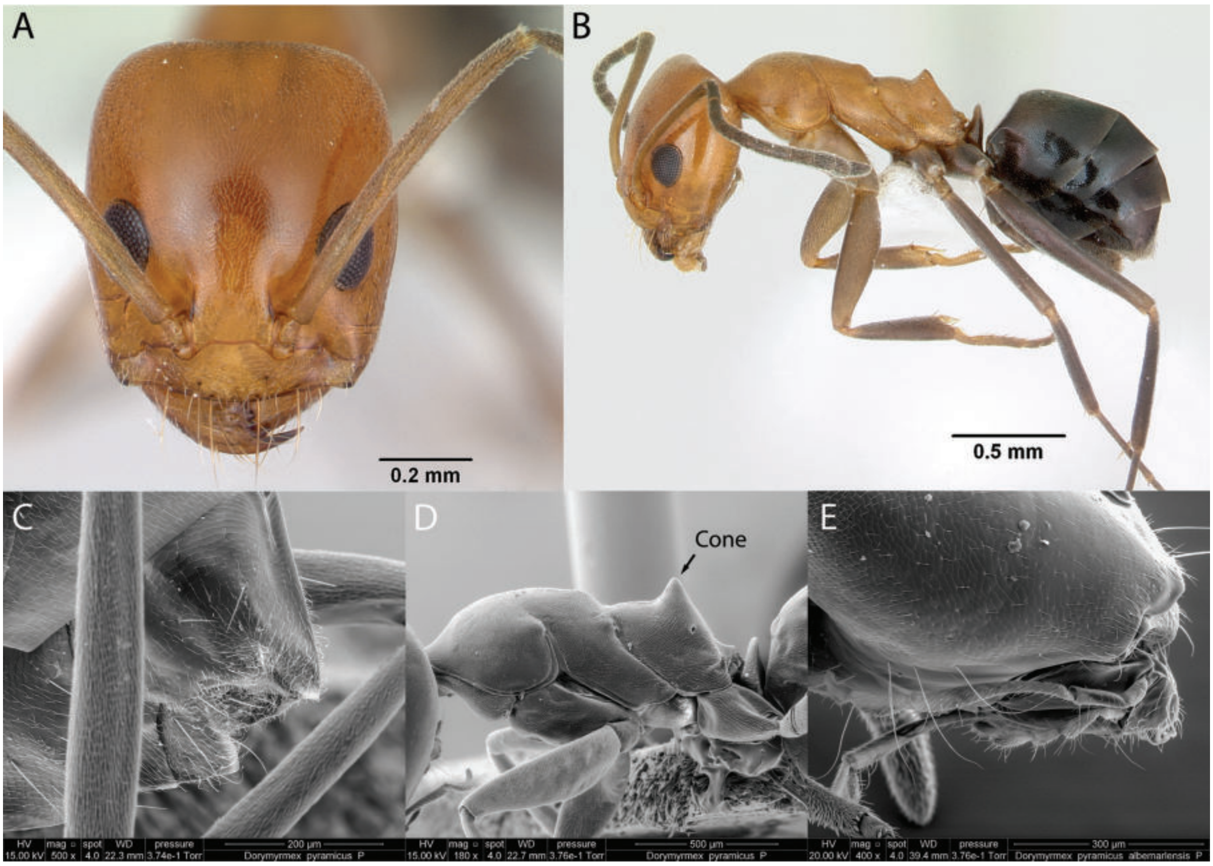

**Figure 4.** *Dorymyrmex pyramicus albemarlensis* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** apex of abdomen **D** mesosoma in profile **E** maxillary and labial palps.

### Genus *Tapinoma* Foerster, 1850

### *Tapinoma melanocephalum* (Fabricius, 1793)
Fig. 5

**Remarks.** Originally described as *Formica melanocephalum* (Fabricius, 1793). First published record Emery (1893), cited also in Wheeler (1919) [CAS], Wheeler (1924), Linsley and Usinger (1966), Clark et al. (1982) [ICCDRS], Lubin (1984) [ICCDRS], McMullen (1987 1990, 1993), Abedrabbo (1994) [ICCDRS], Brandão and Paiva (1994), de la Vega (1994), Meier (1994) [ICCDRS], Peck et al. (1998), Pezzatti et al. (1998) [ICCDRS], Roque-Albelo et al. (2000) [ICCDRS], von Aesch and Cherix (2005) [ICCDRS], Boada (2005) [ICCDRS], von Aesch (2006) [ICCDRS], Causton et al. (2006), McMullen (2009), Herrera and Causton (2010) [ICCDRS], McMullen (2012), Chamorro et al. (2012) [ICCDRS], Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2016) [ICCDRS, RBINS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS, RBINS].

**Taxonomic history**. Kempf (1972), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution**. Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution**. Introduced: Albany, Baltra, Champion, Española, Fernandina, Floreana, Genovesa, Isabela (CA, SN, VA), Marchena, Pinta, Plaza Sur, Rábida, Santiago, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé (Herrera et al. 2020).

**New record**. Mariela Mediana Islet.

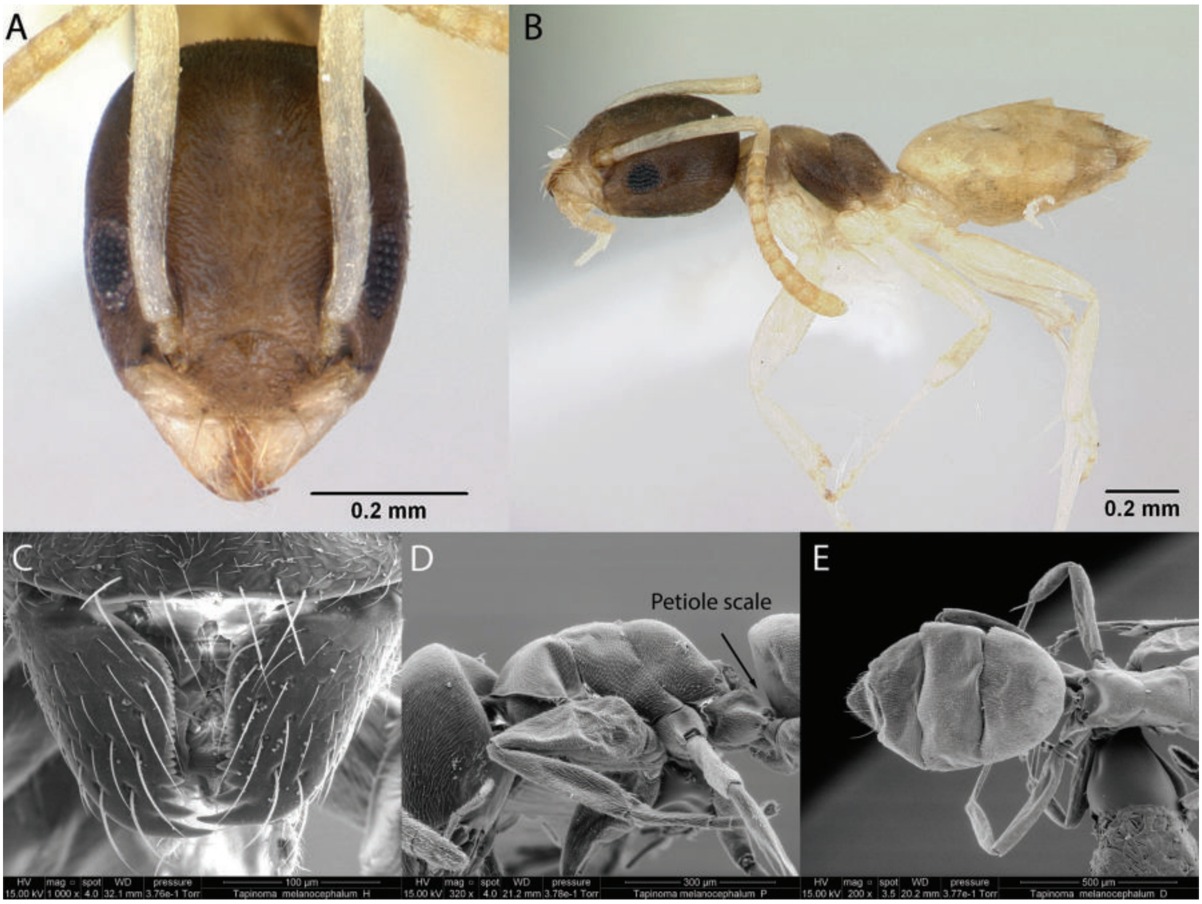

**Figure 5.** *Tapinoma melanocephalum* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up mandibles showing dentition **D** mesosoma in profile **E** gaster in dorsal view.

### *Tapinoma* sp. hh07
Fig. 6

**Remarks.** In Herrera et al. (2014) [ICCDRS], Herrera (2015), and Herrera et al. (2020) [ICCDRS].

**Distribution.** Undetermined origin: Santa Cruz (Herrera et al. 2014).

## Genus *Cylindromyrmex* Mayr, 1870

### *Cylindromyrmex whymperi* (Cameron, 1891)
Fig. 7

**Remarks.** Originally described as *Holcoponera whymperi* (Cameron, 1891). Cited as *Cylindromyrmex striatus* in Wheeler (1919) [CAS]. *Cylindromyrmex williamsi* in Wheeler (1924). *Cylindromyrmex striatus tibialis* in Stitz (1932). *Cylindromyrmex williamsi* in Linsley and Usinger (1966), *Cylindromyrmex* sp. in Silberglied (1972). *Cylindromyrmex striatus* in Lubin (1984), *Cylindromyrmex* sp. in de la Vega (1994). *Cylindromyrmex whymperi* in De Andrade (1998), *Cylindromyrmex striatus* in Causton et al. (2006), *Cylindromyrmex whymperi* Herrera and Causton (2010) [ICCDRS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

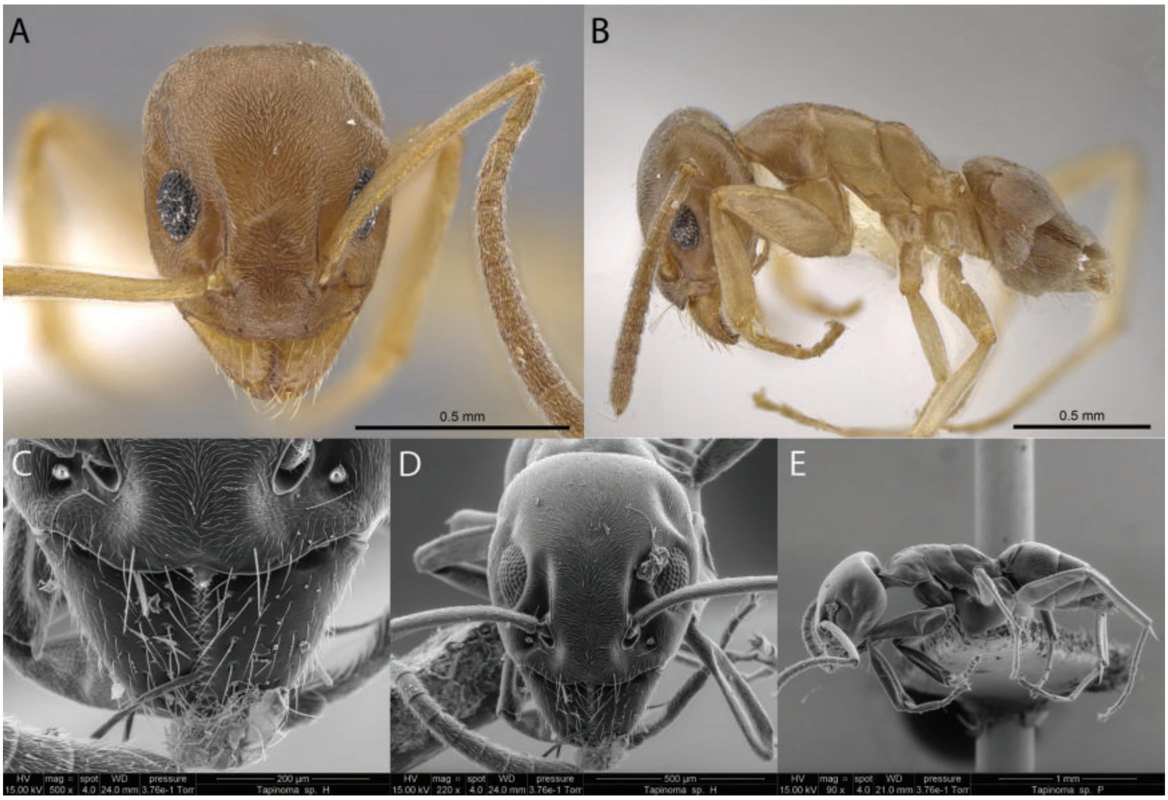

**Figure 6.** *Tapinoma* sp. hh07 worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up mandibles showing dentition **D** head in full-face view **E** view in profile.

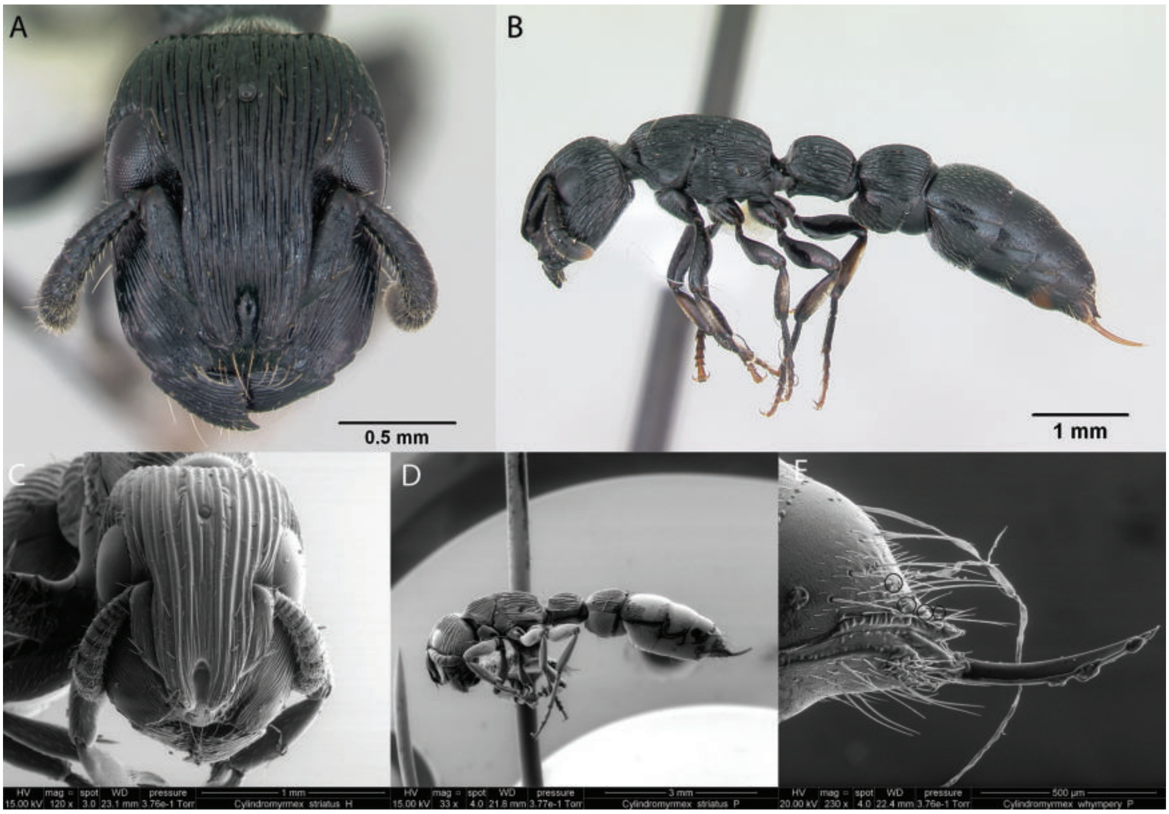

**Figure 7.** *Cylindromyrmex whymperi* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** view in profile **E** stinging apparatus. The small circles indicate spines on the pygidium.

**Taxonomic history**. Kempf (1972), Bolton (1995, 2014), De Andrade (1998), Bolton et al. (2006).

**Distribution**. Neotropical.

**Galápagos distribution**. Introduced: Baltra, Fernandina, Isabela (VA, VW), Santa Cruz (Herrera and al. 2020).

**New record**. Santiago Island.

## Key to the genera and species of the subfamily Formicinae

1 Antenna, including scape, with 9 segments (Fig. 8C) (*Brachymyrmex*) .......... ***Brachymyrmex heeri***

– Antenna, including scape, with > 9 segments (Fig. 11C) .......... **2**

2 Polymorphic, minor workers > 4 mm (total length); antennal insertions located distantly from posterior margin of the clypeus (Fig. 11D); head in dorsal view with frontal carinae (Fig. 11D) (*Camponotus*) .......... **3**

– Monomorphic, workers of small size, < 4 mm (total length), with antennal insertions located near to posterior margin of clypeus (Fig. 12A, C); head in dorsal view with frontal carinae hardly visible (Fig. 11C) .......... **5**

3 In lateral view, promesonotum and dorsum of propodeum flat; propodeal declivity angulate (Fig. 11E); short and erect hairs distributed evenly along mesosoma; head, mesosoma, and gaster black with antennae and legs reddish (Fig. 11A, B) .......... ***Camponotus planus***

– In lateral view, promesonotum and propodeum rounded until the base of the declivity of propodeum, forming a single convexity (Figs 9B, E,10B, C); long and erect hairs distributed unevenly along mesosoma; ants yellowish (Figs 9B, 10B) .......... **4**

4 Longitudinal carina visible in middle of the clypeus (major workers); head in frontal view with frontal carinae closing towards the middle of eyes; mesosoma with > 10 erect hairs (Fig. 9B, E) .......... ***Camponotus zonatus***

– Longitudinal carina in the middle of clypeus inconspicuous or absent (major workers); head in frontal view with frontal carinae opening from base of fronto-clypeal suture towards middle of eyes; mesosoma with < 10 erect hairs (Fig. 10B, C) .......... ***Camponotus macilentus***

5 Scape obviously elongate without erect setae and extending at least twice the length of the head in lateral view (Fig. 13D); mandibles with 5 teeth; mesosoma smooth with absence of appressed hairs (Fig. 13B, E) (*Paratrechina*) .......... ***Paratrechina longicornis***

– Scape with abundant erect setae and never extending twice the length of the head in lateral view (Fig. 12C, D); mandible with 6 or 7 teeth; mesosoma with appressed hairs (Fig. 12E) (*Nylanderia*) .......... **6**

6 Head, mesosoma, gaster and legs dark brown with trochanters yellowish; mesopleuron and metapleuron smooth and shiny (Fig. 12A, B) .......... ***Nylanderia steinheili***

– Species without combination of characteristics described above .......... ***Nylanderia* spp**.

### Genus *Brachymyrmex* Mayr, 1868

### *Brachymyrmex heeri* Forel, 1874
Fig. 8

**Remarks.** First published record in Herrera and Longino (2008) [ICCDRS]. Cited as *Brachymyrmex* sp. in Causton et al. (2006). *Brachymyrmex heeri* in Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2014) [ICCDRS], Wauters et al. (2016) [ICCDRS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history**. Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Nearctic, Neotropical, and Palearctic.

**Galápagos distribution**. Introduced: Floreana, Isabela (SN, VE), Marchena, San Cristóbal, Santa Cruz (Herrera et al. 2020).

### Genus *Camponotus* Mayr, 1861

### *Camponotus zonatus* Emery, 1894
Fig. 9

**Remarks.** First published record (Herrera and Causton 2010) [ICCDRS]. Cited in Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS, RBINS].

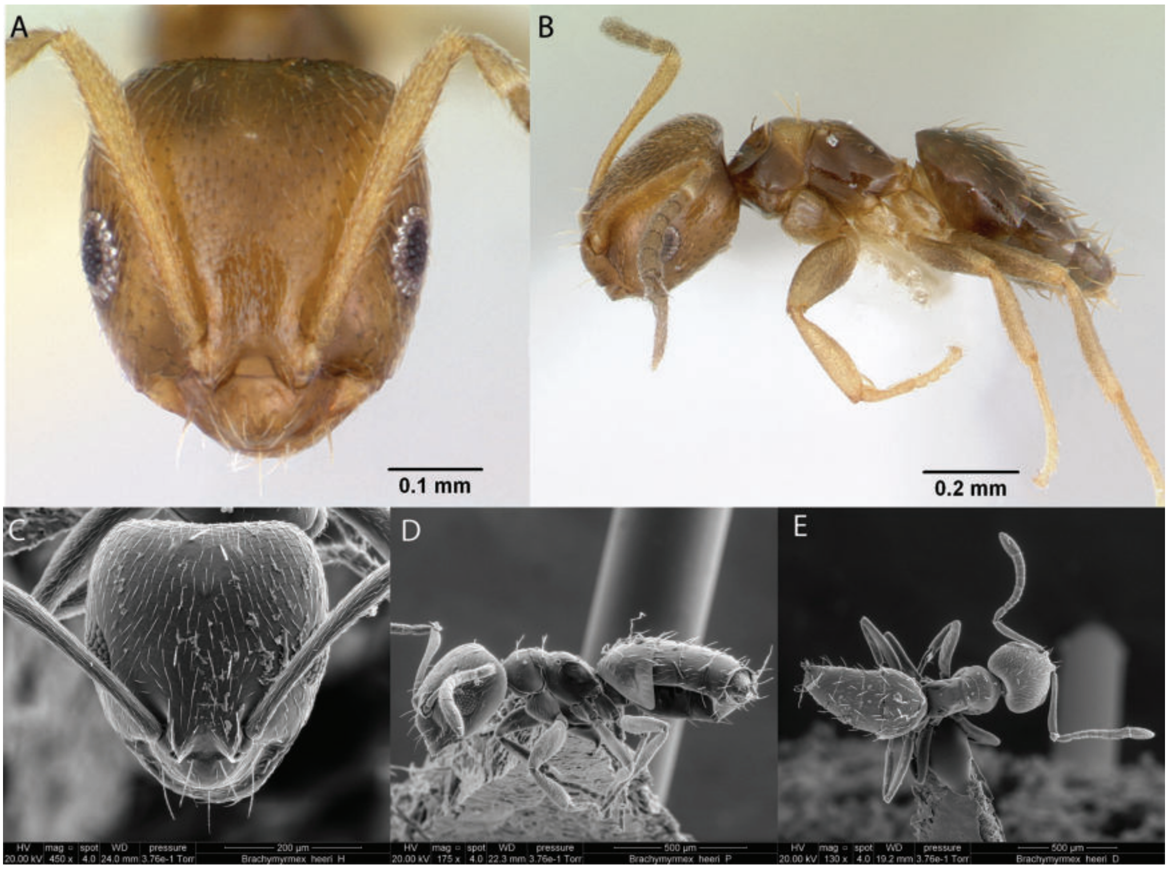

**Figure 8.** *Brachymyrmex heeri* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** view in profile **E** head and antenna in dorsal view.

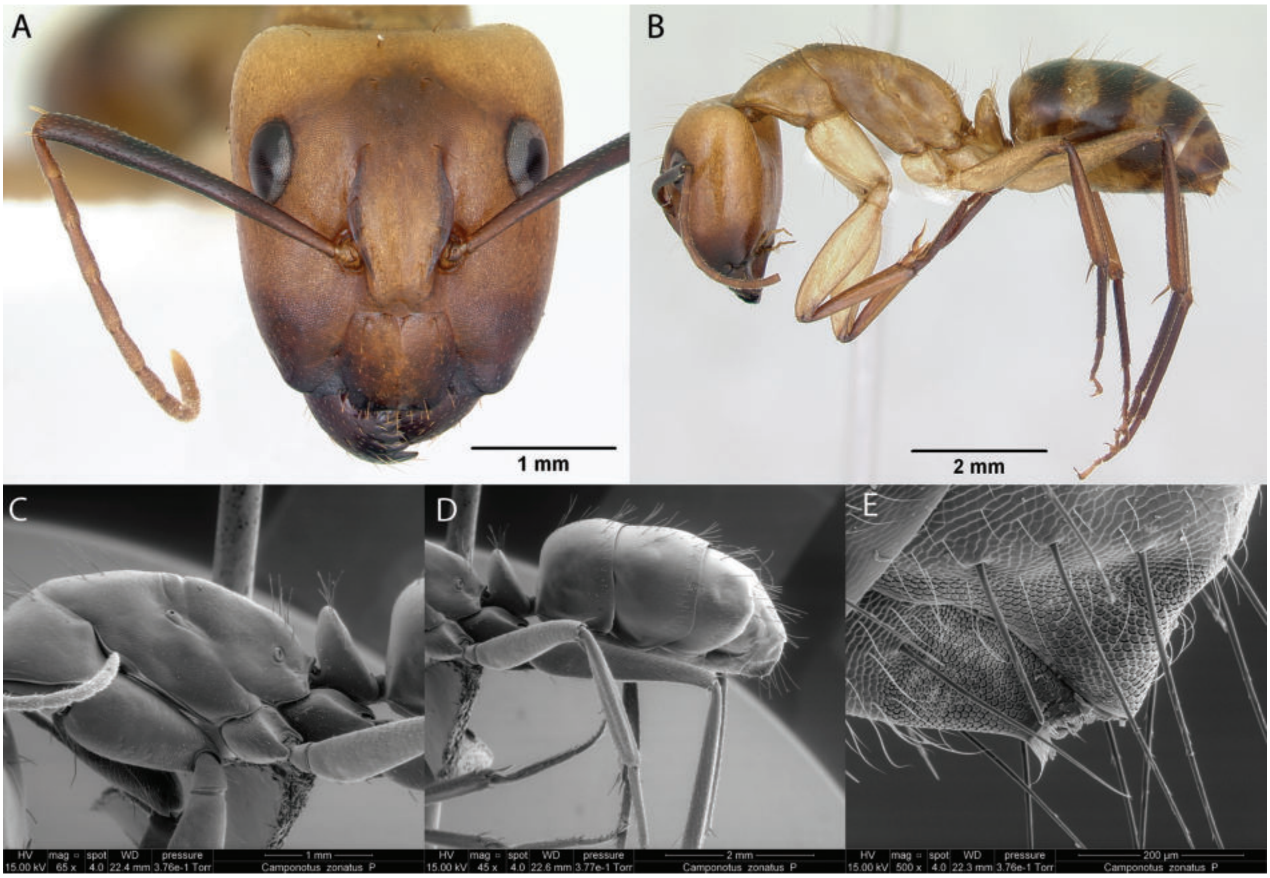

**Figure 9.** *Camponotus zonatus* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** gaster in profile view **E** close up of acidopore.

**Taxonomic history**. Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Neotropical.

**Galápagos distribution**. Introduced: Bainbridge #1, Bainbridge #3, Bainbridge #4, Bainbridge #5, Bainbridge #6, Baltra, Champion, Cuevas, Daphne Mayor, Eden, Floreana, Genovesa, Isabela (CA, SN, VA, VD, VW), Mao, Marchena, Pinta, Pinzón, Plaza Norte, Plaza Sur, San Cristóbal, Santa Cruz, Santa Fé, Santiago, Seymour Norte (Herrera et al. 2020).

### ***Camponotus macilentus*** **Smith, 1877**

Fig. 10

**Remarks.** Cited as *Camponotus* (*Myrmamblys*) *macilentus* in Wheeler (1919). *Camponotus* (*Pseudocolobopsis*) *macilentus* in Emery (1920). *Camponotus* (*Pseudocolobopsis*) *macilentus macilentus* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* in Kempf (1972). *Camponotus macilentus* in Clark et al. (1982), Lubin (1983) [ICCDRS], Lubin (1984, 1985), Brandão and Paiva (1994), Meier (1994), Peck (1994b), Bolton (1995), Roque-Albelo et al. (2000) [ICCDRS], Boada (2005) [ICCDRS], McMullen (2011, 2012). Misidentification in Pezzatti et al. (1998) [ICCDRS], von-Aesch and Cherix (2005), von Aesch (2006) [ICCDRS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS, RBINS].

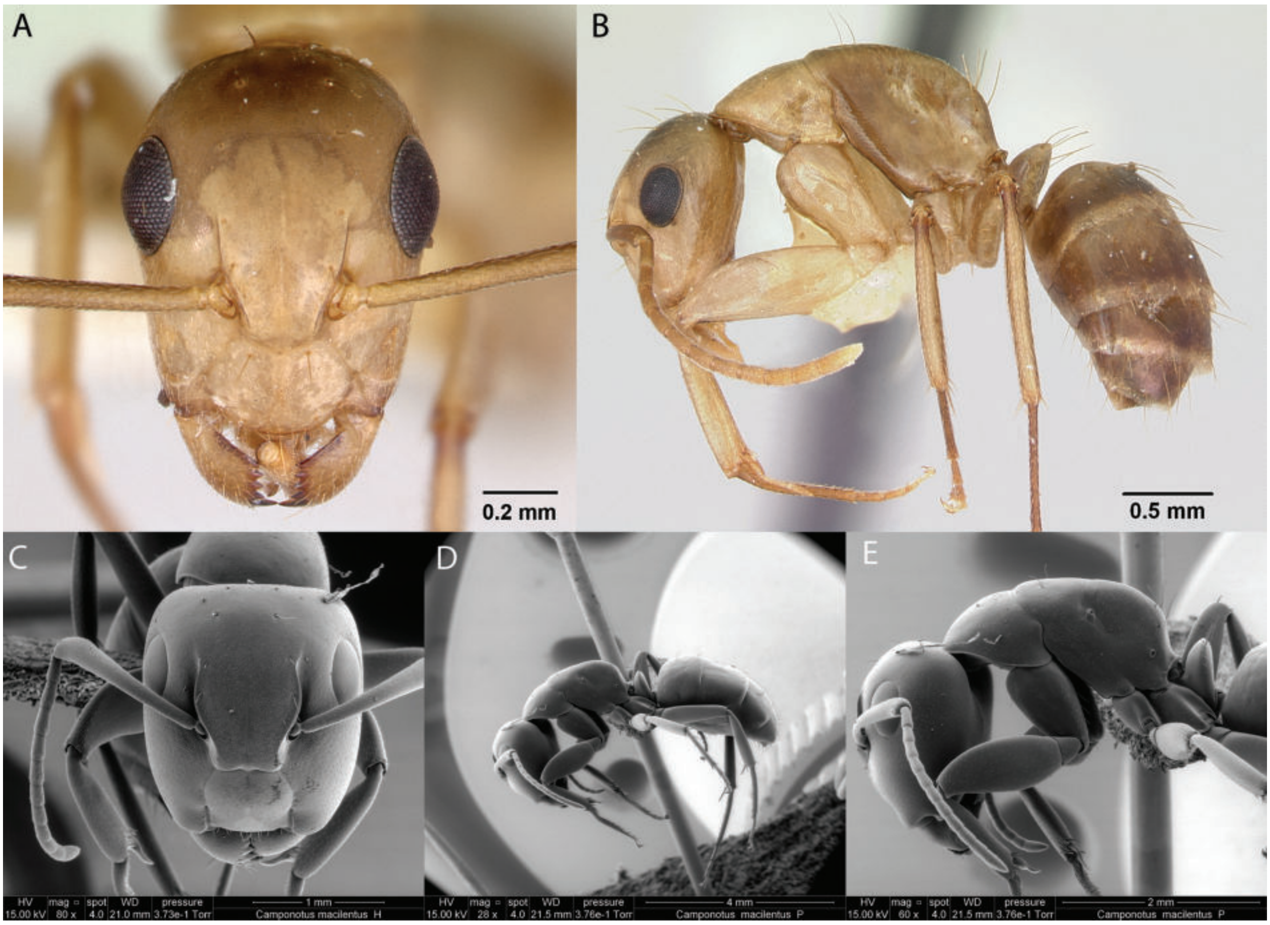

**Figure 10.** *Camponotus macilentus* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** view in profile **E**. mesosoma and head profile view.

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Baltra, Champion, Española, Fernandina, Floreana, Genovesa, Isabela (SN, VA, VD, VW), Marchena, Pinta, Pinzón, Plaza Norte, Rábida, Santa Cruz, Santa Fé, Santiago, (Herrera and al. 2020).

**Citations.**

***Camponotus macilentus albemarlensis*** **Wheeler**, **1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *albemarlensis* Wheeler, 1919: 284. *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *albemarlensis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus albemarlensis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *albemarlensis* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus albemarlensis* in (Bolton, 1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Isabela Island.

***Camponotus macilentus altinotus*** **Stitz**, **1932**. Cited as *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *altinota* Stitz, 1932: 370. *Camponotus* (*Pseudocolobopsis*) *macilentus altinotus* in Linsley and Usinger (1966). *Camponotus macilentus* var. *altinotus* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus altinotus* in (Bolton, 1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Floreana Island (Stitz 1932).

***Camponotus macilentus barringtonensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *barringtonensis* Wheeler, 1919: 282. *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *barringtonensis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus barringtonensis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *barringtonensis* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus barringtonensis* in (Bolton, 1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santa Fé Island (Wheeler 1919).

***Camponotus macilentus bindloensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *bindloensis* Wheeler, 1919: 286. *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *bindloensis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus bindloensis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *bindloensis* in Kempf (1972), *Camponotus* (*Pseudocolobopsis*) *macilentus bindloensis* in Bolton (1995). *Camponotus macilentus bindloensis* in Herrera (2015, 2019).

**Taxonomic history.** Bolton et al. (2006), Bolton (2014).

**Distribution.** Endemic: Marchena Island (Wheeler 1919).

***Camponotus macilentus castellanus* Wheeler, 1924**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *castellanus* Wheeler, 1924: 116. Cited as *Camponotus* (*Pseudocolobopsis*) *macilentus castellanus* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *castellanus* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus castellanus* Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Genovesa Island (Wheeler 1924).

***Camponotus macilentus duncanensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *duncanensis* Wheeler, 1919: 283. *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *duncanensis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus duncanensis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *duncanensis* in Kempf (1972). *Camponotus macilentus duncanensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Floreana, Pinzón Islands (Wheeler 1919, Stitz 1932).

***Camponotus macilentus hoodensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *hoodensis* Wheeler, 1919: 285. Cited ad *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *hoodensis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus hoodensis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *hoodensis* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus hoodensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Española Island (Wheeler 1919).

***Camponotus macilentus jacobensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *jacobensis* Wheeler, 1919: 280. *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *jacobensis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus jacobensis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *jacobensis* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus jacobensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santiago Island (Wheeler 1919).

***Camponotus macilentus narboroensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *narboroensis* Wheeler, 1919: 286. *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *narboroensis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus narboroensis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *narboroensis* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus narboroensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Fernandina Island (Wheeler 1919, 1933).

***Camponotus macilentus pervicus* Wheeler, 1924**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *pervicus* Wheeler, 1924: 115. *Camponotus* (*Pseudocolobopsis*) *macilentus pervicus* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *pervicus* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus pervicus* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santa Cruz Island (Wheeler 1924).

***Camponotus macilentus sapphirinus* Wheeler, 1924**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *sapphirinus* Wheeler, 1924: 114. Cited as *Camponotus* (*Pseudocolobopsis*) *macilentus sapphirinus* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *sapphirinus* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus sapphirinus* in Bolton (1995), Herrera (2015).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santa Cruz, Baltra Islands (Wheeler 1924).

***Camponotus macilentus vulcanalis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *vulcanalis* Wheeler, 1919: 284. *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *vulcanalis* in Emery (1925). *Camponotus* (*Pseudocolobopsis*) *macilentus vulcanalis* in Linsley and Usinger (1966). *Camponotus* (*Pseudocolobopsis*) *macilentus* var. *vulcanalis* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus vulcanalis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Isabela Island (Wheeler 1919).

***Camponotus macilentus wollebaeki* Stitz, 1932**. Cited as *Camponotus* (*Myrmamblys*) *macilentus* var. *wollebaeki* Stitz, 1932: 371. *Camponotus* (*Pseudocolobopsis*) *macilentus wollebaeki* in Linsley and Usinger (1966). *Camponotus macilentus* var. *wollebaeki* in Kempf (1972). *Camponotus* (*Pseudocolobopsis*) *macilentus wollebaeki* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Floreana Island (Stitz 1932).

### *Camponotus planus* Smith, 1877

Fig. 11

**Remarks.** Cited as *Camponotus* (*Myrmorhachis*) *planus* in Wheeler (1919), Emery (1920). *Camponotus* (*Myrmocladoecus*) *planus* in Wheeler (1924), Stitz (1932). *Camponotus* (*Myrmocladoecus*) *planus planus* in Linsley and Usinger (1966).

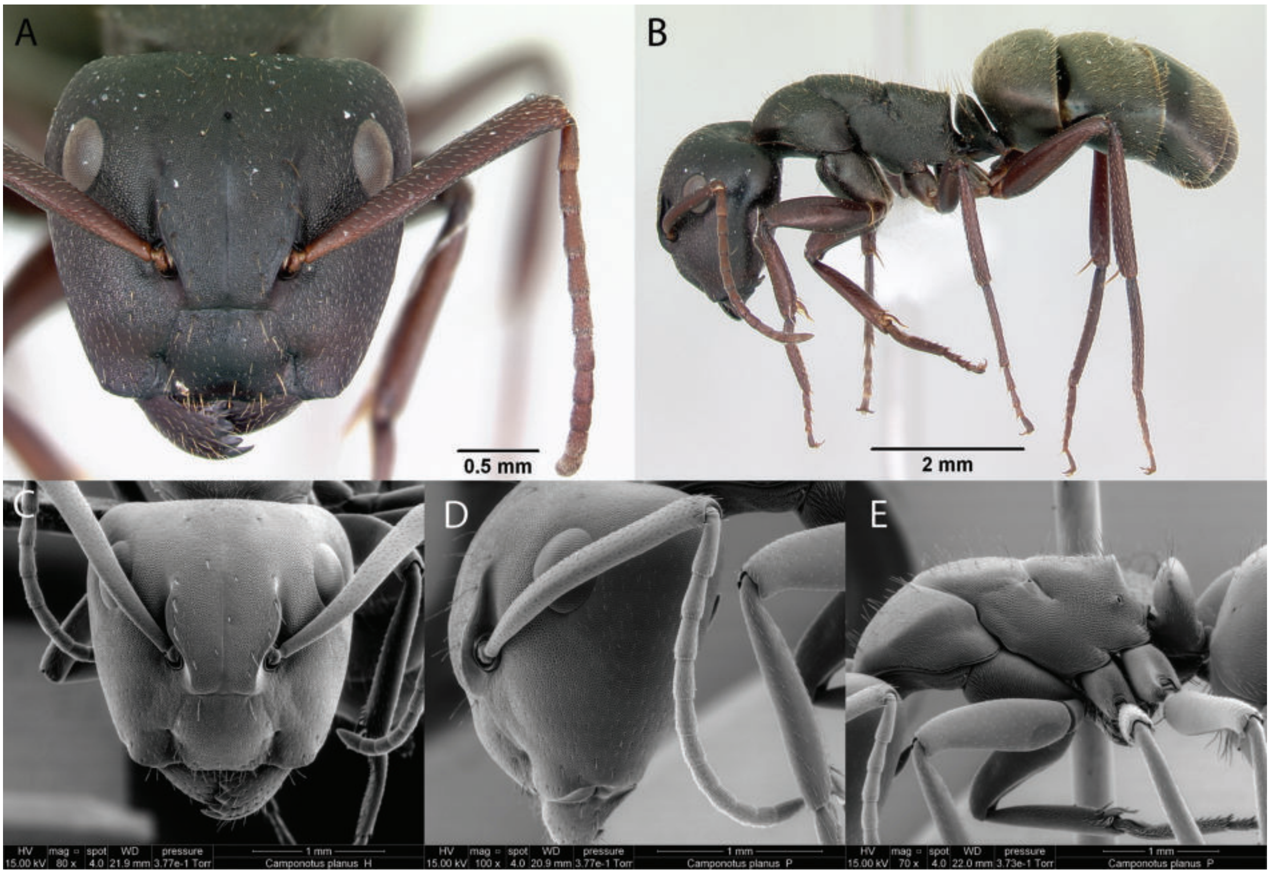

**Figure 11.** *Camponotus planus* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** head profile view **E** mesosoma in profile.

*Camponotus* (*Myrmocladoecus*) *planus* in Kempf (1972). *Camponotus planus* in Clark et al. (1982) [ICCDRS], Lubin (1983, 1984, 1985) [ICCDRS], McMullen (1993), Brandão and Paiva (1994), de la Vega (1994), Meier (1994) [ICCDRS]. *Camponotus* (*Myrmocladoecus*) *planus* in Bolton (1995). *Camponotus planus* in Pezzatti et al. (1998) [ICCDRS], Roque-Albelo et al. (2000) [ICCDRS], von Aesch and Cherix (2005) [ICCDRS], Boada (2005) [ICCDRS], von Aesch (2006) [ICCDRS], Jaramillo et al. (2010), Herrera and Causton (2010) [ICCDRS], Chamorro et al. (2012) [ICCDRS], Herrera (2015, 2019) [ICCDRS] and Wauters (2016) [ICCDRS; RBINS].

**Taxonomic history.** Kempf (1972), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Bainbridge #1, Baltra, Bartolomé, Cousin, Fernandina, Floreana, Isabela (CA, SN, VA, VD, VE, VW), Logie, Marchena, Pinzón, Plaza Sur, Rábida, Santiago, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé (Herrera et al. 2020).

**Citations.**

***Camponotus planus fernandinensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *fernandinensis* Wheeler, 1919: 296. *Camponotus* (*Myrmocladoecus*) *planus fernandinensis* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *fernandinensis* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus fernandinensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Fernandina Island (Wheeler 1919).

***Camponotus planus fidelis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *fidelis* Wheeler, 1919: 295. *Camponotus* (*Myrmocladoecus*) *planus* var. *fidelis* in Emery (1925). *Camponotus* (*Myrmocladoecus*) *planus fidelis* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *fidelis* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus fidelis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santa Fé (Wheeler 1919).

***Camponotus planus hephaestus* Wheeler, 1933**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *hephaestus* Wheeler, 1933: 59. *Camponotus* (*Myrmocladoecus*) *planus hephaestus* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *hephaestus* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus hephaestus* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Isabela Island (Wheeler 1933).

***Camponotus planus indefessus* Wheeler, 1919**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *indefessus* Wheeler, 1919: 294. *Camponotus* (*Myrmocladoecus*) *planus indefessus* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *indefessus* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus indefessus* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santa Cruz Island (Wheeler 1919).

***Camponotus planus isabelensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *isabelensis* Wheeler, 1919: 293. *Camponotus* (*Myrmocladoecus*) *planus isabelensis* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *isabelensis* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus isabelensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Isabela Island (Wheeler 1919, 1933).

***Camponotus planus peregrinus* Emery, 1893**. Cited as *Camponotus peregrinus* Emery, 1893: 91. *Camponotus* (*Myrmorhachis*) *planus peregrinus* in Wheeler (1919). *Camponotus* (*Myrmocladoecus*) *planus* var. *peregrinus* in Wheeler (1924), Stitz (1932). *Camponotus* (*Myrmocladoecus*) *planus peregrinus* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *peregrinus* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus peregrinus* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Floreana, San Cristóbal Island (Wheeler 1919; Stitz 1932; Wheeler 1933).

***Camponotus planus pinzonensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *pinzonensis* Wheeler, 1919: 297. *Camponotus* (*Myrmocladoecus*) *planus* var. *pinzonensis* in Emery (1925). *Camponotus* (*Myrmocladoecus*) *planus pinzonensis* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *pinzonensis* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus pinzonensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Pinzón Island (Wheeler 1919).

***Camponotus planus sansalvadorensis* Wheeler, 1924**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *sansalvadorensis* Wheeler, 1924: 119. Cited as *Camponotus* (*Myrmocladoecus*) *planus sansalvadorensis* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *sansalvadorensis* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus sansalvadorensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santiago Island (Wheeler 1924).

***Camponotus planus santacruzensis* Wheeler, 1919**. Cited as *Camponotus* (*Myrmorhachis*) *planus* var. *santacruzensis* Wheeler, 1919: 294. *Camponotus* (*Myrmocladoecus*) *planus* var. *santacruzensis* in Wheeler (1924). *Camponotus* (*Myrmocladoecus*) *planus santacruzensis* in Linsley and Usinger (1966). *Camponotus* (*Myrmocladoecus*) *planus* var. *santacruzensis* in Kempf (1972). *Camponotus* (*Myrmocladoecus*) *planus santacruzensis* in Bolton (1995), Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Endemic: Santa Cruz, Baltra Island (Wheeler 1919, 1924, 1933).

***Camponotus senex* (Smith, 1858).** Originally described as *Formica senex* (Smith, 1858). Cited in Smith (1877), Wheeler (1919). Doubtful record for Galápagos (Wheeler 1924). Cited also in Linsley and Usinger (1966), Kempf (1972), Brandão and Paiva (1994) and Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Neotropical.

**Galápagos distribution.** Uncertain: San Cristóbal Island (Smith 1877).

### Genus *Nylanderia* Emery, 1906

#### *Nylanderia fulva nesiotis* (Wheeler, 1919)

**Remarks.** Cited as *Prenolepis fulva nesiotis* in Wheeler (1919, 1924, 1933) [CAS]. As *Paratrechina fulva nesiotis* in Linsley and Usinger (1966) and *Nylanderia fulva nesiotis* in Kempf (1972), *Paratrechina nesiotis* in Lubin (1983, 1984, 1985), see also Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Neotropical.

**Galápagos distribution.** Introduced: Española, Isabela, Santiago, San Cristobal, Santa Cruz (Wheeler 1919, 1924, 1933).

#### *Nylanderia guatemalensis itinerans* (Forel, 1901)

**Remarks.** Cited as *Prenolepis vividula guatemalensis itinerans* in Wheeler (1919, 1924), *Nylanderia vividula guatemalensis* var. *itinerans* in Wheeler (1933) [CAS], *Paratrechina vividula itinerans* in Linsley and Usinger (1966), *Nylanderia guatemalensis* var. *itinerans* in Kempf (1972), *Paratrechina vividula itinerans* in Brandão and Paiva (1994) and *Paratrechina guatemalensis itinerans* in Pezzatti et al. (1998). See also Herrera (2015, 2019).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Neotropical.

**Galápagos distribution.** Introduced: Floreana, San Cristobal, Santa Cruz (Wheeler 1919, 1924, 1933).

### ***Nylanderia steinheili* (Forel, 1893)**

Fig. 12

**Remarks.** Cited as *Prenolepis steinheili* in (Forel, 1893). First record in Herrera et al. (2014), cited also in Dekoninck et al. (2014), Herrera (2015a. b), Wauters et al. (2016) [ICCDRS].

**Taxonomic history.** Kempf (1972), Brandão (1991), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Malagasy, Nearctic, Neotropical.

**Galápagos distribution.** Introduced: Floreana, Gardner (next to Floreana), Isabela (CA), Pinzón, San Cristóbal, Santa Cruz (Herrera et al. 2014, 2020) [ICCDRS].

**New record.** Santiago Island.

### ***Nylanderia vaga* (Forel, 1901)**

**Remarks.** Cited as *Prenolepis vaga* in (Forel, 1901). Cited as *Paratrechina vaga* in Clark et al. (1982), McMullen (1987), McMullen (1990), McMullen (1993), Causton et al. (2006) and McMullen (2007). Cited as possibly *N. vaga* in Pezzatti et al. (1998).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

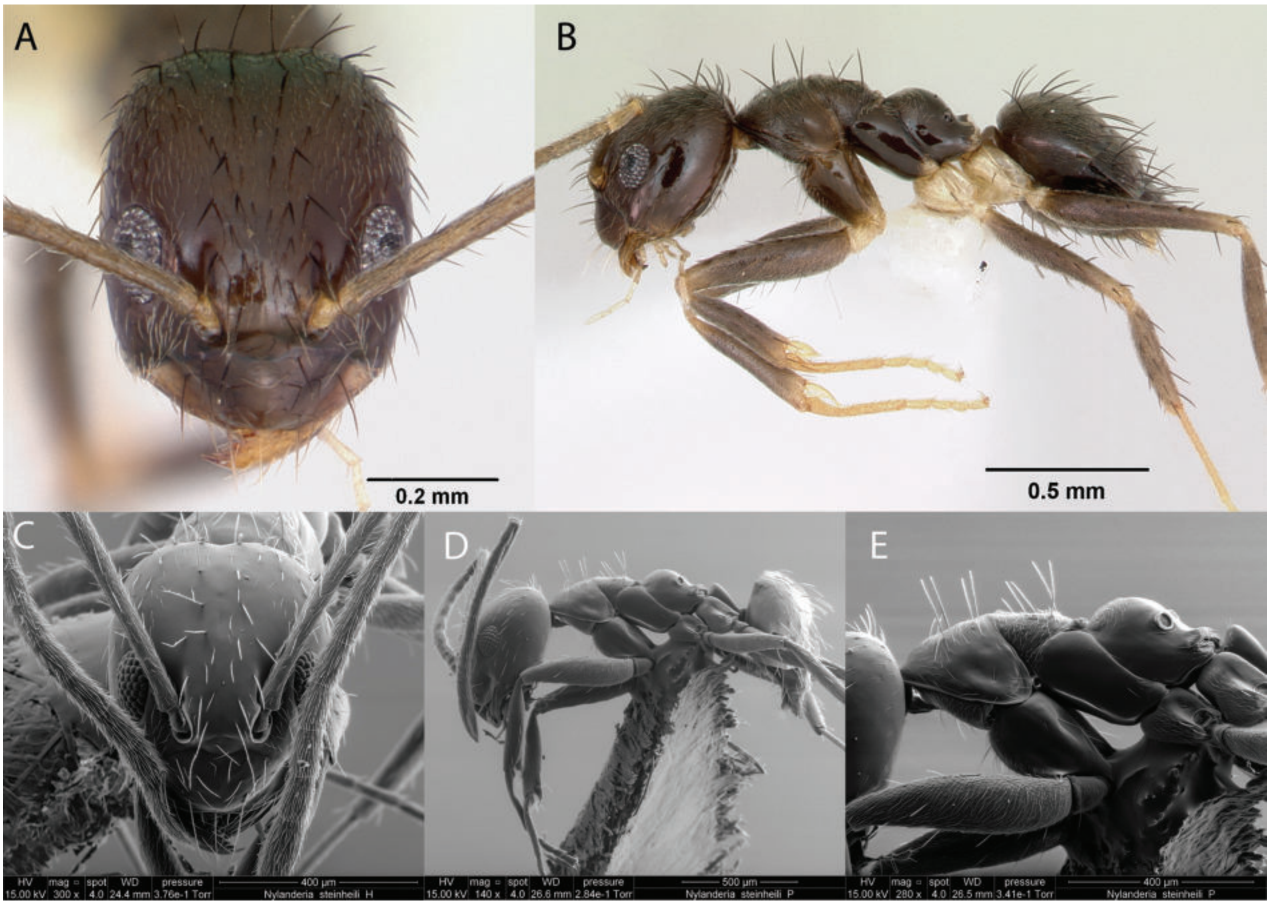

**Figure 12.** *Nylanderia steinheili* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** view in profile **E** mesosoma in profile.

**Distribution.** Australasia, Indomalaya, Neotropical, Oceania.

**Galápagos distribution.** Introduced: Floreana, Santa Cruz, Pinta (Clark et al. 1982; McMullen 1987 1990, 1993, 2007).

### Genus *Paratrechina* Motschoulsky, 1863

### *Paratrechina longicornis* (Latreille, 1802)

Fig. 13

**Remarks.** Cited as *Formica longicornis* in (Latreille, 1802). Cited as *Prenolepis longicornis* (Latreille, 1802) in Wheeler (1919), Wheeler (1924) and Stitz (1932). *Paratrechina longicornis* in Wheeler (1933) [CAS], Kempf (1972), Linsley and Usinger (1966), Lubin (1984) [ICCDRS], McMullen (1987), McMullen (1990), McMullen (1993), Brandão and Paiva (1994), Meier (1994) [ICCDRS], Pezzatti et al. (1998) [ICCDRS], von Aesch and Cherix (2005) [ICCDRS], Causton et al. (2006) [ICCDRS], von Aesch (2006) [ICCDRS]. Also, in Herrera and Causton (2010) [ICCDRS]. Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS, RBINS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

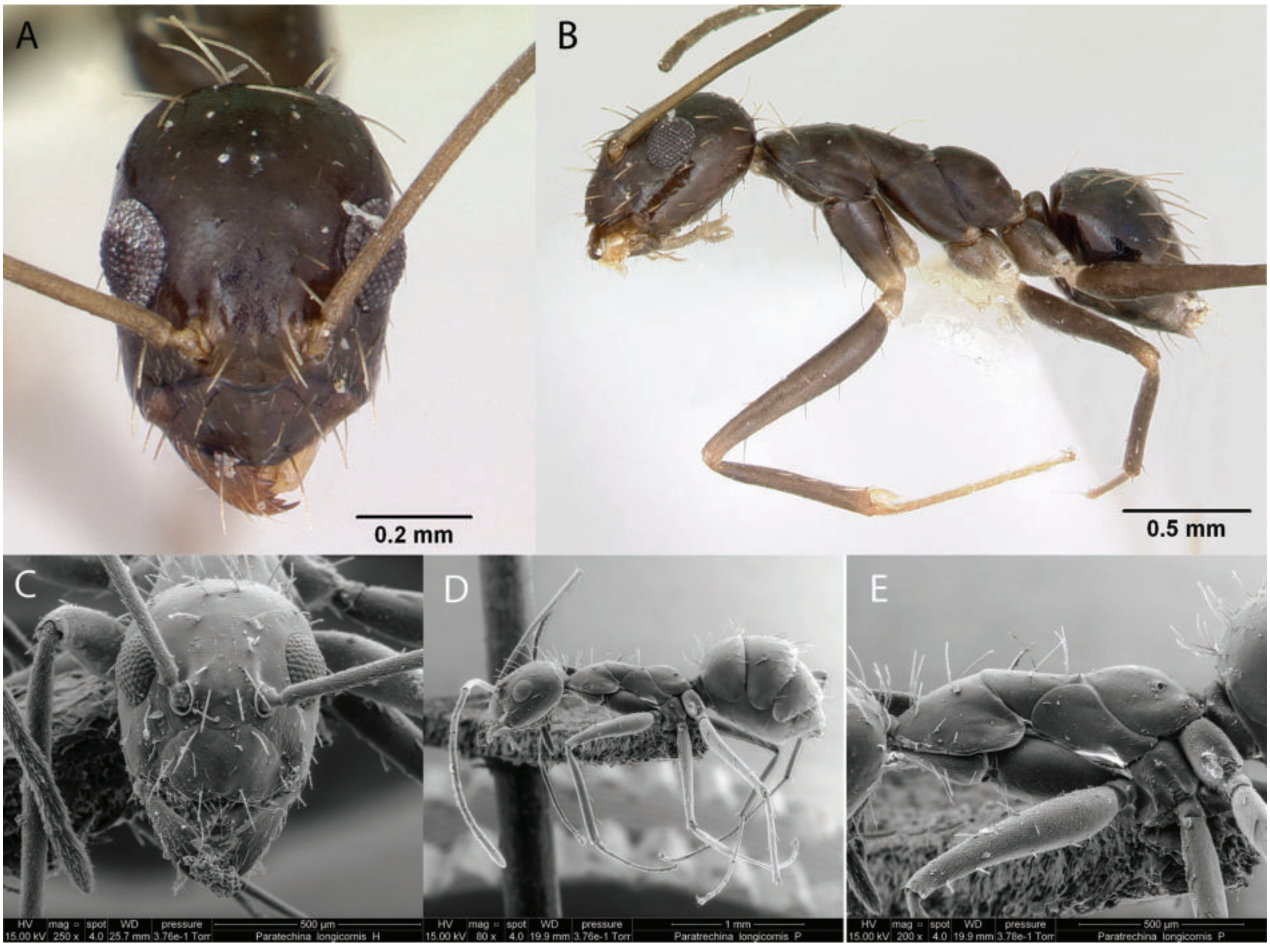

**Figure 13.** *Paratrechina longicornis* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** view in profile **E** mesosoma in profile.

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Baltra, Bartolomé, Champion, Española, Fernandina, Floreana, Gardner (next to Española), Isabela (SN, VA), Marchena, Pinta, Rábida, Santiago, San Cristóbal, Santa Cruz, Santa Fé, Seymour Norte (Herrera et al. 2020).

## Key to the genera and species of the subfamily Myrmicinae

1 Postpetiole attached to the dorsal surface of the first segment of the gaster (*Crematogaster*) (Fig. 17C)............................***Crematogaster* JTL – 022**

– Postpetiole attached on anterior surface of the first segment of the gaster (Figs 14C, 40C) .................................................................................**2**

2 Antenna with 12 segments, scape included (Fig. 14D) .............................**3**

– Antenna with < 12 segments: scape included (Figs 18C, 33C) ...............**19**

3 Antennal club of two segments (Fig. 14D); triangular mandible equipped with a tooth at the basal margin; median portion of clypeus bicarinate with 2 clypeal teeth in the anterior clypeal margin, pointing to the apical margin of the mandibles when these are almost closed (Fig. 14E). Eye composed of 3 ommatidia (Fig. 14F) (*Adelomyrmex*)............... ***Adelomyrmex longinoi***

– Antennal club diffuse or with 2 or 3 segments (Fig. 42A, C); mandible triangular with absence of teeth on the basal margin; pair of apical teeth at the anterior margin of clypeus absent (Fig. 42D)........................................**4**

4 Propodeum without spines (Figs 21C, 22F) ................................................**5**

– Propodeum armed with spines (Figs 16C, 38C, 37C) ................................**8**

5 Posterior surface of the head and propodeal dorsum transversely striate (Fig. 42E, F) (*Trichomyrmex*)............................... ***Trichomyrmex destructor***

– Posterior surface of the head and propodeal dorsum not transversely striate (Figs 22D, 23D); (*Monomorium*) ............................................................**6**

6 Head, mesosoma and gaster smooth and shiny (Fig. 21A, B, D, E); in lateral view mesosoma with > 4 erect setae (Fig. 21C); bicolored with mesosoma pale brown, head and gaster dark brown (Fig. 21A, B) ................................ .....................................................................................***Monomorium floricola***

– Head and mesosoma neither smooth nor shiny (Figs 22A, C, D, E, 23C, D, E); in lateral view mesosoma with ≤ 4erect setae (Fig. 22D), in dorsal and lateral view with appressed hairs (Fig. 23D, E)...........................................**7**

7 In lateral or dorsal view, pronotum with a pair of erect setae (Fig. 22D, E), in lateral view post-petiole almost the same size as petiole (Fig. 22B, F); ant yellowish in its entirety (Fig. 22B) ..........................***Monomorium pharaonis***

– In lateral or dorsal view, pronotum without a pair of erect setae, only appressed pubescence present (Fig. 23E, D); in lateral view post-petiole slightly dilated, 1.5 times larger than petiole (Fig. 23B, F); bicolored with head, mesosoma, and legs reddish yellow and gaster dark brown (Fig. 23B)...........................................................***Monomorium* cf. *pharaonis***

8 Antennal scrobes very well marked, extending posteriorly past the eyes (Fig. 37D); frontal carina clearly differentiated to extending tenuously until or near to the occipital corners (Fig. 41C) (*Tetramorium*) ..........................**9**

– Antennal scrobes absent (Figs 15C, 28C); frontal carinae short and never extending posteriorly past the eyes (Figs 13C, 28D) ...............................**13**

9 Propodeal spines long, strong, and acute (Figs 37C, 41D)........................**10**

– Propodeal spines short and not acute (Figs 38C, 40C)............................**12**

10 Sculpture on the cephalic dorsum of the head strigose (Fig. 41E); body dark brown to black; legs, antennae, and mandibles pale brown (Fig. 41A) ................................................................................ ***Tetramorium lucayanum***

– Sculpture on the cephalic dorsum of the head alveolate or areolate (Fig. 37E); yellowish and reddish ants (Figs 37B, 38B, 39B, 40B) ............**11**

11 Anterior clypeal margin with a distinct median notch or impression; median portion of the clypeus with 3 longitudinal carinae (Fig. 37E); head, mesosoma, waist and gaster covered by numerous thick erect and suberect hairs (Fig. 37B, C, F); bicolored with gaster dark (Fig. 37B)......................... ............................................................................... ***Tetramorium bicarinatum***

– Anterior clypeal margin without a median notch or impression (Fig. 39C); median portion of the clypeus with a central carina weak or discontinuously marked (Fig. 39B); head, mesosoma, waist, and gaster densely covered by a fine and long white pilosity (Fig. 39D, E, F); entirely reddish (Fig. 39B)............................................................***Tetramorium lanuginosum***

12 Frontal carinae very well marked (Fig. 40D); antennal scrobes shallow, broad and conspicuous (Fig. 40E) mesosoma with < 10 erect hairs ......... ...................................................................................***Tetramorium simillimum***

– Frontal carinae not well marked, scrobes vestigial, feebly developed (Fig. 38D, E); mesosoma with > 10 erect hairs .......***Tetramorium caldarium***

13 Head in full-face view and mesosoma in dorsal view strigose (Fig. 28C, E); mesosoma in lateral view clearly convex, without sutures impressed on the dorsum (Fig. 28B, E); eyes composed of 5 ommatidia (Fig. 28D) (*Rogeria*)....................................................................... ***Rogeria curvipubens***

– Head in full-face view and mesosoma in dorsal view with variable sculpturing, but never uniformly strigose; mesosoma with notopropodeal suture present and grooved in lateral view (Slightly reduced to absent in *Cardiocondyla minutior*); number of ommatidia variable ...............................**14**

14 Monomorphic worker caste; dorsal view of the head and mesosoma densely foveolate with small appressed hairs (Figs 15C, D, 16D, F); promesonotum flat or slightly convex (Figs 15E, 16C); anterior margin of clypeus projected over the basal margin of the mandibles (Fig. 16E); in dorsal view, post-petiole spherical and notably dilated in comparison with petiole (Fig. 15F) *Cardiocondyla*) ....................................................................................**15**

– Polymorphic worker caste; dorsal view of the head with the occipital corners smooth and shiny (major workers) (Fig. 27C); promesonotum convex (Fig. 25C); anterior margin of clypeus not projected over the basal margin of the mandibles (Fig. 25D); postpetiole never spherical (Fig. 26C) (*Pheidole*)............................................................................................................**16**

15 Metanotal groove not impressed on the dorsum of mesosoma (Fig. 16C, F); head, mesosoma, and gaster dark brown; propodeal spines short (Fig. 16C, B) ............................................................***Cardiocondyla minutior***

– Metanotal groove impressed on the dorsum of mesosoma (Fig. 15D, E); mesosoma pale brown or orange, contrasting with darker gaster; propodeal spines longer and more acute than above (Fig. 15E) .......................... ..................................................................................... ***Cardiocondyla emeryi***

16 Major workers orange to reddish; total length ~ 2 mm (Figs 24B, 27B)....**17**

– Major workers dark brown to brown; total length ~ 2.5 mm (Figs 25B, 26B) ....................**18**

17 Major workers: head in frontal view with antennal scrobe weakly developed and alveolate (Fig. 24D, E); mesosoma in lateral view alveolate (Fig. 24C, E) .................... ***Pheidole flavens***

– Major workers: head in frontal view with antennal scrobe absent (Fig. 27A, C, B); mesosoma in lateral view, with the pronotum in major proportion smooth and shiny (Fig. 27B, D), but rugulose and alveolate between the mesonotum and propodeum (Fig. 27D) ....................***Pheidole* hh01**

18 Promesonotum in lateral view convex until it reaches the metanotal groove (Fig. 25C); post-petiole hexagonal in dorsal view exaggeratedly swollen relative to petiole (Fig. 25E); subpostpetiolar process slightly bulging (Fig. 25F) ....................***Pheidole megacephala***

– Promesonotum in lateral view forming two convexities, truncated before reaching the metanotal groove (Fig. 26D); postpetiole not swollen compared to petiole (Fig. 26E); subpostpetiolar process absent or reduced (Fig. 26F).................... ***Pheidole williamsi***

19 Antenna with 10 or 11 segments (Figs 29C, 43C)....................**20**

– Antenna with < 6 segments (Fig. 33F), (*Strumigenys*) ....................**24**

20 Antenna with 10 segments; funiculus with 2-segmented club (Fig. 29C); antennal scrobes absent (Fig. 30C); propodeum without spines (Fig. 31C) (*Solenopsis*) ....................**21**

– Antenna with 11 segments (Figs 18C, 43E); funiculus with a diffuse 3-segmented club (Figs 18C, 43C) antennal scrobes present (Figs 19E, 43E); spines on propodeum present or not (Figs 20C, 43D) ....................**27**

21 Large (Fig. 29B), second and usually third segments of funiculus at least 1½ times as long as broad (Fig. 29A, C); petiole with thin flange ventrally; dark brown to black (Fig. 29B) ....................***Solenopsis geminata***

– Smaller (Figs 30B, 31B, 32B), second and third segments of funiculus at most only slightly longer than broad, usually broader than long (Fig. 31D); petiole lacking flange ventrally, reddish to orange and dark brown (Figs 30B, 31B, 32B) ....................**22**

22 Postpetiole greatly dilated, wider than petiole (seen from above), globose; eye with 15–25 ommatidia (Fig. 30D, E)....................***Solenopsis globularia***

– Postpetiole not dilated nor globose (Fig. 32C); eye with 3–5 ommatidia (Fig. 31D) ....................**23**

23 In full face view, occipital margin of the head slightly concave (Fig. 31E); anterior clypeal margin with the median portion concave and oriented onward; frontal lobes longitudinally striated (Fig. 31E) .....***Solenopsis gnoma***

– In full face view, occipital margin of the head relatively straight to convex rather than concave (Fig. 32E); anterior clypeal margin with the median portion erect and not oriented onward; frontal lobes smooth and shiny, not striated (Fig. 32E)....................***Solenopsis* cf. *basalis* (hh06)**

24 Mandibles long and straight (Figs 33C, 35C) ....................**25**

– Mandibles short and curved downwards in profile, otherwise triangular (Figs 34D, 36C) ....................**26**

25 Mandibles with a small preapical tooth, without denticles on inner border (Fig. 35C); head and mesosoma with appressed spatulate hairs (Figs 34E, 35D, E, F) ................................................................***Strumigenys louisianae***

– Mandibles armed with small denticles on inner border (Fig. 33C); head and mesosoma without appressed (spatulate) circular hairs (Fig. 33D, E) ........................................................................................ ***Strumigenys eggersi***

26 Triangular mandibles armed with denticles (Fig. 36A); antenna with 6 segments, head and mesosoma with few appressed hairs (Fig. 36D); petiole and post-petiole with spongiform tissue (Fig. 36E) ........................................................................................................................................... ***Strumigenys membranifera***

– Mandibles in appearance curved and short, armed with an apical fork (Fig. 33D); antenna with four segments (Fig. 33C); head and mesosoma with appressed spatulate hairs (Fig. 33E); petiole and post-petiole without spongiform tissue ....................................................... ***Strumigenys emmae***

27 Head in frontal view with the antennal insertions hidden under the frontal lobes, which are exceptionally broad or expanded (Figs 18C, 20A, D); promesonotum tuberculated and propodeum unarmed by spines (Figs 18D; 19C, 20C); first segment of the gaster covered with appressed hairs, dull and opaque (Figs 19E, 20E) (*Cyphomyrmex*).....................................**28**

– Head in full face view with the antennal insertions partly visible (Fig. 43A); frontal lobes not distended; promesonotum not tuberculated (Fig. 43D); propodeum armed with a pair of acute spines (Fig. 43D); first segment of the gaster smooth and shiny with few erect setae (Fig. 43F) (*Wasmannia*)........................................................................ ***Wasmannia auropunctata***

28 Pair of tubercles absent in the anterior median region of the pronotum (Fig. 18E); dark brown (Fig. 18B)............................***Cyphomyrmex nesiotus***

– Pair of tubercles present in the anterior median region of the pronotum (Figs 19D, 20E)...............................................................................................**29**

29 In dorsal view, propodeal declivity with a pair of tubercles located at the level of spiracles (Fig. 20E, F); head and body black (Fig. 20B) ........................................................................................... ***Cyphomyrmex* sp. hh04**

– In dorsal view, propodeal declivity without a pair of tubercles situated at level of spiracles (Fig. 19C, D); head and gaster brown, mesosoma and legs pale brown (Fig. 19B) ...................................... ***Cyphomyrmex rimosus***

## Genus *Adelomyrmex* Emery, 1897

### *Adelomyrmex longinoi* Fernández, 2003

Fig. 14

**Remarks.** Misidentification in Herrera and Longino (2008). Cited in Longino (2012) and Herrera (2015, 2019) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Central America.

**Galápagos distribution.** Introduced: Isabela Island (Herrera et al. 2014).

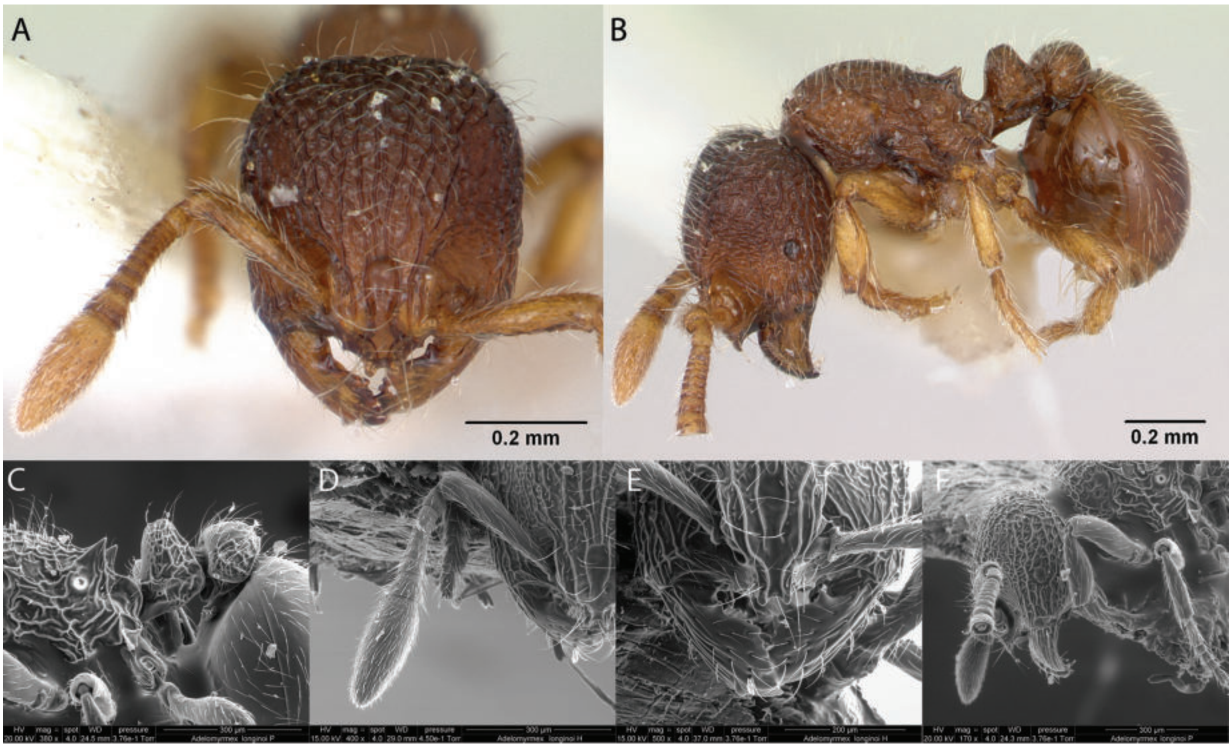

**Figure 14.** *Adelomyrmex longinoi* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** propodeum, petiole and postpetiole in profile **D** antennae in front view **E** mandibles in front view **F** head in profile.

## Genus *Cardiocondyla* Emery, 1869

### *Cardiocondyla emeryi* Forel, 1881

Fig. 15

**Remarks.** Cited in Lubin (1984), Lubin (1985), Pezzatti et al. (1998), Roque-Albelo et al. (2000) [ICCDRS], von Aesch and Cherix (2005), von Aesch (2006) [ICCDRS], Causton et al. (2006), McMullen (2007), Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS; RBINS]. Probably *C. minutior* or *C. emeryi* in Peck (1994a) and Peck (1994b).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Albany, Bainbridge #1, Bainbridge #3, Bainbridge #4, Bainbridge #5, Bainbridge #6, Bainbridge #8, Bar, Cousin, Darwin, Eden, Fernandina, Floreana, Gardner (next to Floreana), Genovesa, Gran Felipe, Isabela (CA, SN, VA, VD, VE, VW), Mariela Grande, Mao, Marchena, Pinta, Pinzón, Plaza Sur, Rábida, Santiago, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé, Wolf (Herrera et al. 2020).

### *Cardiocondyla minutior* Forel, 1899

Fig. 16

**Remarks.** Cited as *Cardiocondyla nuda* in Lubin (1984), Lubin (1985), [ICCDRS], Roque-Albelo et al. (2000) [ICCDRS], Pezzatti et al. (1998) [ICCDRS], von Aesch

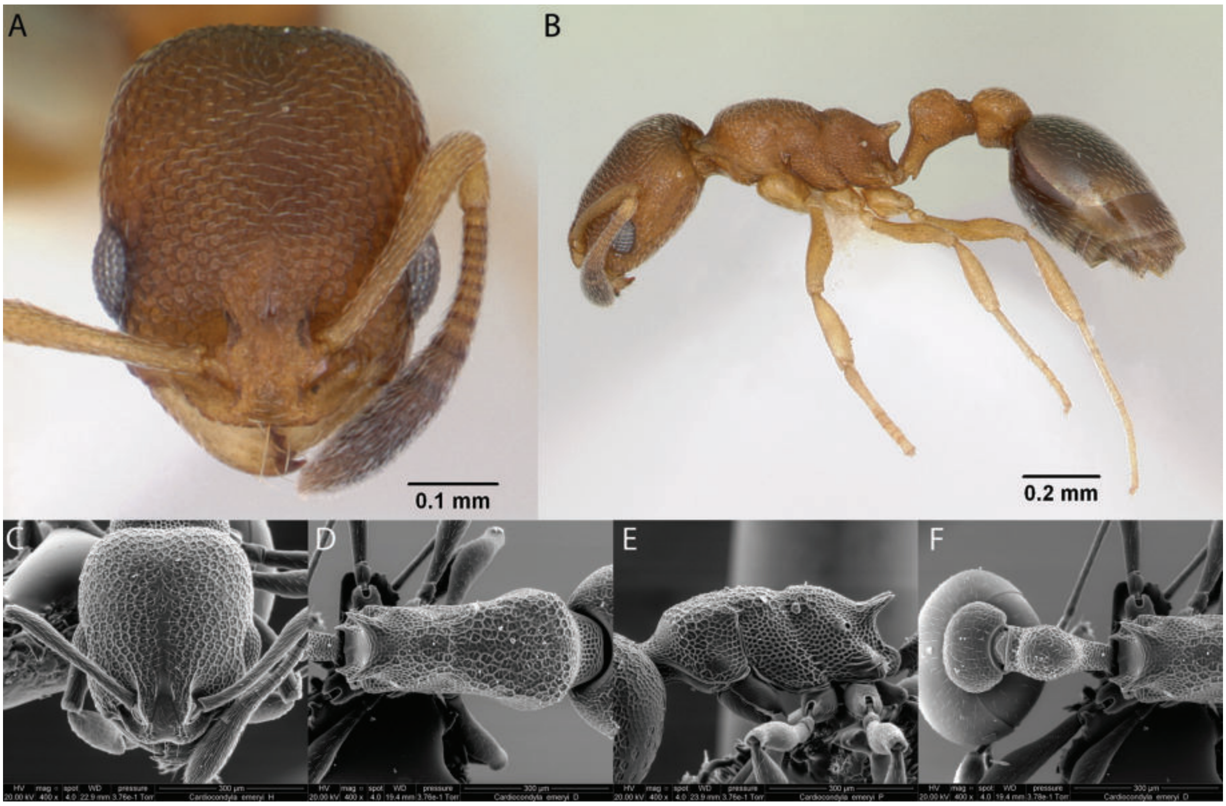

**Figure 15.** *Cardiocondyla emeryi* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** mesosoma in dorsal view **E** mesosoma in profile **F** propodeum, petiole and postpetiole in dorsal view.

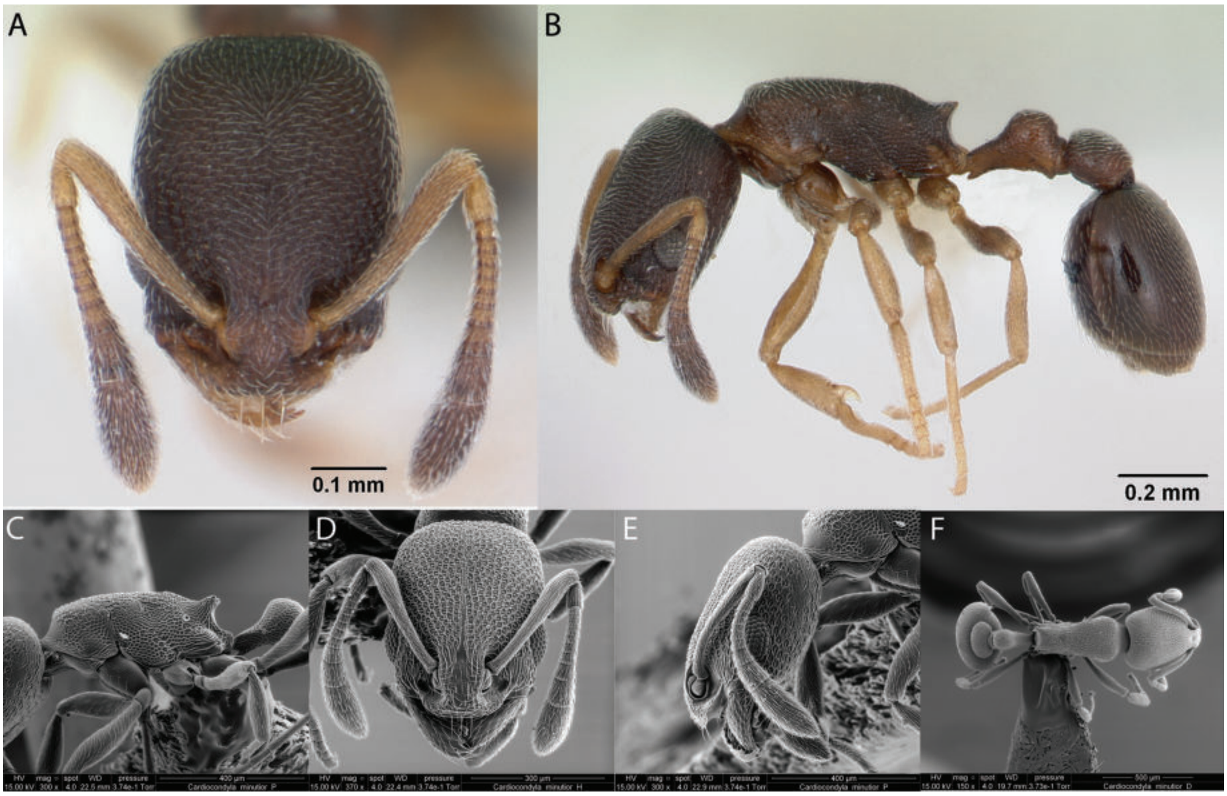

**Figure 16.** *Cardiocondyla minutior* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** head in full-face view **E** head in profile **F** mesosoma in dorsal view.

and Cherix (2005), von Aesch (2006) [ICCDRS]. Cited as *C. nuda* in Causton et al. (2006). Probably *C. minutior* in McMullen (1993). *Cardiocondyla minutior* or *C. emeryi* in Peck (1994a, 1994b). *Cardiocondyla minutior* in Wauters et al. (2016), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania.

**Galápagos distribution.** Introduced: Bainbridge #1, Cousin, Daphne Mayor, Darwin, Fernandina, Floreana, Gardner (next to Floreana), Isabela (CA, SN, VA, VD, VE), Mariela Grande, Marchena, Pinta, Santiago, San Cristóbal, Santa Cruz, Santa Fé, Wolf (Herrera et al. 2020).

### Genus *Crematogaster* Lund, 1831

#### *Crematogaster crinosa* Mayr, 1862

**Remarks.** Cited as *Crematogaster* (*Orthocrema*) *brevispionsa chatamensis* in Wheeler (1933), Kempf (1972), Linsley and Usinger (1966). *Crematogaster chatamensis* in Lubin (1984). *Crematogaster crinosa* in Longino (2003) [CAS], Herrera et al. (2014), Herrera (2015, 2019) and Herrera et al. (2020).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Neotropical.

**Galápagos distribution.** Uncertain: San Cristóbal (Wheeler 1933).

### Genus *Crematogaster* Lund, 1831

#### *Crematogaster* JTL-022

Fig. 17

**Remarks.** First published record Herrera et al. (2014), cited also in Traveset et al. (2013), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS, JTLC].

**Distribution.** Introduced: San Cristóbal Island (Herrera et al. 2014, 2020).

### Genus *Cyphomyrmex* Mayr, 1862

#### *Cyphomyrmex nesiotus* Snelling & Longino, 1992

Fig 18

**Remarks.** Cited in Snelling and Longino (1992), Herrera and Longino (2008), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS, JTLC].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Probably endemic: Isabela (Snelling and Longino 1992).

#### *Cyphomyrmex rimosus* (Spinola, 1851)

Fig. 19

**Remarks.** First published record Herrera and Longino (2008) [ICCDRS]. Cited also in Dekoninck et al. (2014), Wauters et al. (2016), Herrera (2015, 2019)

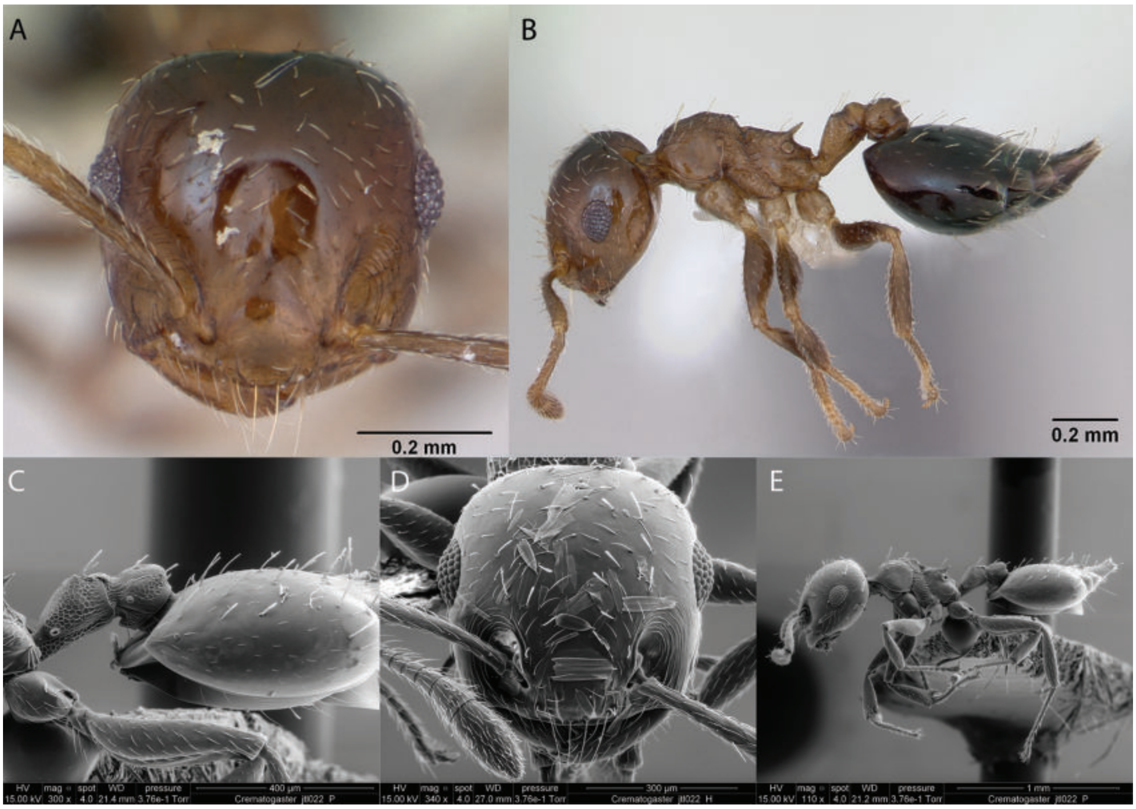

**Figure 17.** *Crematogaster* JTL-022 worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** petiole and postpetiole in profile **D** head in full-face view **E** view in profile.

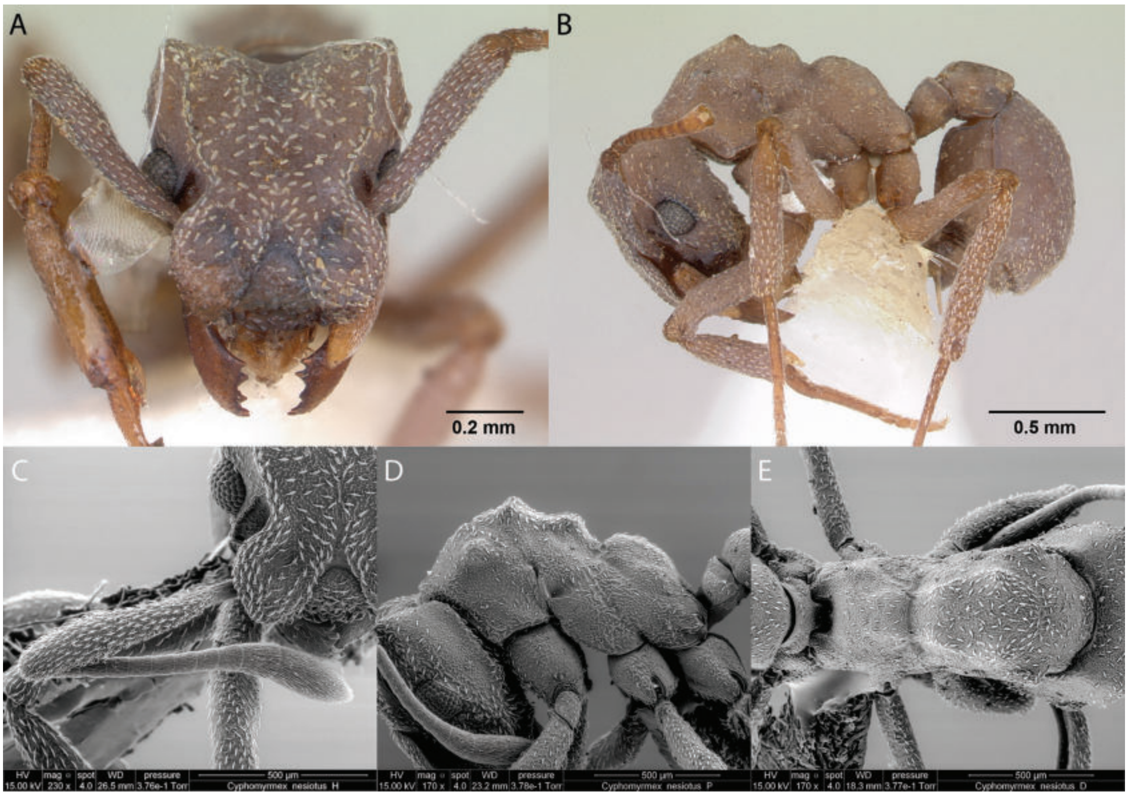

**Figure 18.** *Cyphomyrmex nesiotus* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** antennae in front view **D** mesosoma in profile **E** mesosoma in dorsal view.

and Herrera et al. (2020) [ICCDRS]. Probably *C. rimosus* in Lubin (1984) and Brandão and Paiva (1994).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Nearctic and Neotropical.

**Galápagos distribution.** Introduced: Gardner (next to Floreana), Isabela (SN), San Cristóbal, Santa Cruz (Herrera et al. 2020).

### *Cyphomyrmex* sp. hh04

Fig. 20

**Remarks.** First published record as dark form of *C. rimosus* in Herrera and Longino (2008). Cited as *Cyphomyrmex* sp. hh04 in Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS, RBINS].

**Distribution.** Origin uncertain: Isabela (SN) Pinzón, Santa Cruz (Herrera et al. 2020).

**New record.** Santiago Island.

## Genus *Monomorium* Mayr, 1855

### *Monomorium floricola* (Jerdon, 1851)

Fig. 21

**Remarks.** Originally cited as *Atta floricola* in (Jerdon, 1851). Cited as *Monomorium floreanun* in Stitz (1932). *Monomorium floricola* in Linsley and Usinger (1966). *Monomorium floreanun* in Kempf (1972). *Monomorium floricola* in Kempf (1972), Clark et al. (1982), Lubin (1984) [ICCDRS], McMullen (1993), Meier (1994) [ICCDRS], Abedrabbo (1994) [ICCDRS], de la Vega (1994), Peck (1994a), Peck et al. (1998), Pezzatti et al. (1998) [ICCDRS], Roque-Albelo et al. (2000) [ICCDRS], von Aesch and Cherix (2005), Boada (2005) [ICCDRS], von Aesch (2006) [ICCDRS], Causton et al. (2006), Herrera and Causton (2010) [ICCDRS], McMullen (2012), Chamorro et al. (2012) [ICCDRS], Dekoninck et al. (2014) [ICCDRS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Bainbridge #5, Baltra, Bartolomé, Bayas, Bowditch South, Champion, Cousin, Daphne Mayor, Española, Fernandina, Floreana, Gardner (next to Floreana), Genovesa, Isabela (CA, SN, VA, VD), Mariela Grande, Mariela Mediana, Marchena, Pinta, Plaza Norte, Plaza Sur, Rábida, Santiago, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé (Herrera et al. 2020).

**New record.** Sombrero Chino.

### *Monomorium pharaonis* (Linnaeus, 1758)

Fig. 22

**Remarks.** Originally cited as *Formica pharaonis* in (Linnaeus, 1758). Galápagos first published record in Wheeler (1919). Cited also in Linsley and Usinger (1966),

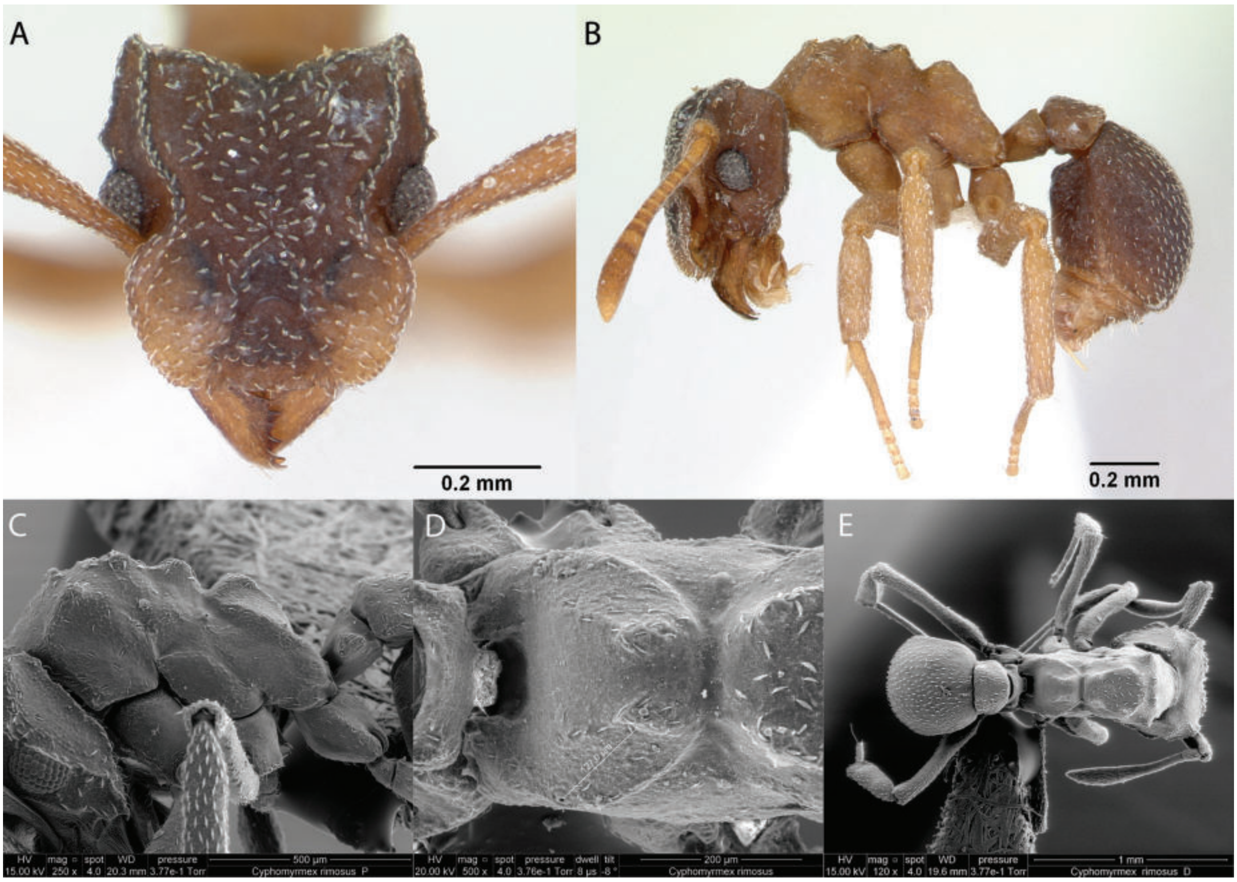

Figure 19. *Cyphomyrmex rimosus* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head and mesosoma in profile **D** propodeum in dorsal view **E** dorsal view.

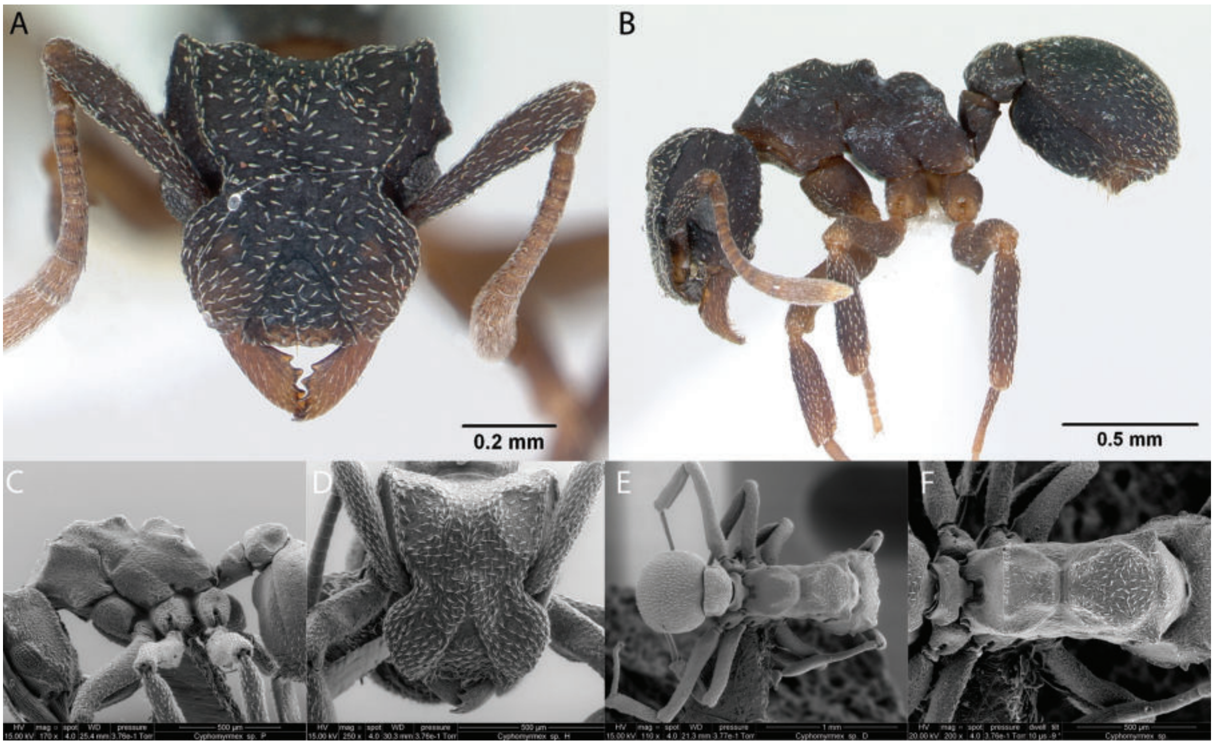

Figure 20. *Cyphomyrmex* sp. hh004 worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** head in full-face view **E** dorsal view **F** mesosoma in dorsal view.

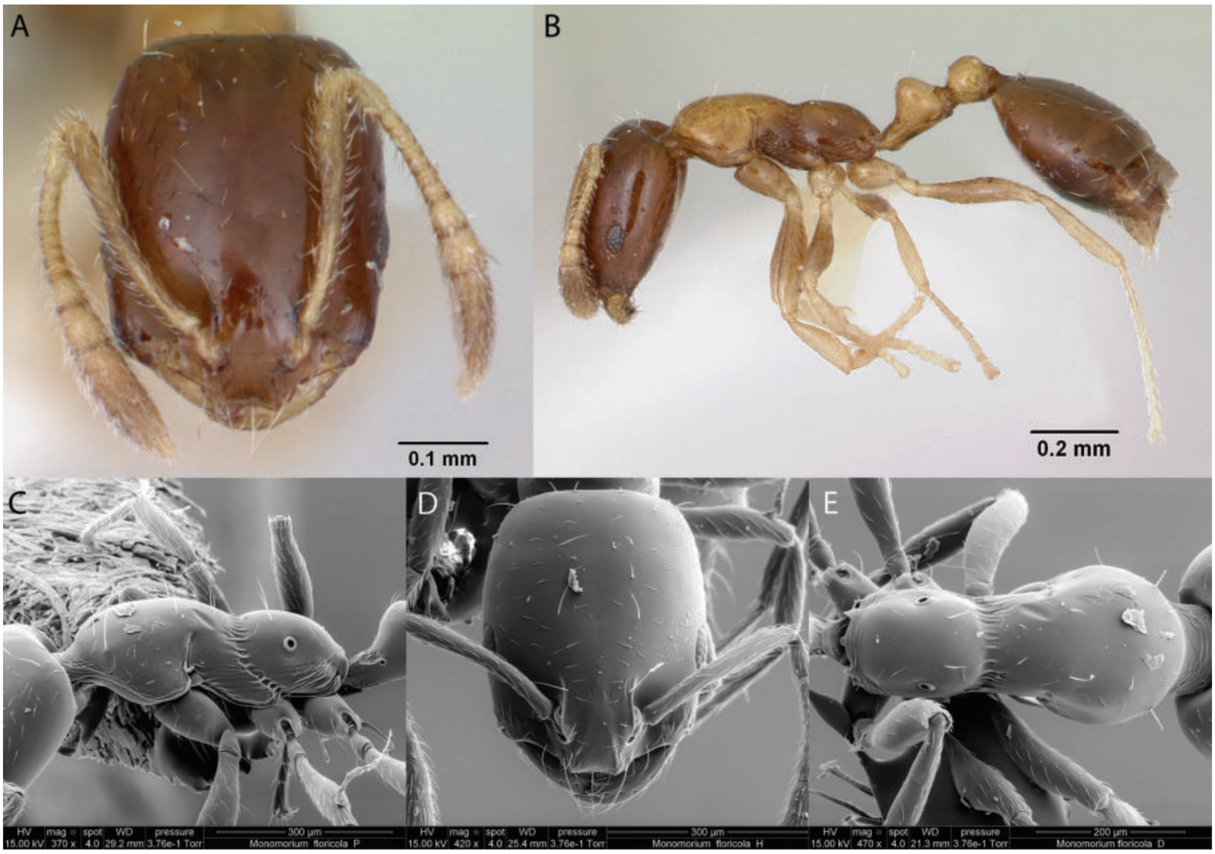

**Figure 21.** *Monomorium floricola* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** head in full-face view **E** mesosoma in dorsal view.

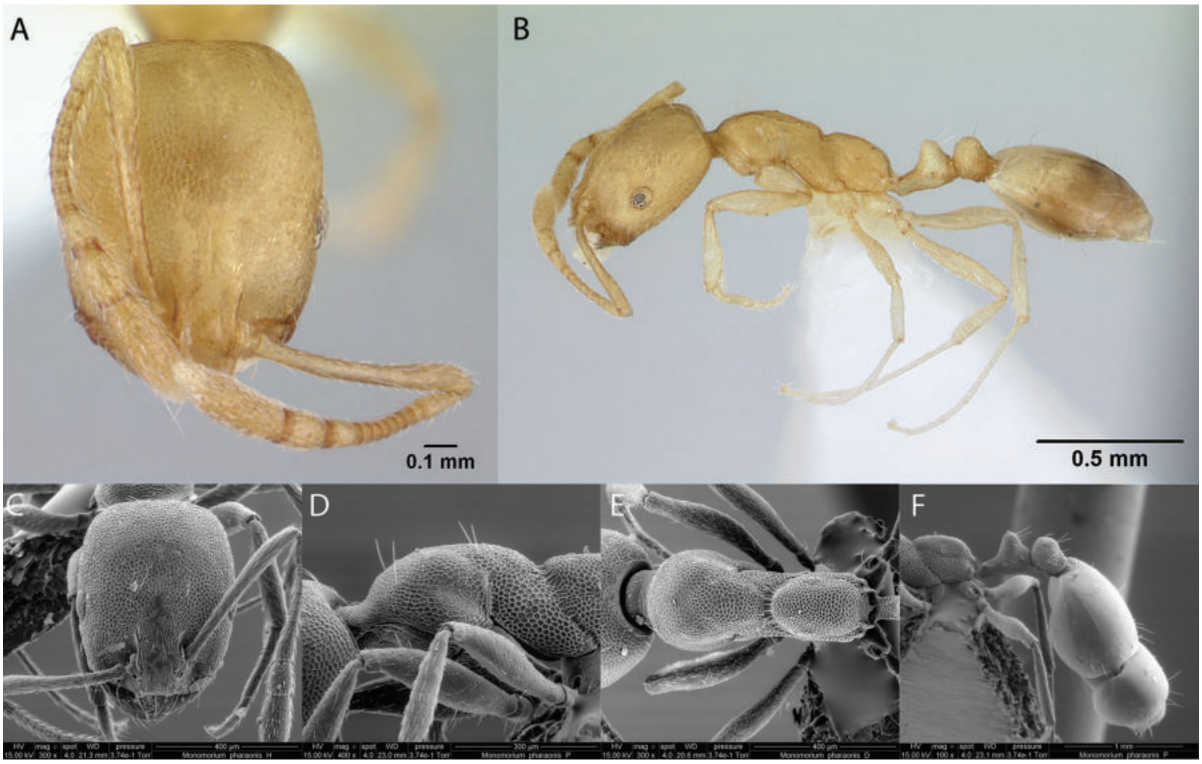

**Figure 22.** *Monomorium pharaonis* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** mesosoma in profile **E** mesosoma in dorsal view **F** petiole and postpetiole in profile.

Kempf (1972), Lubin (1984) [ICCDRS], Brandão and Paiva (1994), Peck et al. (1998), Causton et al. (2006), Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Baltra, Isabela (SN), Pinta, Santa Cruz (Herrera et al. 2020).

### *Monomorium* cf. *pharaonis*

Fig. 23

**Remarks.** First record in Herrera and Causton (2010) [ICCDRS]. Cited also in Dekoninck et al. (2014) [ICCDRS], Wauters et al. (2016) [ICCDRS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Distribution.** Undetermined origin: Baltra, Fernandina, Floreana, Isabela (SN), Marchena, Pinta, San Cristóbal, Santa Cruz, Santa Fé (Herrera et al. 2020).

## Genus *Pheidole* Westwood, 1839

### *Pheidole flavens* Roger, 1863

Fig. 24

**Remarks.** Cited in Wheeler (1919), Clark et al. (1982), Herrera et al. (2014) [ICCDRS], Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

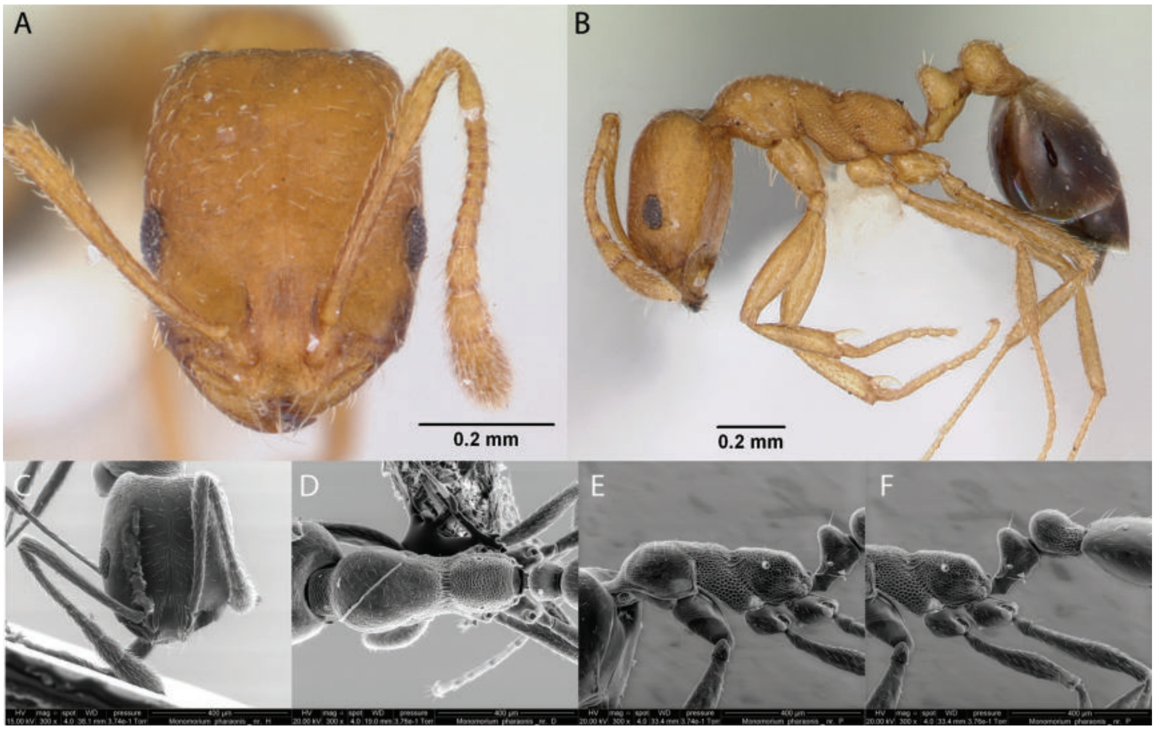

**Figure 23.** *Monomorium* sp. nr. *pharaonis* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** mesosoma in dorsal view **E** mesosoma in profile **F** petiole and postpetiole in profile.

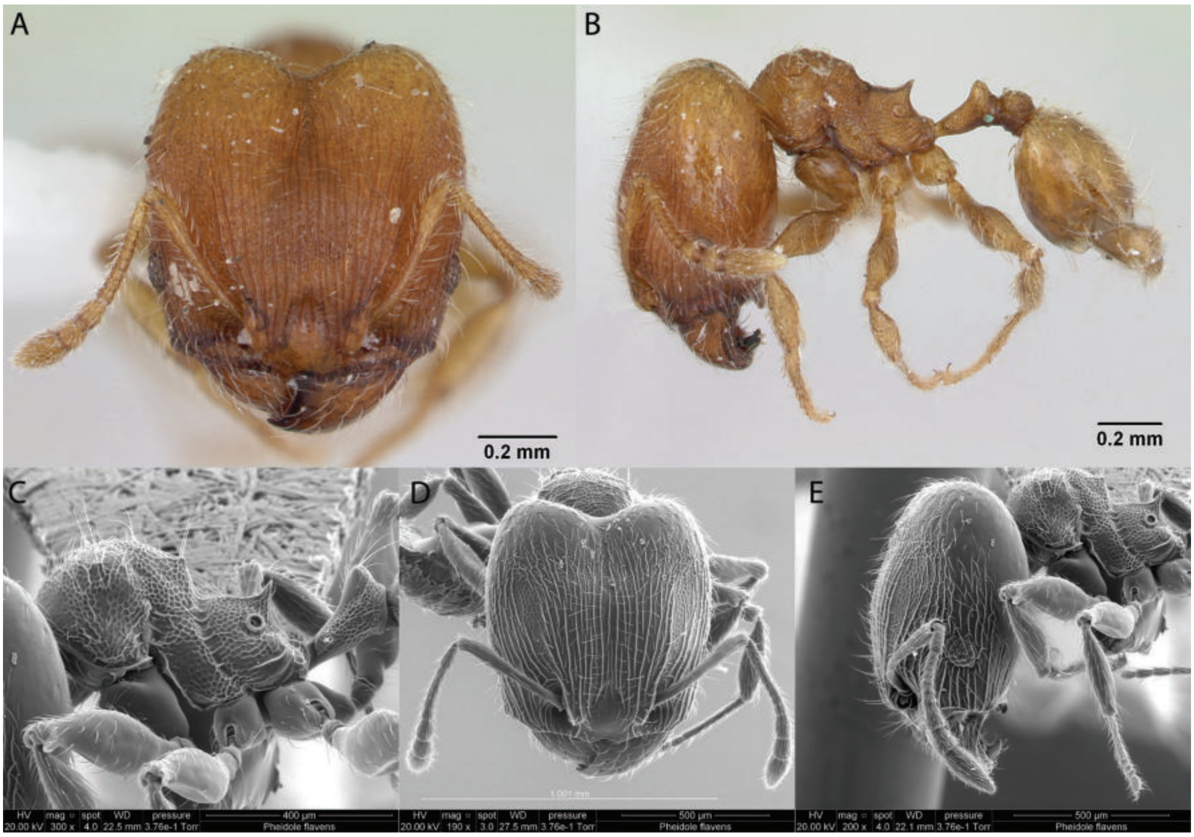

Figure 24. *Pheidole flavens* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** head in full-face view **E** head in profile.

**Distribution.** Neotropical.

**Galápagos distribution.** Introduced: Isabela (CA, SN, VA, VD, VW), San Cristóbal, Santa Cruz (Herrera et al. 2020).

### *Pheidole megacephala* (Fabricius, 1793)

Fig. 25

**Remarks.** Originally cited as *Formica megacephala* (Fabricius, 1793). Cited in Herrera et al. (2013) [ICCDRS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019) and Herrera et al. (2020).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Isabela (SN), San Cristóbal, Santa Cruz (Herrera et al. 2013).

### *Pheidole williamsi* Wheeler, 1919

Fig. 26

**Remarks.** Cited as *Pheidole williamsi* in (Wheeler 1919). *Pheidole williamsi* var. *seymourensis* in Wheeler (1924), Linsley and Usinger (1966). *Pheidole williamsi williamsi* in Linsley and Usinger (1966). *Pheidole williamsi* in Clark et al. (1982),

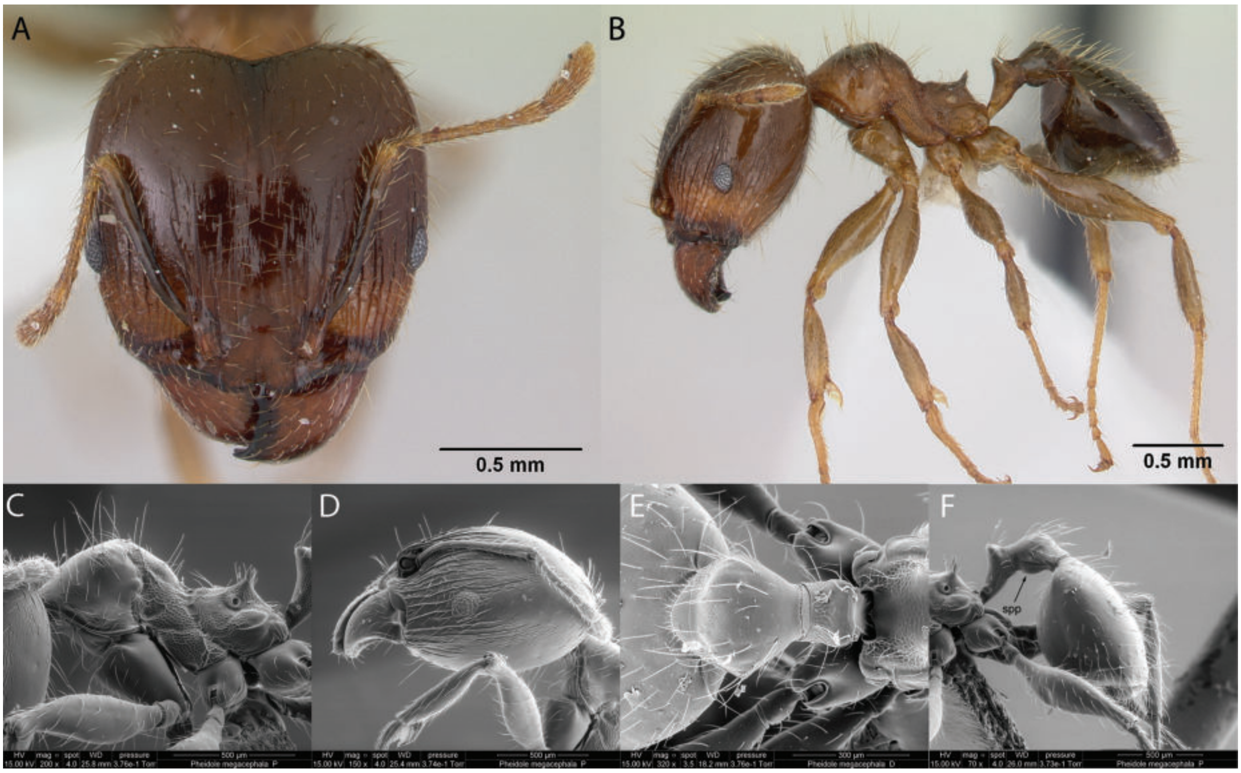

Figure 25. *Pheidole megacephala* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** head in profile **E** petiole and postpetiole in dorsal view **F** petiole and postpetiole in profile (spp = subpetiolar process).

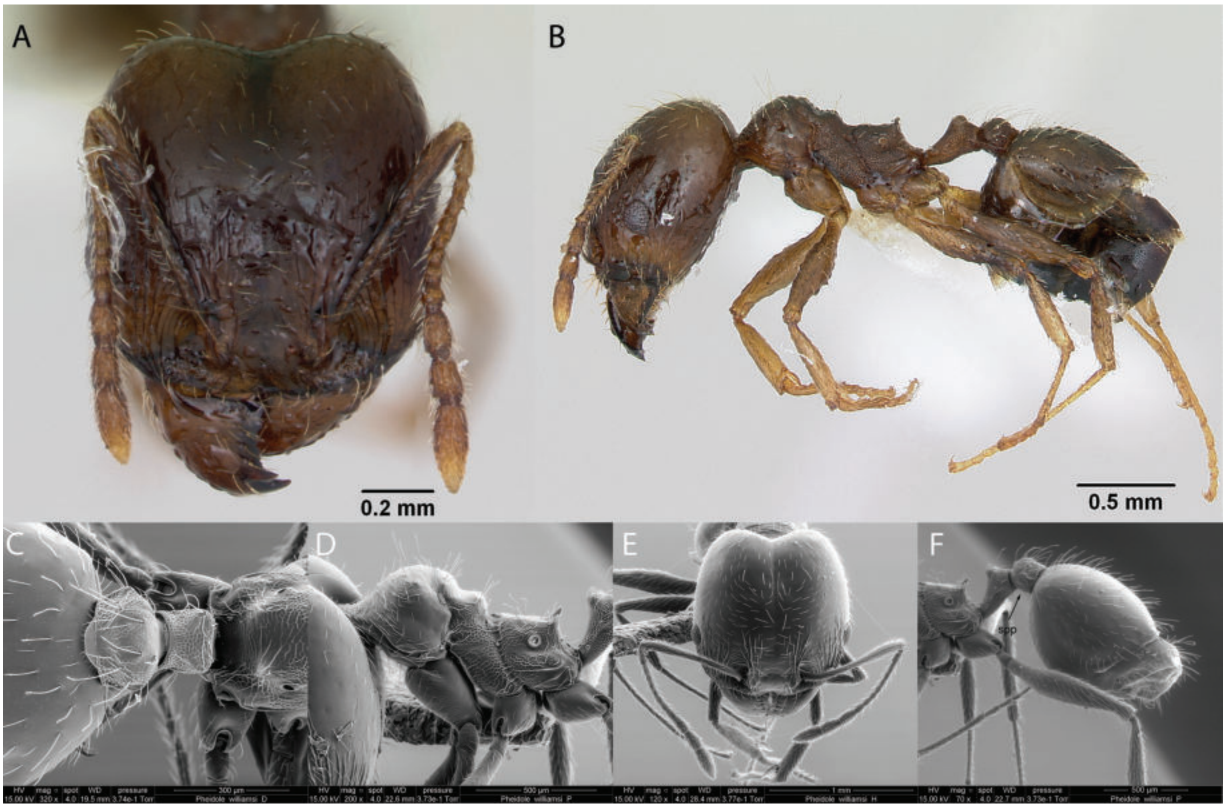

Figure 26. *Pheidole williamsi* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** petiole and postpetiole in profile **D** mesosoma in profile **E** head in profile **F** petiole and postpetiole in profile (spp = subpetiolar process).

Lubin (1984, 1985), Espadaler (1997), Wilson (2003), Herrera et al. (2014) [ICCDRS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Kempf (1972), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Possibly endemic: Albany, Bainbridge #1, Bainbridge #2, Bainbridge #3, Bainbridge #4, Bainbridge #5, Bainbridge #6, Baltra, Bowditch South, Daphne Mayor, Fernandina, Floreana, Gardner (next to Floreana), Isabela (SN, VA, VD, VW), Mariela Grande, Mariela Mediana, Pinta, Plaza Sur, Rábida, Santiago, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé, Tortuga (Herrera et al. 2020).

**New records.** Bartolomé and Beagle.

### *Pheidole* sp. hh01

Fig. 27

**Remarks.** In Herrera et al. (2014), Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Distribution.** Origin uncertain: Bowditch South, Eden, Floreana, Isabela (CA, SN, VA, VD, VE, VW), Logie, Pinzón, Santiago, San Cristóbal, Santa Cruz (Herrera et al. 2020).

## Genus *Rogeria* Emery, 1894

### *Rogeria curvipubens* Emery, 1894

Fig. 28

**Remarks.** Galápagos first published record (Herrera and Longino 2008), cited also in Dekoninck et al. (2014), Wauters et al. (2016), Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Neotropical.

**Galápagos distribution.** Introduced: Isabela (SN), San Cristóbal, Santa Cruz (Herrera et al. 2020).

## Genus *Solenopsis* Westwood, 1840

### *Solenopsis geminata* (Fabricius, 1804)

Fig. 29

**Remarks.** Originally cited as *Atta geminata* in (Fabricius, 1804). Cited as *Solenopsis geminata* in Emery (1893). *Solenopsis geminata galapageia* in Wheeler (1919), Linsley and Usinger (1966), and Kempf (1972). *Solenopsis geminata* in Lubin (1984), Williams (1987), Trager (1991), Williams and Whelan (1991), Brandão and Paiva (1994), Meier (1994), de la Vega (1994), Peck et al. (1998), Pezzatti et al. (1998), von Aesch and Cherix (2005) [ICCDRS], Boada (2005) [ICCDRS], von Aesch (2006) [ICCDRS], Causton et al. (2006), Pacheco et al. (2007), Herrera and Causton (2010) [ICCDRS], Herrera and Longino (2008), Herrera and Causton (2010) [ICCDRS], Herrera et al. (2013), Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2014) [RBINS], Wauters et al. (2016), [RBINS] Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

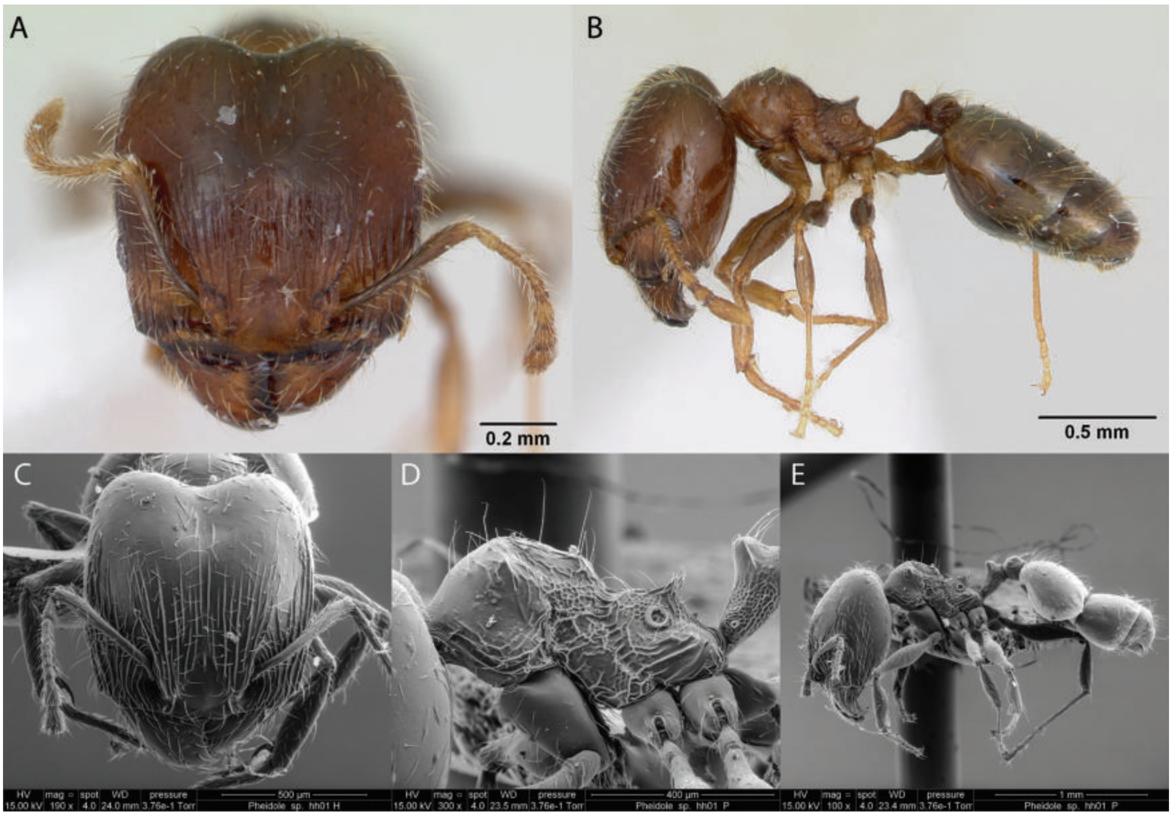

**Figure 27.** *Pheidole* sp. hh01 worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** mesosoma in profile **E** view in profile.

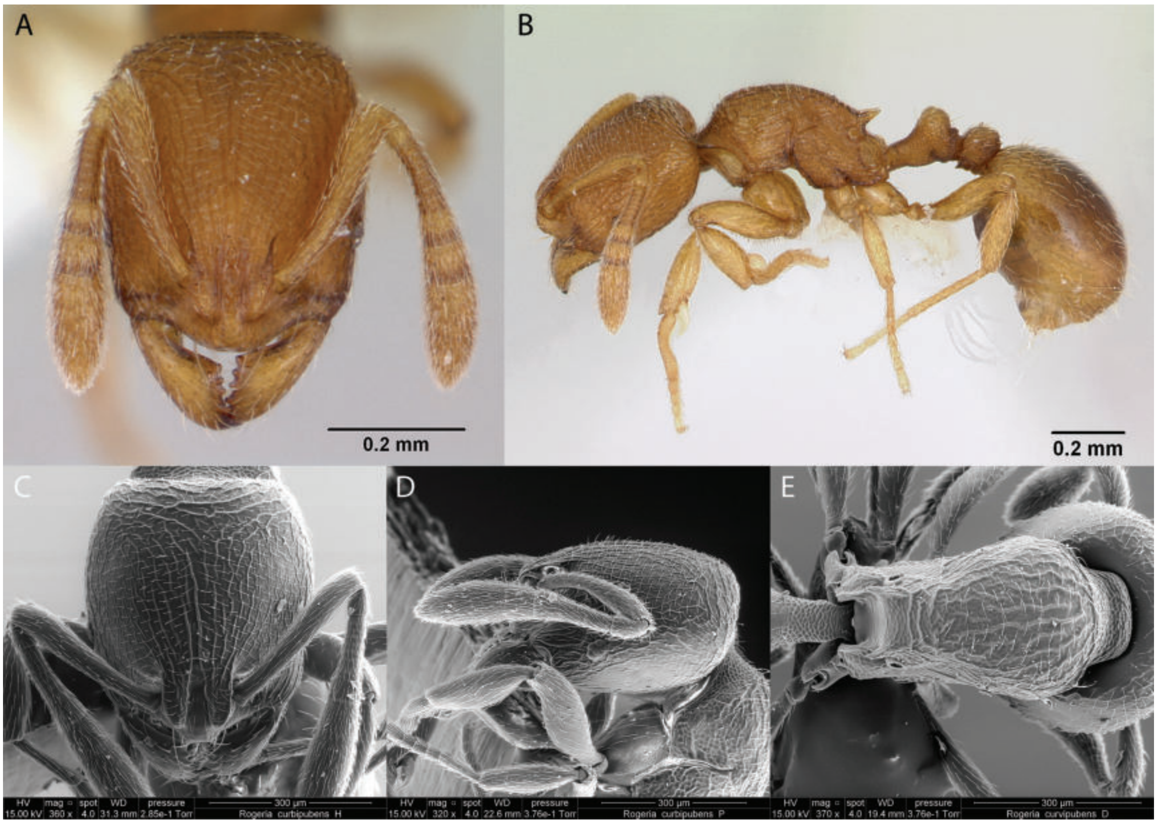

**Figure 28.** *Rogeria curvipubens* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** head in profile **E** mesosoma in dorsal view.

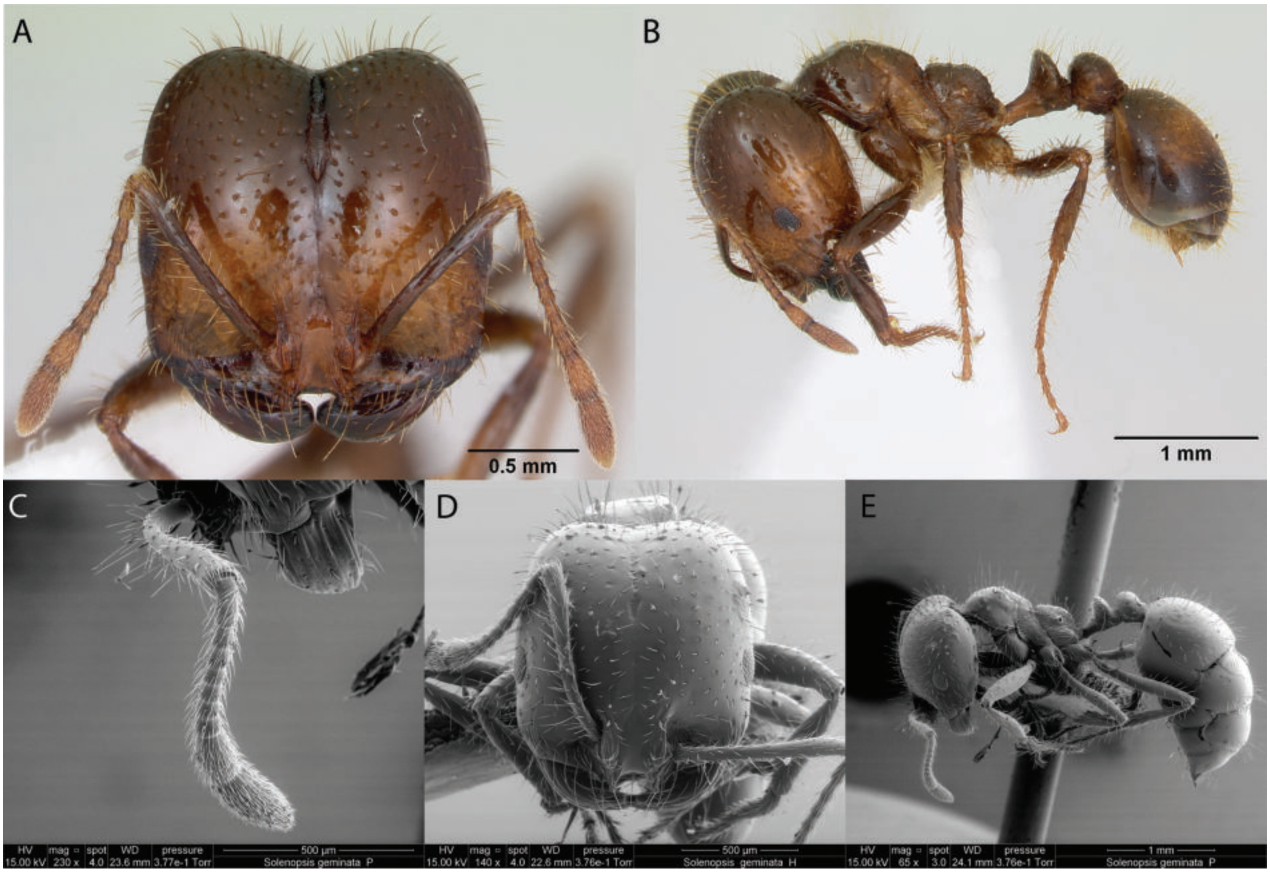

**Figure 29.** *Solenopsis geminata* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** antennae funiculi in profile **D** head in full-face view **E** view in profile.

**Taxonomic history.** Trager (1991), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Albany, Bainbridge #1, Baltra, Bayas, Champion, Cuevas, Eden, Enderby, Fernandina, Floreana, Gardner (next to Floreana), Isabela (CA, SN, VA), Mariela Grande, Mao, Mariela Mediana, Plaza Sur, Santa Fé, Santiago, San Cristóbal, Santa Cruz, Seymour Norte (Herrera et al. 2020).

### *Solenopsis globularia* (Smith, 1858)

Fig. 30

**Remarks.** Originally cited as *Myrmica globularia pacifica* in (Smith, 1858). Cited as *Solenopsis globularia pacifica* in Wheeler (1919, 1924). *Solenopsis globularia pacifica* var. *rubida* in Wheeler (1919, 1924), *Solenopsis globularia pacifica* in Linsley and Usinger (1966). *Solenopsis globularia rubida* in Linsley and Usinger (1966). *Solenopsis globularia pacifica* and *Solenopsis globularia pacifica* var. *rubida* in Kempf (1972). *Solenopsis globularia* in Clark et al. (1982). *Solenopsis pacifica* in Lubin (1984). *Solenopsis globularia* in Lubin (1985) [ICCDRS], Meier (1994), Abedrabbo (1994) [ICCDRS], Peck et al. (1998), (Pezzatti et al. (1998), Roque-Albelo et al. (2000) [ICCDRS], von Aesch and Cherix (2005), von Aesch (2006), Causton et al. (2006), Pacheco et al. (2007), Herrera and Causton (2010)

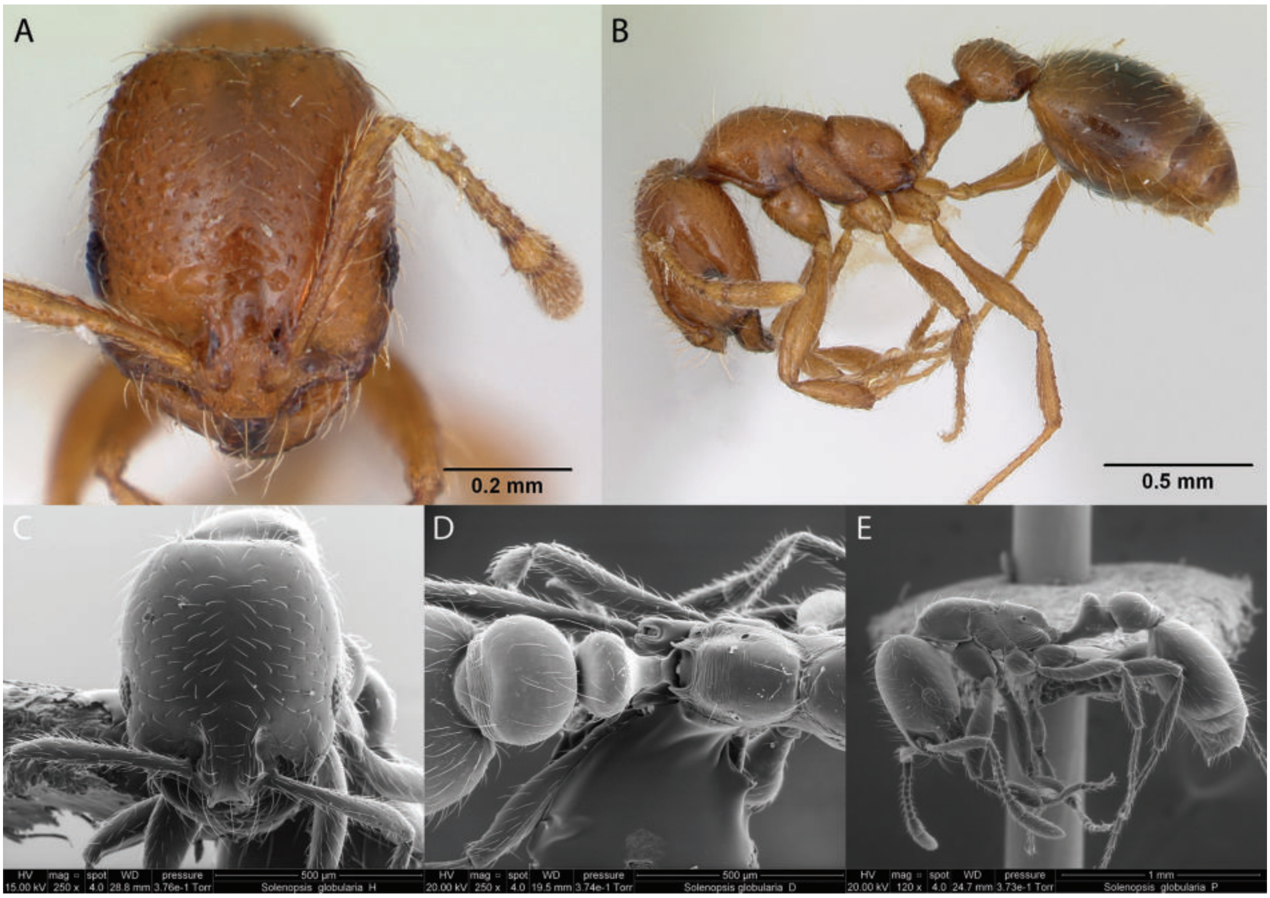

**Figure 30.** *Solenopsis globularia* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** petiole and postpetiole in dorsal view **E** head and mesosoma in profile.

[ICCDRS], McMullen (2012), Pacheco and Mackay (2013), Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006), Pacheco and Mackay (2013).

**Distribution.** Afrotropical, Nearctic, Neotropical.

**Galápagos distribution.** Introduced: Albany, Bainbridge #1, Bainbridge #3, Bainbridge #5, Bainbridge #7, Bainbridge #8, Baltra, Bowditch South, Champion, Daphne Mayor, Darwin, Eden, Enderby, Española, Fernandina, Floreana, Gardner (next to Española), Gardner (next to Floreana), Genovesa, Isabela (CA, SN, VA, VD, VE, VW), Mariela Grande, Mao, Mariela Pequeña, Marchena, Pinta, Pinzón, Plaza Sur, Rábida, Santiago, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé, Tortuga (Herrera et al. 2020).

**New record.** Sombrero Chino.

### *Solenopsis gnoma* Pacheco, Herrera & Mackay, 2007

Fig. 31

**Remarks.** Cited also in Dekoninck et al. (2014), Wauters et al. (2016), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Pacheco and Mackay (2013), Bolton (2014).

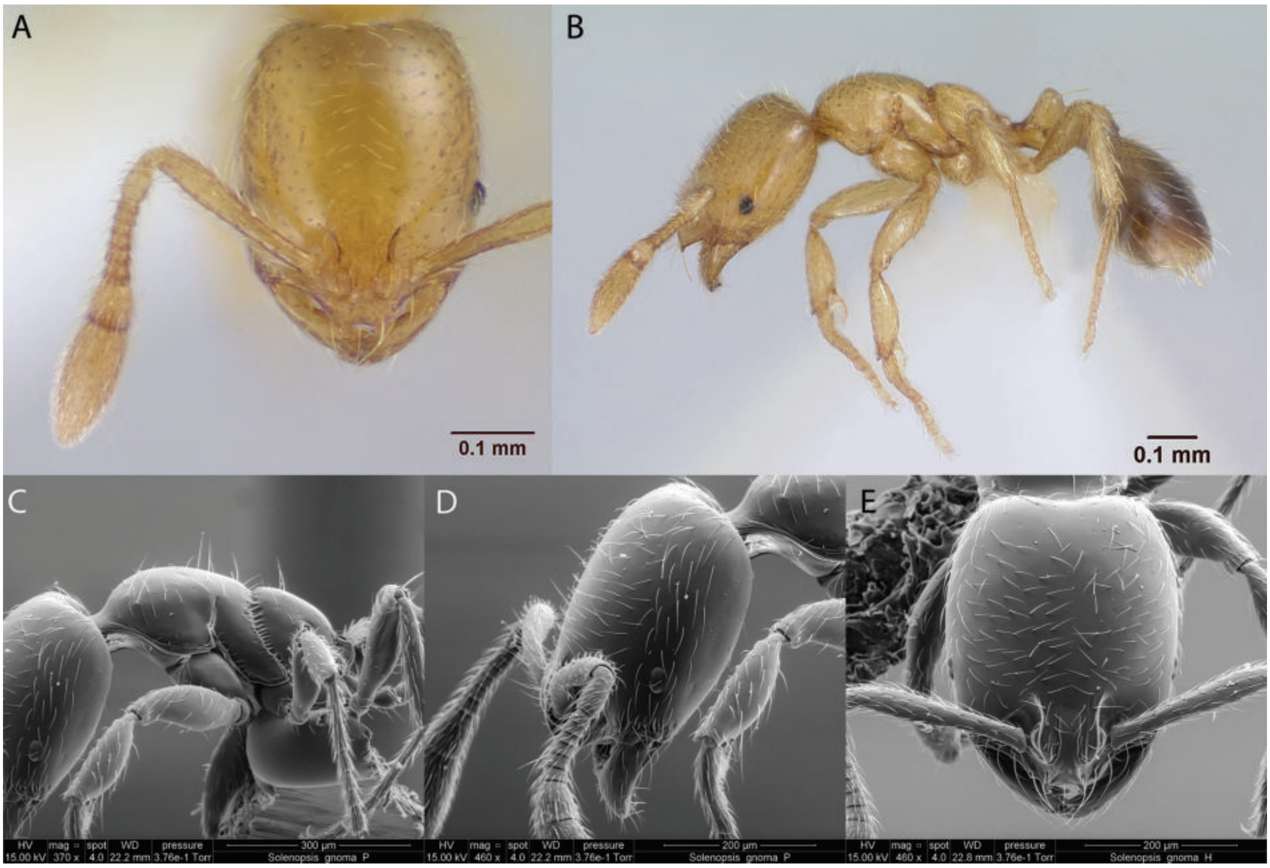

**Figure 31.** *Solenopsis gnoma* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** head in profile **E** head in full-face view.

**Distribution.** Probably endemic: Albany, Bowditch South, Española, Floreana, Isabela (SN, VA, CA), Marchena, San Cristóbal, Santa Cruz (Pacheco et al. 2007; Herrera et al. 2020).

**New record.** Santiago.

### *Solenopsis saevissima* (Smith, 1855)

**Remarks.** Originally cited as *Myrmica saevissima* (Smith, 1855). Doubtful record for Galápagos (Herrera et al. 2020). Cited in Wheeler (1919, 1924), Linsley and Usinger (1966) and Brandão and Paiva (1994), probably misidentification in Peck et al. (1998). Cited also from literature in Causton et al. (2006).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Nearctic, Neotropical.

**Galápagos distribution.** Uncertain: Santa Cruz Island (Wheeler 1919; Peck et al. 1998).

### *Solenopsis* cf. *basalis* (hh06)

Fig. 32

**Remarks.** First record in Herrera et al. (2014), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

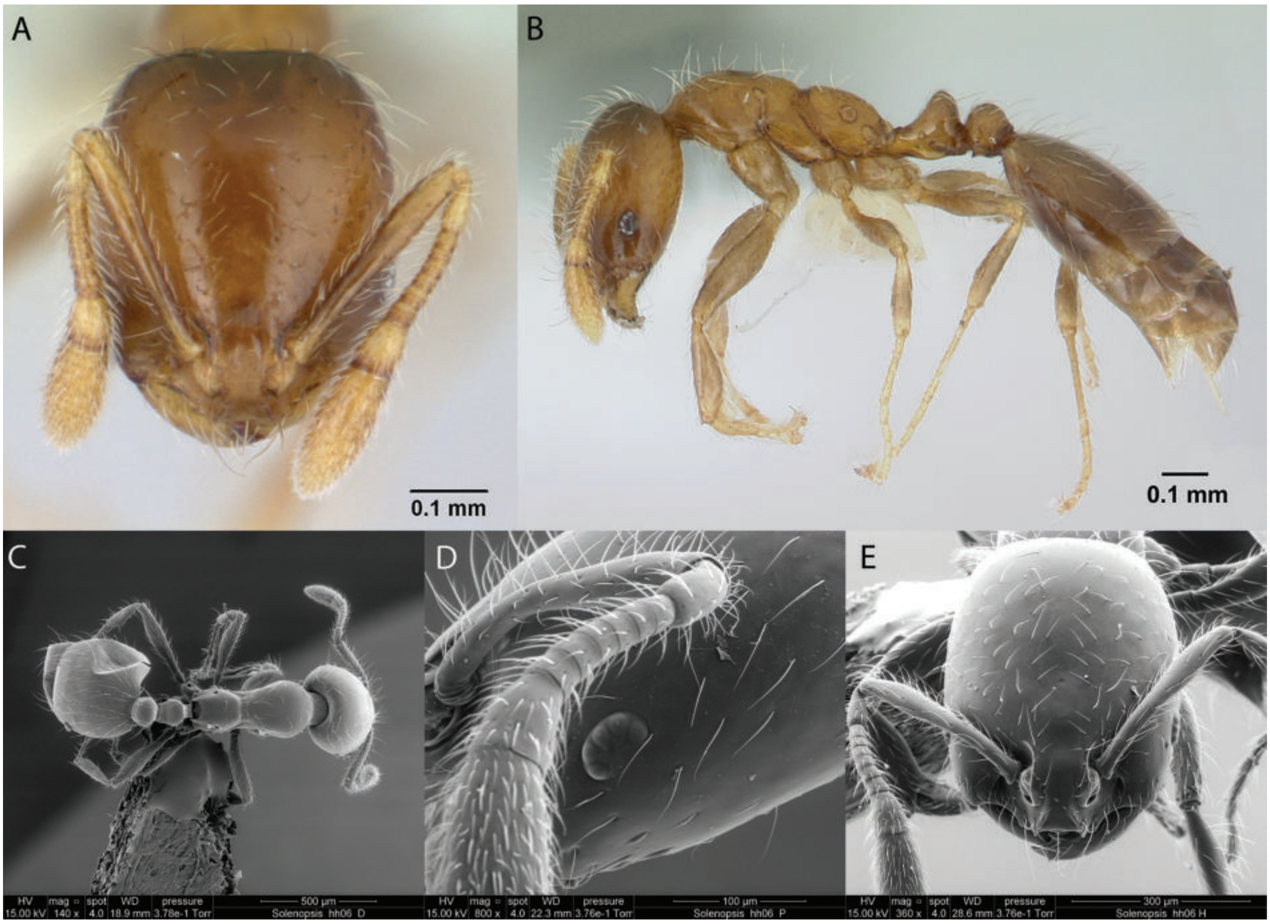

**Figure 32.** *Solenopsis* sp. basalis (hh06) worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma in profile **D** head in profile **E** head in full-face view.

**Distribution.** Origin uncertain: Bainbridge #5, Santa Cruz, Santiago (Herrera et al. 2014).

### Genus *Strumigenys* Smith, 1860

#### *Strumigenys eggersi* Emery, 1890

Fig. 33

**Remarks.** Galápagos first published record in Herrera et al. (2014). Cited also in Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Indomalaya, Nearctic, Neotropical.

**Galápagos distribution.** Introduced: Santa Cruz (Herrera et al. 2014).

#### *Strumigenys emmae* (Emery, 1890)

Fig. 34

**Remarks.** Originally cited as *Epitritus emmae* in (Emery, 1890). Cited as *Quadristruma emmae* in Pezzatti et al. (1998) and Causton et al. (2006). Also, in Herrera et al. (2014). Wauters et al. (2016), Herrera et al. 2020) [ICCDRS].

**Taxonomic history.** Kempf (1972), Bolton (1995, 2014), Bolton et al. (2006).

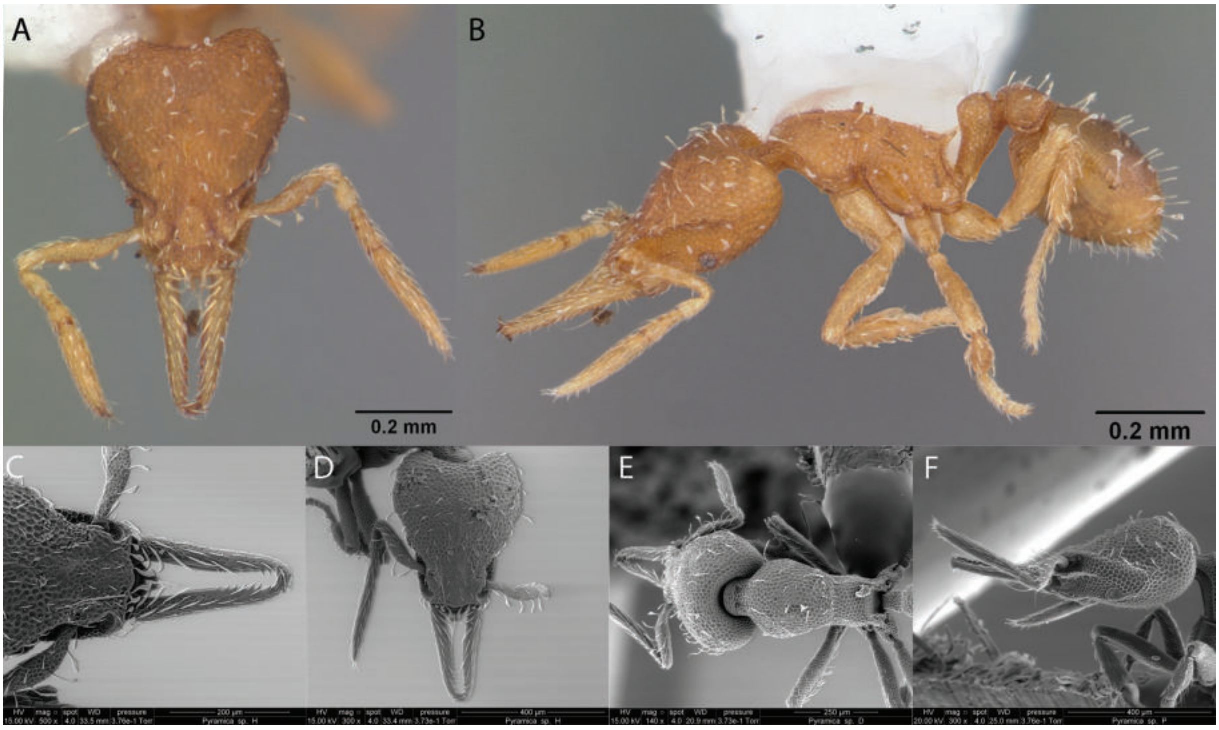

**Figure 33.** *Strumigenys eggersi* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on mandibles **D** head in full-face view **E** mesosoma in dorsal view **F** head in profile.

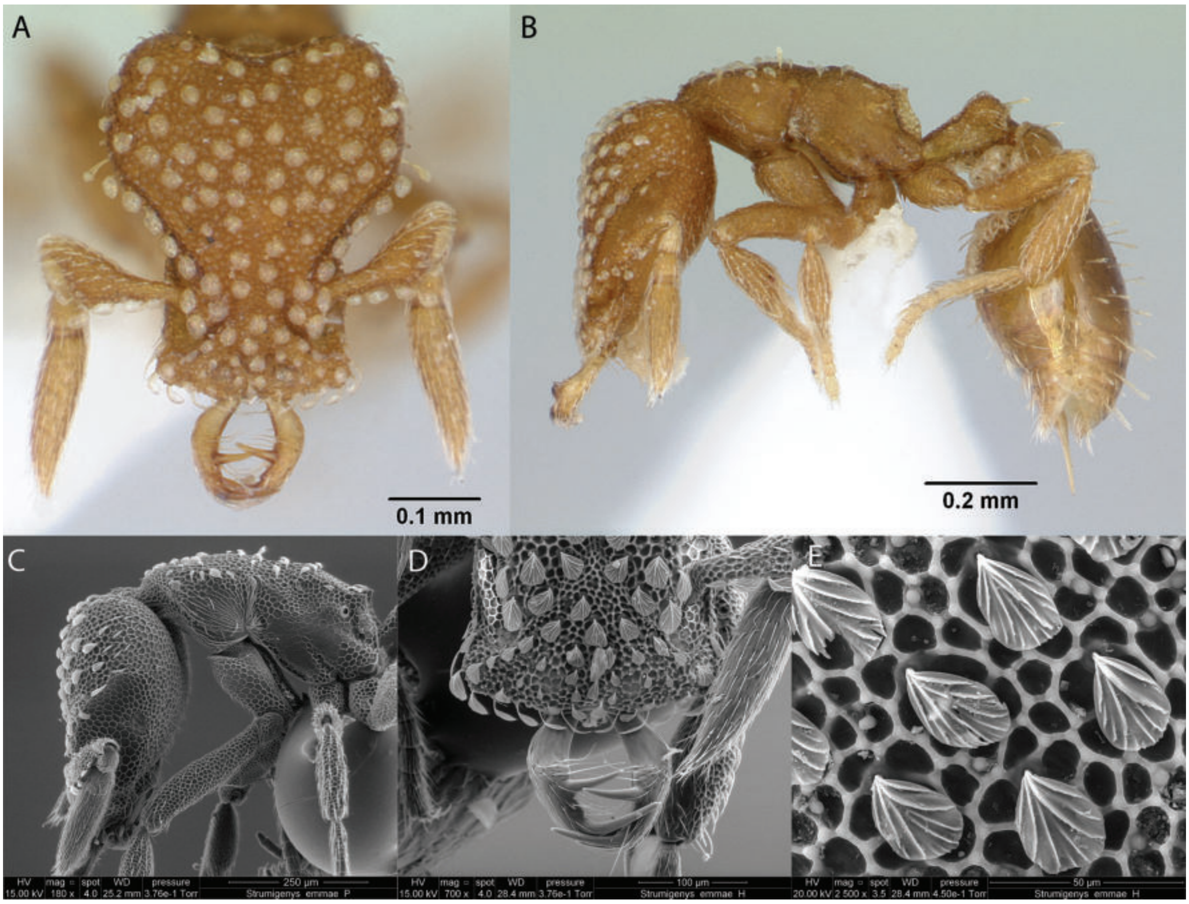

**Figure 34.** *Strumigenys emmae* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in profile **D** close-up of mandibles **E** close-up of spatulate setae.

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Floreana, Isabela (SN, VA), San Cristóbal, Santa Cruz (Herrera et al. 2020).

### *Strumigenys louisianae* Roger, 1863

Fig 35

**Remarks.** Cited in Lubin (1984), (Pezzatti et al. (1998), von Aesch (2006) [ICCDRS], Causton et al. (2006), Herrera et al. (2014), Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2016), Herrera et al. (2020), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** In Kempf (1972), Brandão (1991), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Nearctic, Neotropical.

**Galápagos distribution.** Introduced: Floreana, Isabela (CA, SN, VA), San Cristóbal, Santa Cruz (Herrera et al. 2020).

**New record.** Santiago.

### *Strumigenys membranifera* Emery, 1869

Fig. 36

**Remarks.** Galápagos first published record in Herrera et al. (2014). Cited in Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** In Kempf (1972), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Isabela (VA, VW), Santiago (Herrera et al. 2020).

### Genus *Tetramorium* Mayr, 1855

### *Tetramorium bicarinatum* (Nylander, 1846)

Fig. 37

**Remarks.** Originally cited as *Myrmica bicarinatum* in (Nylander, 1846). Cited as *Tetramorium guineense* in Emery (1893), Wheeler (1919) [CAS], Wheeler (1924), Wheeler (1933) [CAS], Linsley and Usinger (1966), Kempf (1972), Clark et al. (1982), Brandão and Paiva (1994). As *T. bicarinatum* in Lubin (1984), Lubin (1985) [QCAZ], Abedrabbo (1994) [ICCDRS], de la Vega (1994), Meier (1994) [ICCDRS], Pezzatti et al. (1998) [ICCDRS], von Aesch and Cherix (2005), von Aesch (2006) [ICCDRS], Causton et al. (2006), Herrera and Causton (2010) [ICCDRS], Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Kempf (1972), Brandão (1991), Bolton (1995, 2014), Bolton et al. (2006).

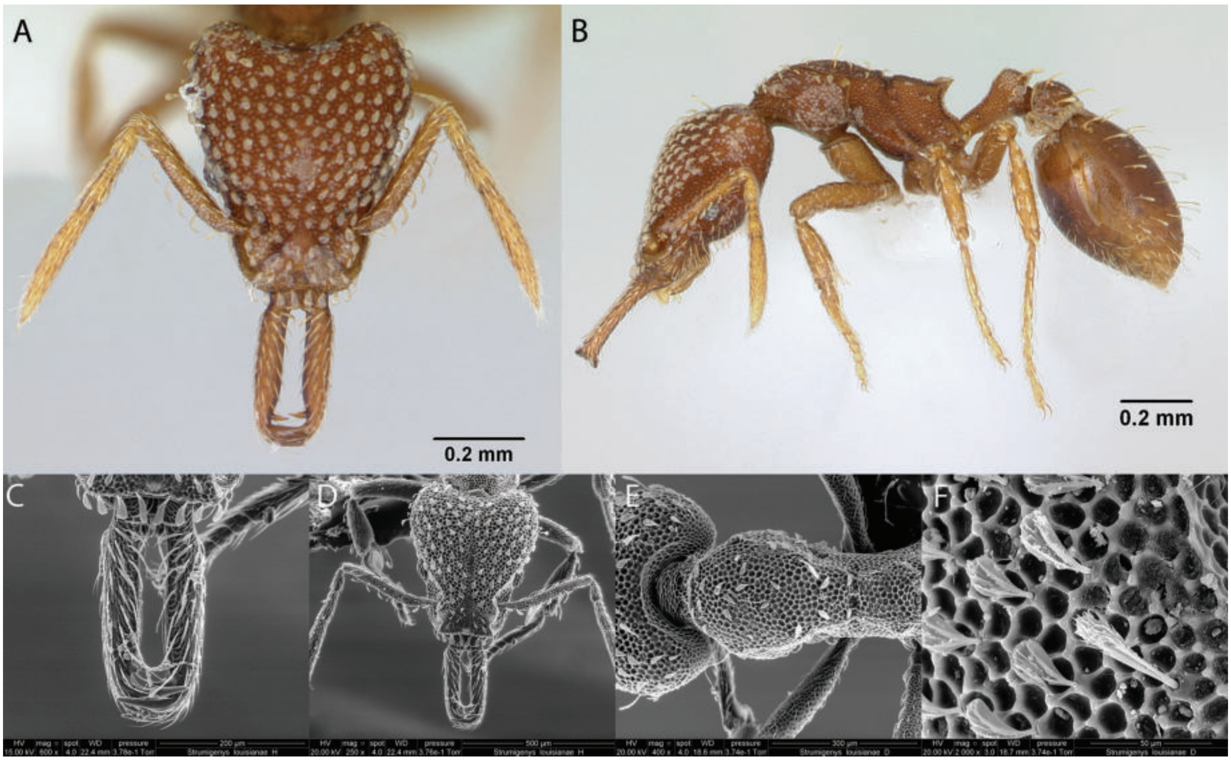

**Figure 35.** *Strumigenys louisianae* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on mandibles **D** head in full-face view **E** mesosoma in dorsal view **F** close-up on spatulate setae.

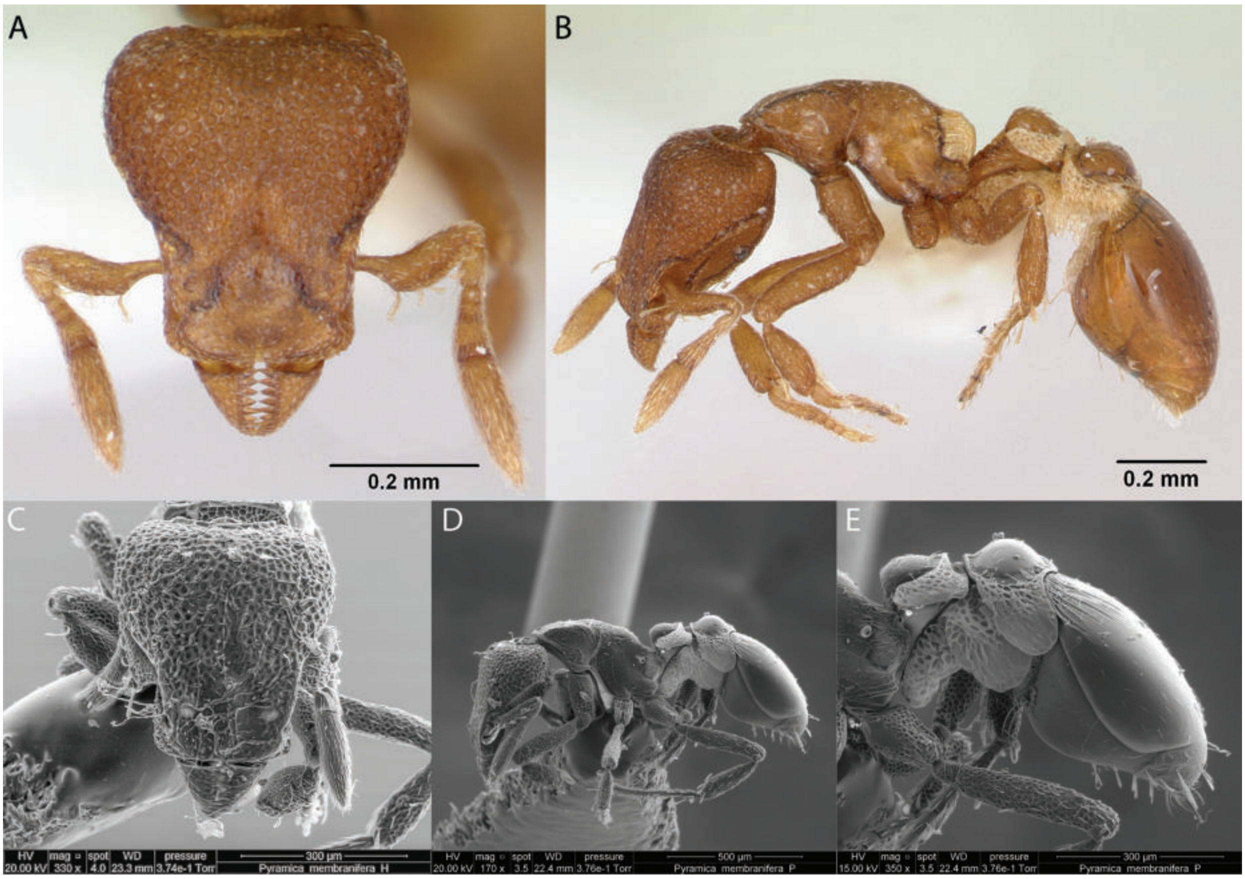

**Figure 36.** *Strumigenys membranifera* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** head in profile **E** petiole and postpetiole with developed spongiform tissue.

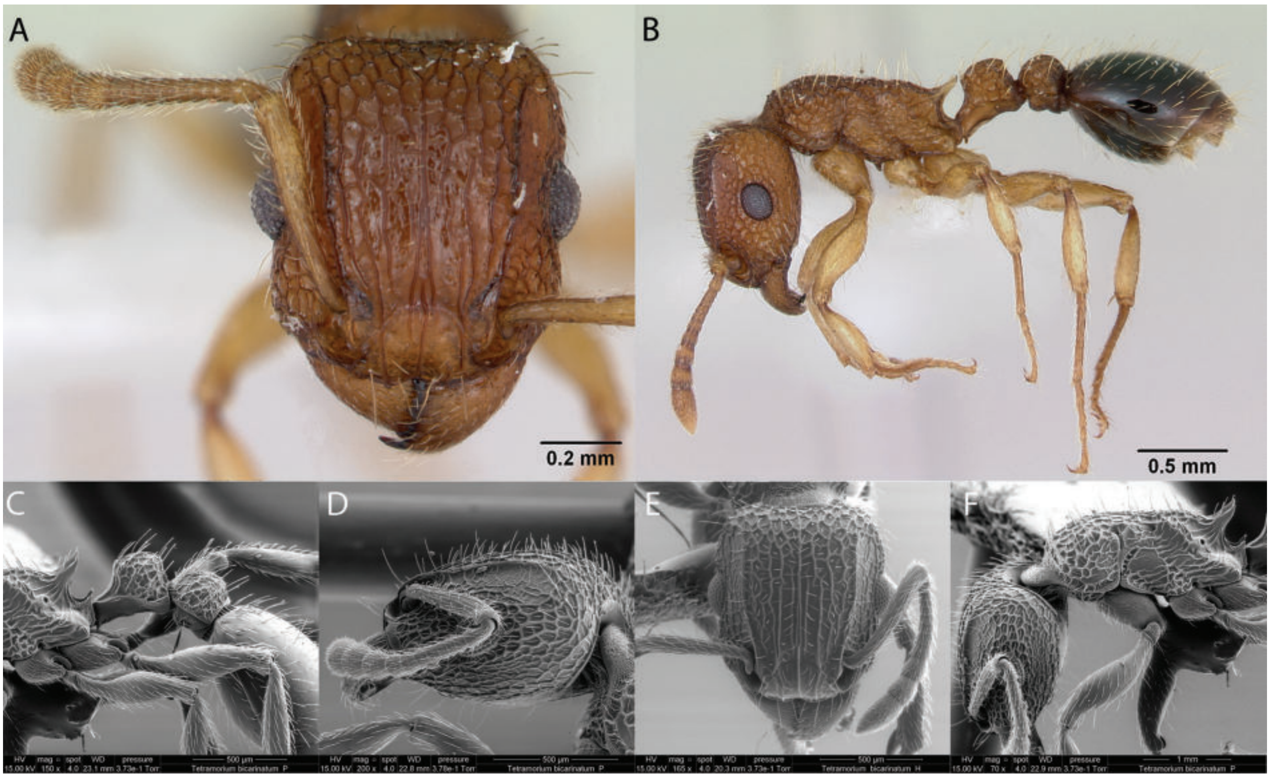

Figure 37. *Tetramorium bicarinatum* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** petiole and postpetiole in profile **D** head in profile **E** head in full-face view **F** mesosoma in profile.

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Bainbridge #1, Bainbridge #2, Bainbridge #3, Bainbridge #4, Bainbridge #5, Bainbridge #6, Bainbridge #8, Baltra, Bar, Bayas, Caldwell, Daphne Mayor, Española, Fernandina, Floreana, Gardner (next to Floreana), Gardner (next to Española), Genovesa, Guy Fawkes, Isabela (CA, SN, VA, VD, VE, VW), Mariela Grande, Mariela Mediana, Marchena, Pinzón, Plaza Norte, Plaza Sur, Rábida, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé, Sombrero Chino (Herrera et al. 2020).

**New records.** Beagle #2, Beagle #3, Santiago Island.

### *Tetramorium caldarium* (Roger, 1857)

Fig. 38

**Remarks.** Originally cited as *Tetrogmus caldarium* in (Roger, 1857). Cited in Brandão and Paiva (1994), Meier (1994), Pezzatti et al. (1998), von Aesch and Cherix (2005), von Aesch (2006), Causton et al. (2006), Dekoninck et al. (2014) [RBINS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Kempf (1972), Brandão (1991), Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Floreana, Santa Cruz (Herrera et al. 2020).

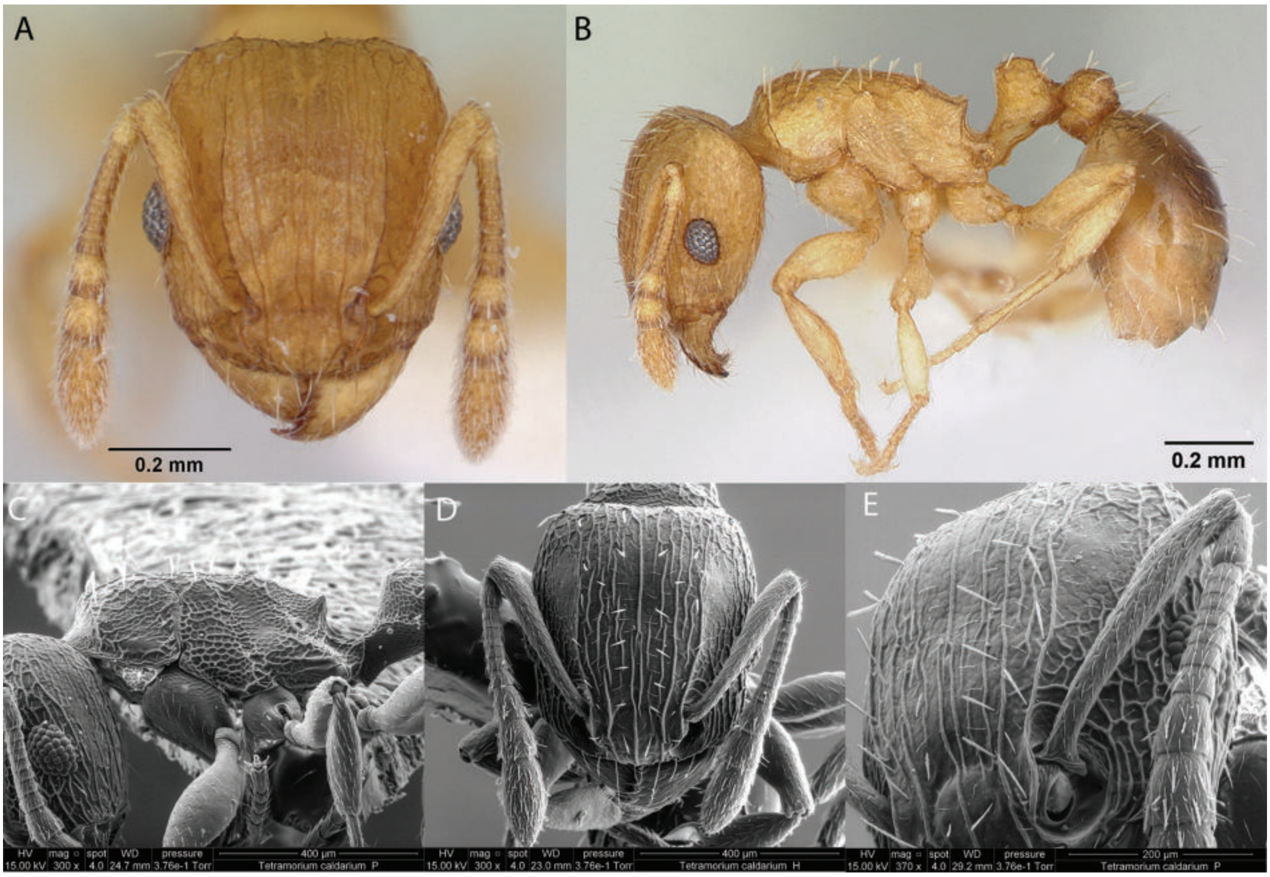

**Figure 38.** *Tetramorium caldarium* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** mesosoma profile **D** head in full-face view **E** close-up on the antennal scrobe.

### *Tetramorium lanuginosum* Mayr, 1870
Fig. 39

**Remarks.** First published record (Pezzatti et al. (1998) [ICCDRS]. Cited also in Causton et al. (2006), Herrera and Causton (2010) [ICCDRS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** In Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Bainbridge #3, Bainbridge #8, Baltra, Floreana, Gardner (next to Española), Isabela (VD), Pinzón, Plaza Norte, Plaza Sur, Rábida, San Cristóbal, Santa Cruz, Santa Fé, Seymour Norte, Wolf (Herrera et al. 2020).

**New records.** Bainbridge #1, Bartolomé, Beagle #2, Beagle #3, Champion, Mao, Marchena, Santiago, Sombrero Chino.

### *Tetramorium simillimum* (Smith, 1851)
Fig. 40

**Remarks.** Originally cited as *Myrmica simillimum* in (Smith, 1851). First published record in Wheeler (1919). Cited also in Wheeler (1933), Kempf (1972),

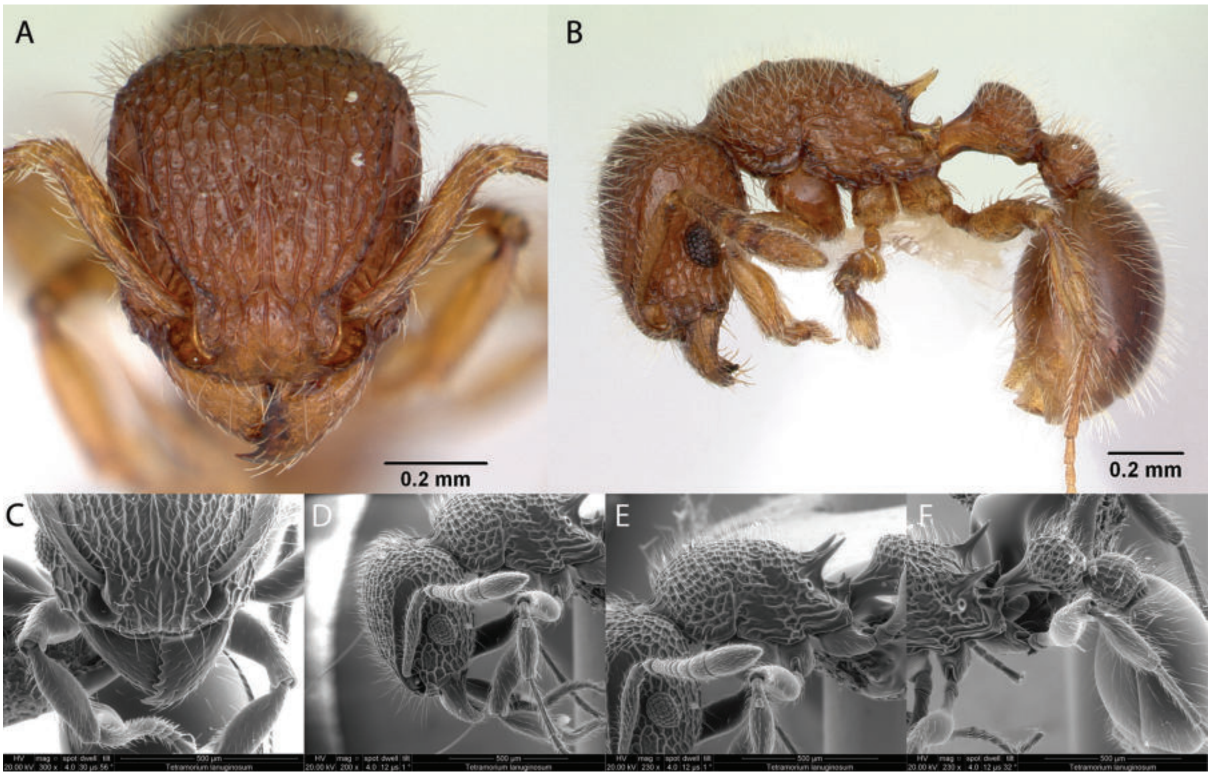

**Figure 39.** *Tetramorium lanuginosum* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on mandibles and clypeus **D** head in profile **E** mesosoma in profile **F** petiole and postpetiole in profile.

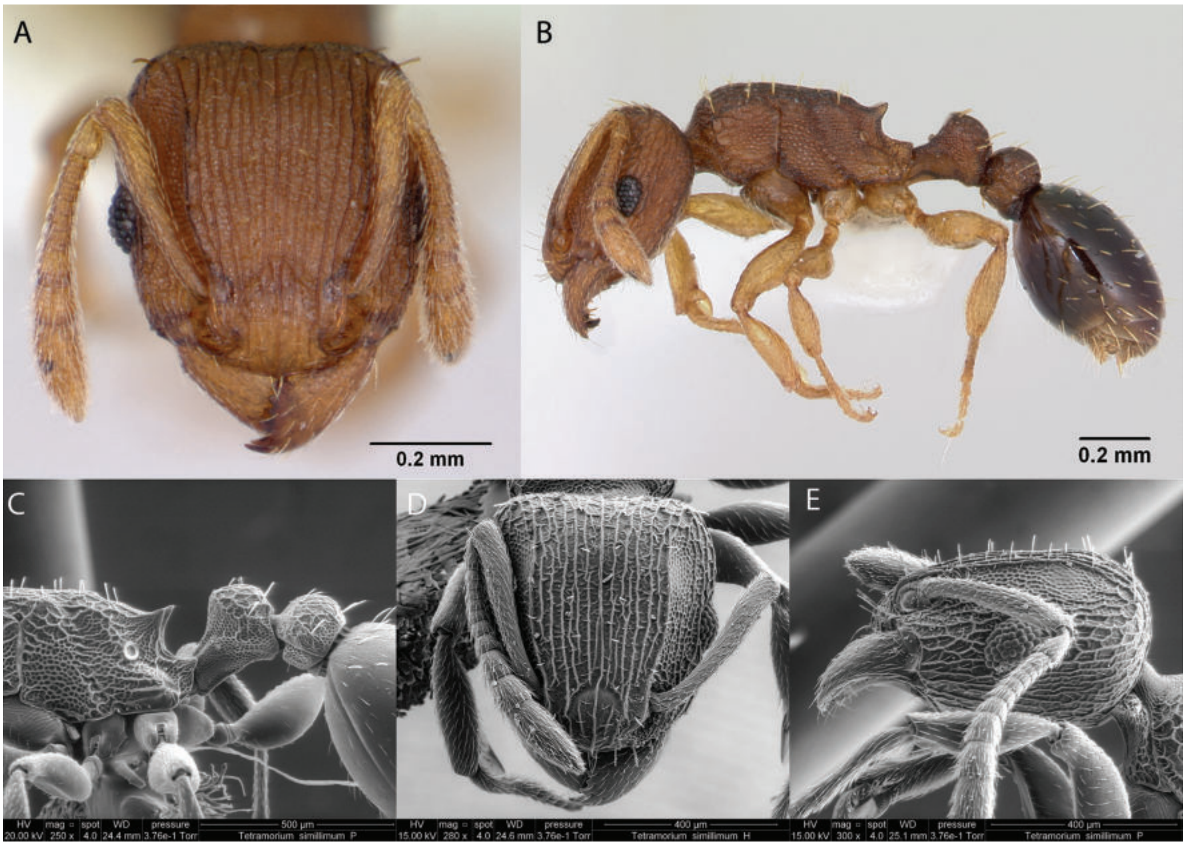

**Figure 40.** *Tetramorium simillimum* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** petiole and postpetiole in profile **D** head in full-face view **E** head in profile.

Linsley and Usinger (1966), Clark et al. (1982), Lubin (1984), Lubin (1985), Brandão and Paiva (1994), Abedrabbo (1994) [ICCDRS], Peck et al. (1998), (Pezzatti et al. (1998) [ICCDRS], Roque-Albelo et al. (2000) [ICCDRS], von Aesch and Cherix (2005), von Aesch (2006) [ICCDRS], Causton et al. (2006), Herrera and Causton (2010) [ICCDRS], Herrera et al. (2014). Wauters et al. (2016) [RBINS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Bainbridge #6, Baltra, Bar, Cousin, Daphne Mayor, Floreana, Gardner (next to Floreana), Isabela (SN, VA), Marchena, Mariela Grande, Santiago, San Cristóbal, Santa Cruz, Tortuga (Herrera et al. 2020).

**New record.** Mariela Mediana.

### ***Tetramorium lucayanum*** **Wheeler, 1905**

Fig. 41

**Remarks.** First published record in Herrera et al. (2014), Cited also in Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Neotropical, Palearctic.

**Galápagos distribution.** Introduced: Isabela (CA) (Herrera et al. 2014).

**New record.** Isabela (SN).

## **Genus *Trichomyrmex* Mayr, 1855**

### ***Trichomyrmex destructor*** **(Jerdon, 1851)**

Fig. 42

**Remarks.** Originally cited as *Atta destructor* in (Jerdon, 1851). Cited as *Monomorium destructor*, in Pezzatti et al. (1998), von Aesch and Cherix (2005), von Aesch (2006), Causton et al. (2006), Herrera and Causton (2010) [ICCDRS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Baltra, Floreana, Isabela (SN), Santiago (Herrera et al. 2020).

## **Genus *Wasmannia* Forel, 1893**

### ***Wasmannia auropunctata*** **(Roger, 1863)**

Fig. 43

**Remarks.** Originally cited as *Tetramorium auropunctata* in (Roger, 1863). First published record in Silberglied (1972). Cited in Lubin (1983), Lubin (1984) [ICCDRS], Lubin (1985), McMullen (1987), Williams (1987), Ulloa-Chacón et al. (1991), Coppois and Wells (1987), McMullen (1990), Brandão (1991), Williams and Whelan

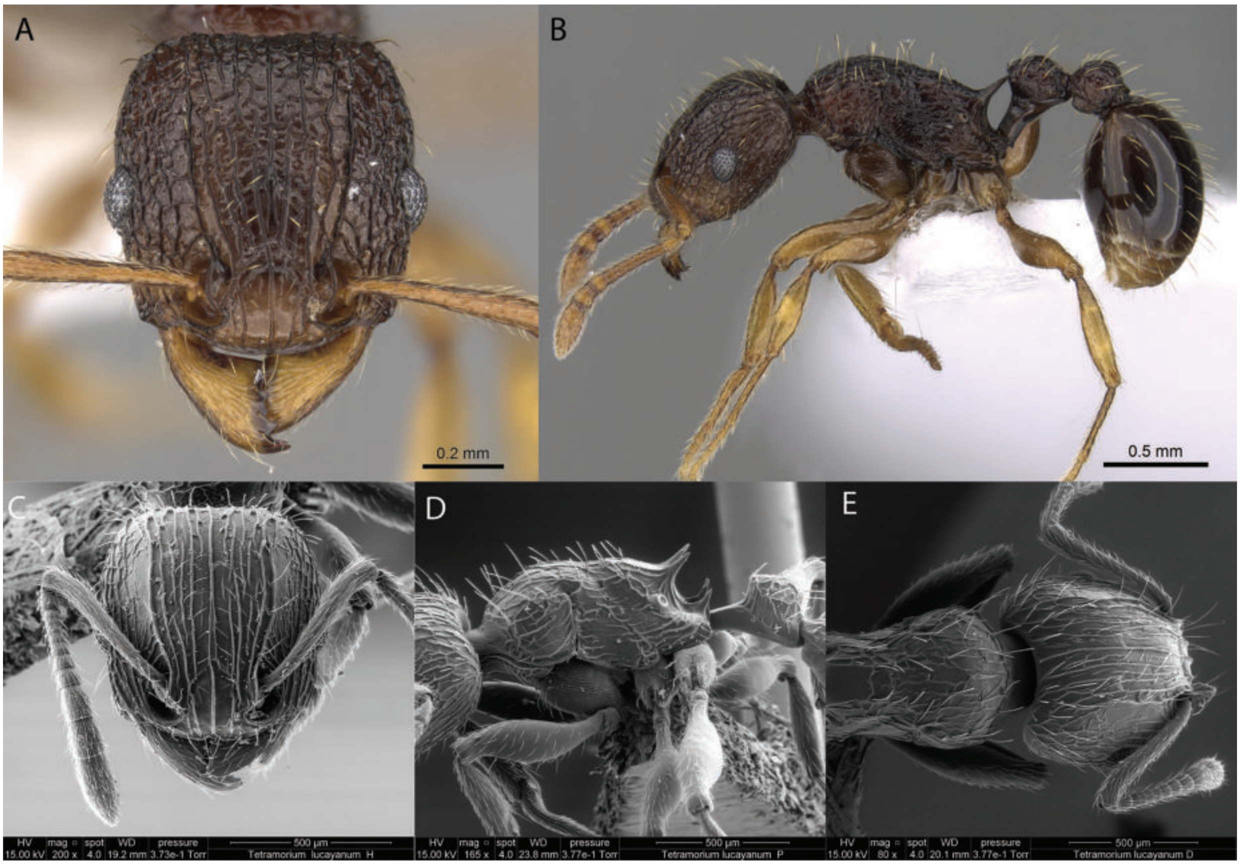

**Figure 41.** *Tetramorium lucayanum* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** mesosoma in profile **E** head in dorsal view.

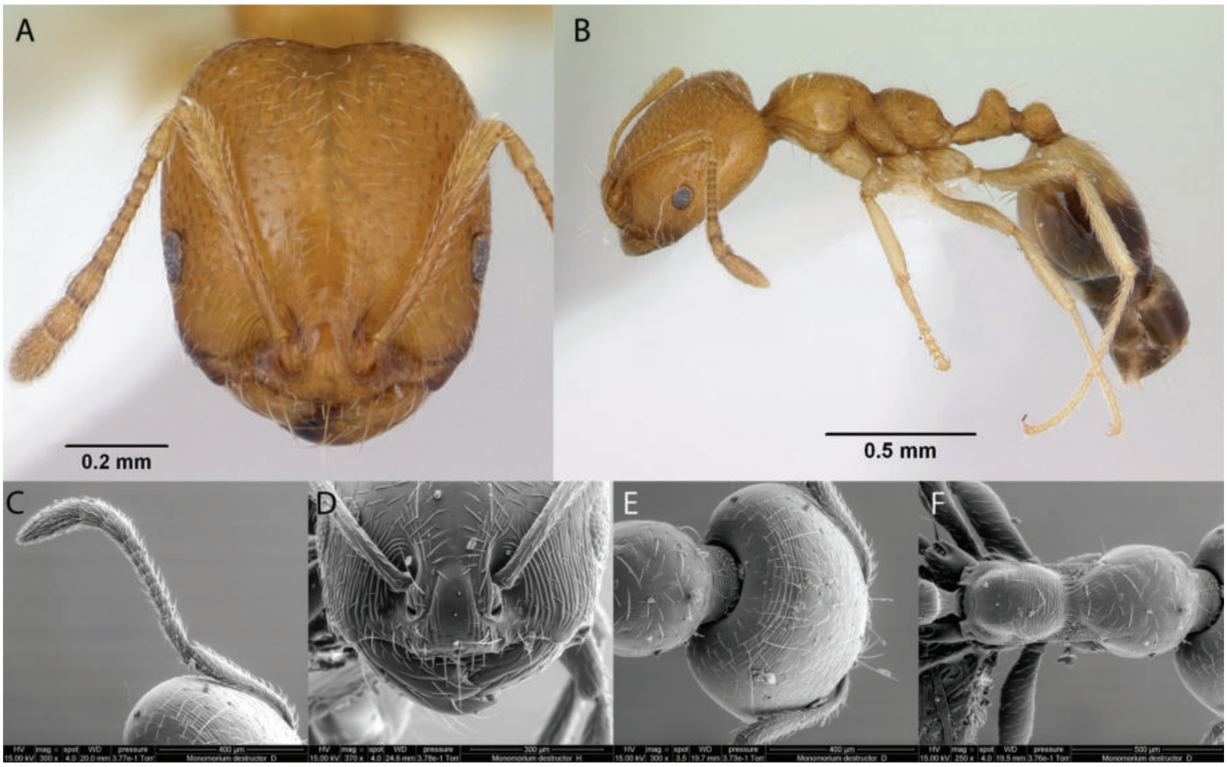

**Figure 42.** *Trichomyrmex destructor* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on antennae **D** close-up on mandibles **E** head in dorsal view **F** mesosoma in dorsal view.

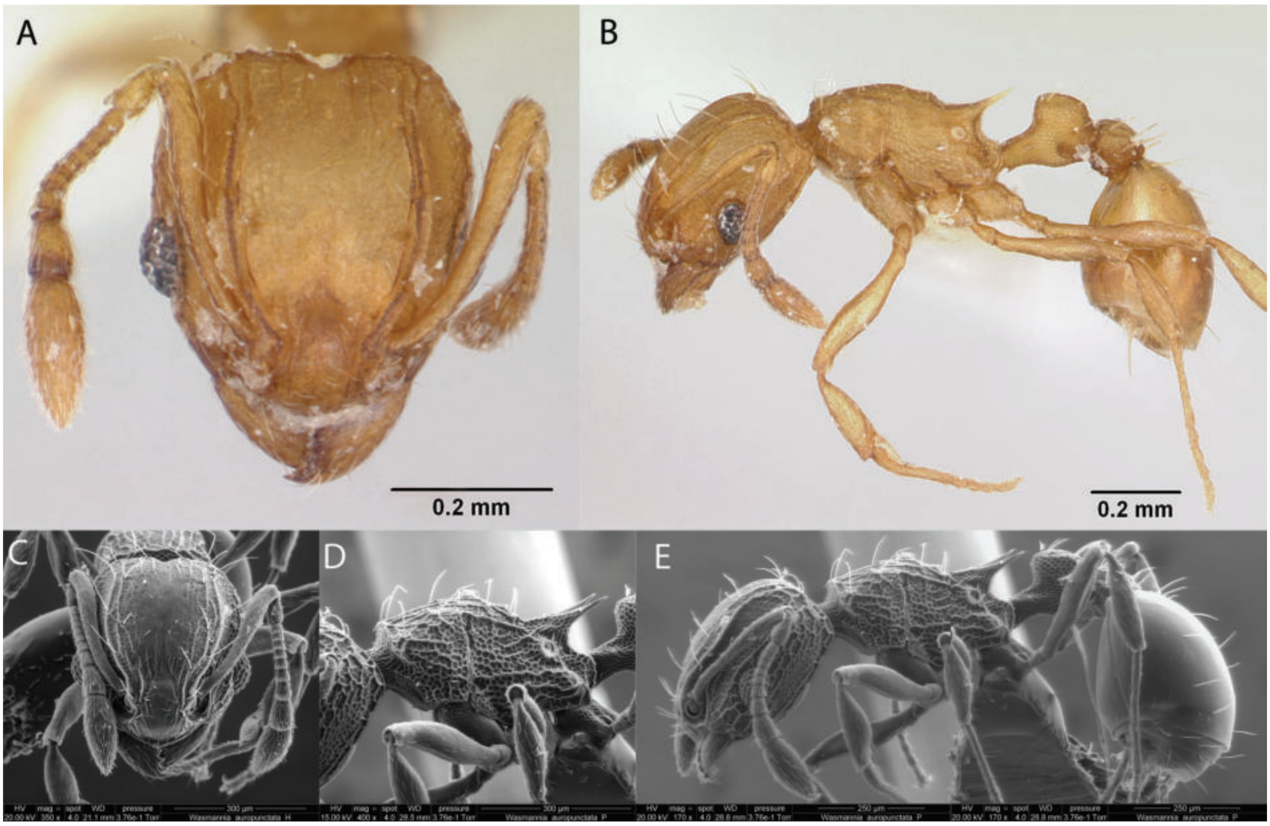

**Figure 43.** *Wasmannia auropunctata* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in full-face view **D** mesosoma in profile **E** head in profile **F** metasoma in profile.

(1992), McMullen (1993), Brandão and Paiva (1994), Meier (1994), Abedrabbo (1994) [ICCDRS], Ulloa-Chacón and Cherix (1994), de la Vega (1994), Lundh (1998), Peck et al. (1998), Pezzatti et al. (1998) [ICCDRS], Roque-Albelo et al. (2000) [ICCDRS], Boada (2005) [ICCDRS], Causton et al. (2005) [ICCDRS], von Aesch (2006) [ICCDRS], Causton et al. (2006), McMullen (2007), Herrera and Causton (2010) [ICCDRS], Herrera and Longino (2008), (McMullen (2011), Herrera et al. (2013), Dekoninck et al. (2014) [ICCDRS, RBINS], Wauters et al. (2014) [RBINS], Wauters et al. (2016) [RBINS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Afrotropical, Australasia, Indomalaya, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Albany, Bainbridge #1, Baltra, Bowditch South, Champion, Cousin, Eden, Española, Floreana, Gran Felipe, Isabela (SN, VA, VD, VE, VW), Mao, Marchena, Pinzón, Rábida, Santiago, San Cristóbal, Santa Cruz, Seymour Norte, Santa Fé, Tortuga (Herrera et al. 2020).

## Key to the genera and species of the subfamily Ponerinae

1 Mandible elongate and linear (Figs 49C, 50C); petiolar node armed with apical spine (Figs 49D, 50D). (*Odontomachus*) .......................................... **2**

– Mandibles not elongate (Figs 44D, 47C, 48C); petiole not armed with apical spine (Figs 44C, B, 47A, C) ....................................................................... **3**

2 Entirely dark brown (Fig. 49A, B); long hairs located below the mandibles, running from the base towards the apex (Fig. 49C); anterior face of the petiole somewhat convex (Fig. 49D)........................... ***Odontomachus bauri***

– Somewhat tricolored: head, antennae and legs orangish, mesosoma reddish brown and gaster dark brown (Fig. 50A, B); ventral face of mandibles with short hairs running from base towards apex (Fig. 50C); anterior face of petiole almost straight or less convex than above (Fig. 50D)........................................................................... ***Odontomachus ruginodis***

3 Mandibles falcate with apical tooth; anterior margin of clypeus triangular with carina conspicuously or slightly visible in median portion (Figs 47C, 48C); anterior legs with finely pectinate tarsal claws (Fig. 48D) (*Leptogenys*)........................................................................................... **4**

– Triangular with dentate mandibles; anterior margin of clypeus without median carina (Fig. 44D; 46D); legs with simple tarsal claws (Fig. 44F) (*Hypoponera*)........................................................................................... **5**

4 Mandibles with basal margin distant from the anterior margin of clypeus when closed (Fig. 47A, C); in lateral view, mesosoma with numerous hairs and petiole higher than wide (Fig. 47D); ~ 5 mm long; body entirely brown (Fig. 47A, B)............................................................... ***Leptogenys santacruzi***

– Mandibles with basal margin almost flush with the anterior border of clypeus when closed (Fig. 48A, C); mesosoma smooth and shiny with few setae; lacking longitudinal striae in the pronotum and propodeum; petiole elongated in lateral view (Fig. 48B, E); ~ 4 mm long; body black, mandibles, legs, and antennae brown (Fig. 48A, B)................. ***Leptogenys* cf. *gorgona***

5 Color dark red brown to black (Fig. 45A, B); scape of antenna reaching the occipital margin of the head (Fig. 45A); petiolar node quadrate (Fig. 45B, C)............................................................................ ***Hypoponera opaciceps***

– Color red brown to dark brown (Figs 44A, B, 46A, B); scape of antenna never reaching the occipital margin of the head (Figs 44A, 46E); petiolar node never quadrate........................................................................................... **6**

6 Lateral surface of petiole relatively coarse with the dorsum somewhat rounded, not totally covered with fine appressed hairs (Fig. 44C)........................................................................................... ***Hypoponera beebei***

– Lateral surface of petiole somewhat more thick than coarse, with the dorsum somewhat triangular, sometimes covered by many fine appressed hairs (Fig. 46F)............................................................. ***Hypoponera opacior***

### Genus *Hypoponera* Santschi, 1938

#### *Hypoponera beebei* (Wheeler, 1924)

Fig. 44

**Remarks.** Originally cited as *Ponera beebei* in Wheeler (1924: 107). *Hypoponera beebei* in Linsley and Usinger (1966), Kempf (1972), Lubin (1985), Peck (1994a), Peck (1994b), Roque-Albelo et al. (2000), Wauters et al. (2016), Lubin (1984), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Kempf (1972), Bolton (1995, 2014), Bolton et al. (2006).

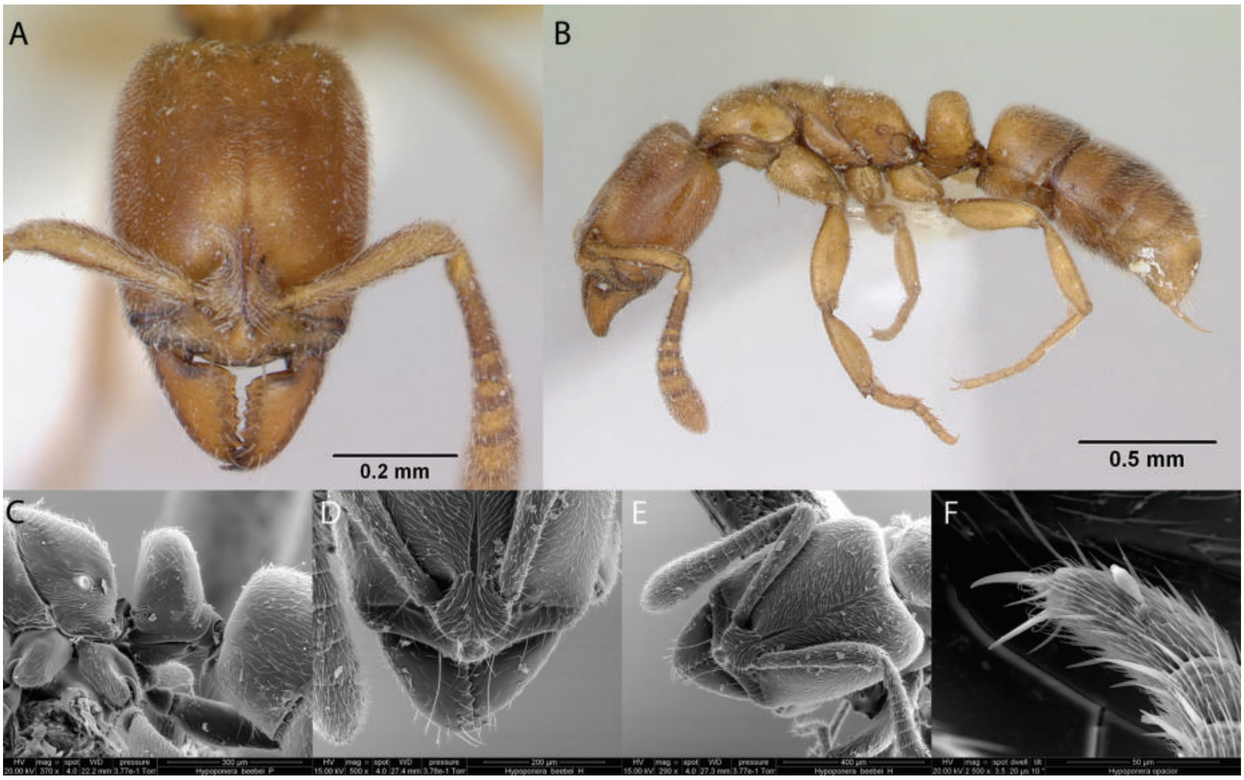

**Figure 44.** *Hypoponera beebei* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on petiole in profile **D** close-up on mandibles **E** head in full-face view **F** close-up on tarsal claws.

**Distribution.** Possibly endemic: Fernandina, Floreana, Isabela (CA, SN, VA, VW), Marchena, San Cristóbal, Santa Cruz, Seymour Norte, Genovesa (Herrera et al. 2020).

### ***Hypoponera opaciceps*** **(Mayr, 1887)**

Fig. 45

**Remarks.** Originally cited as *Ponera opaciceps* in (Mayr, 1887). First published record in (Lubin 1983). Cited also in Lubin (1984), Peck (1994b), Dekoninck et al. (2014), Herrera (2015), Wauters et al. (2016), and Herrera et al. (2020).

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Australasia, Indomalaya, Nearctic, Neotropical, Oceania, Palearctic.

**Galápagos distribution.** Introduced: Baltra, Fernandina, Floreana, Isabela (CA, SN, VA, VD) Marchena, San Cristóbal, Santa Cruz, Santiago (Herrera et al. 2020).

### ***Hypoponera*** **cf.** ***opacior*** **(Forel, 1893)**

Fig. 46

**Remarks.** Originally cited as *Ponera opacior* (Forel, 1893). In Herrera et al. (2014), Dekoninck et al. (2014) [RBINS], Herrera (2015, 2019), and Herrera et al. (2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

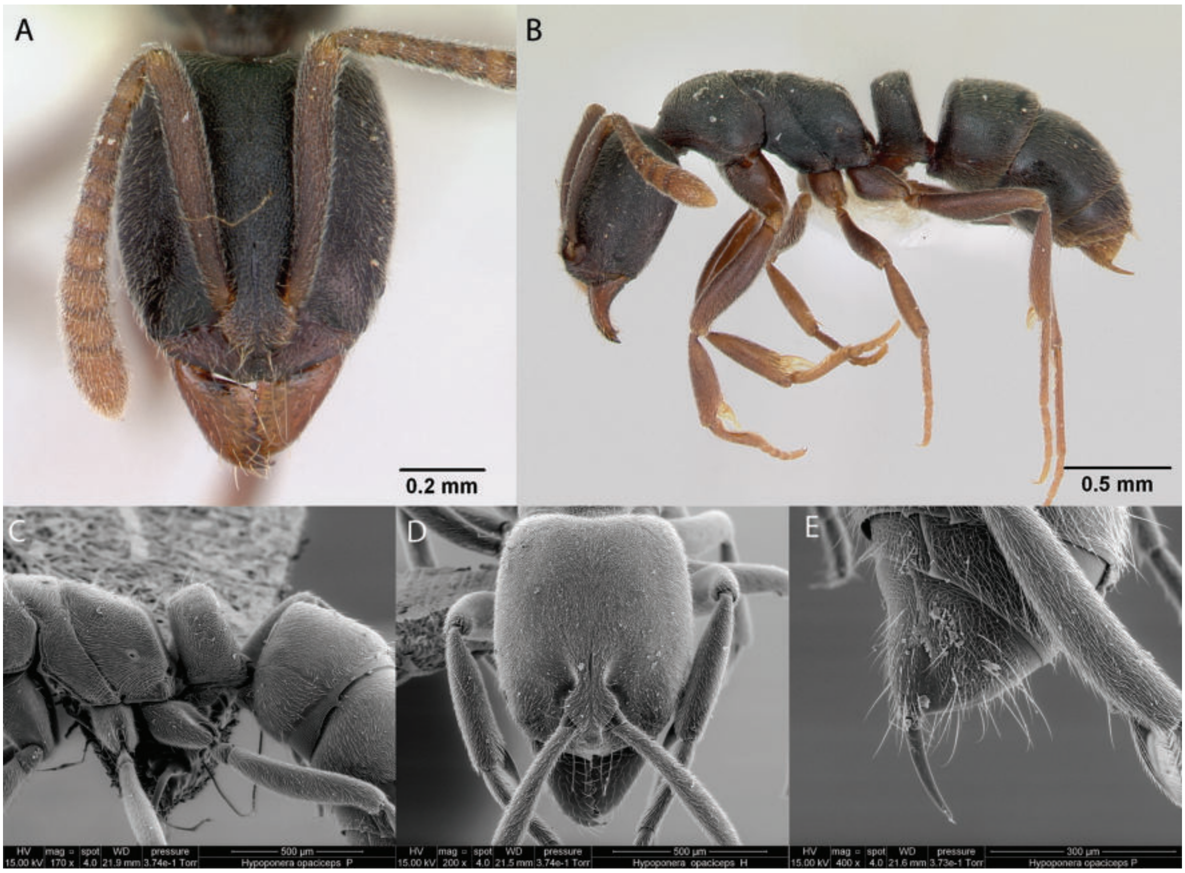

**Figure 45.** *Hypoponera opaciceps* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on petiole in profile **D** head in full-face view **E** stinging apparatus.

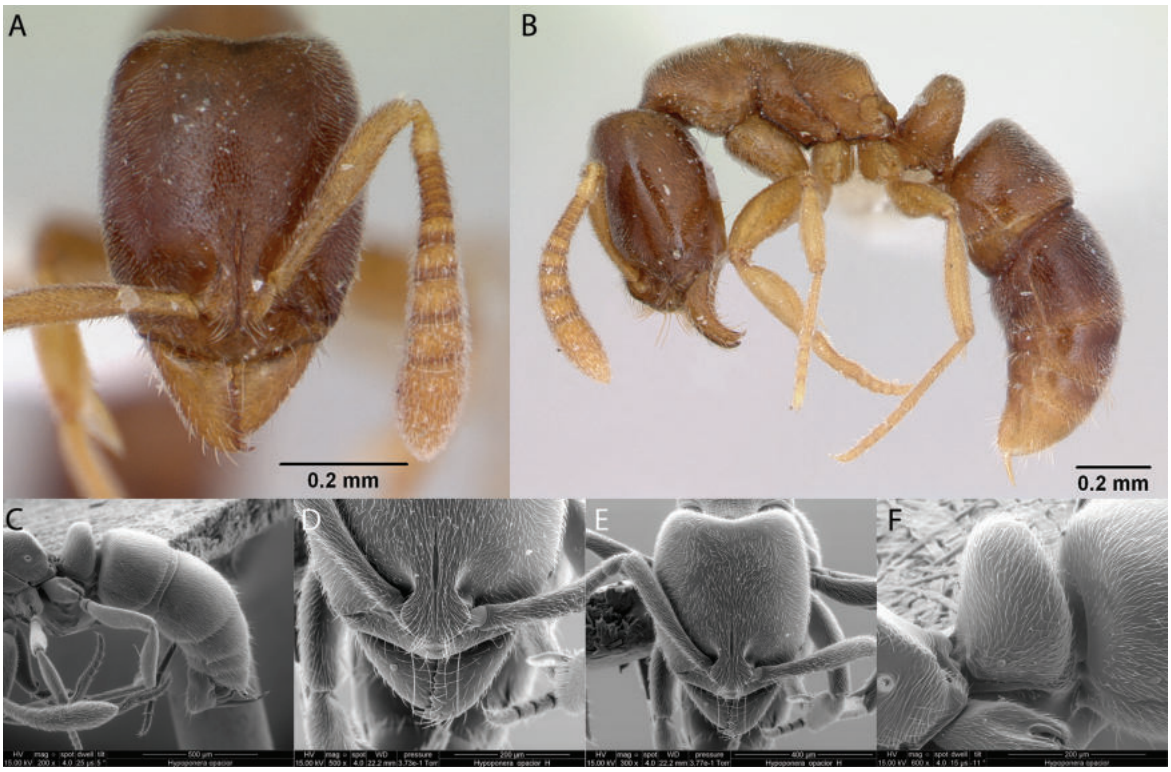

**Figure 46.** *Hypoponera* cf. *opacior* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** metasoma in profile **D** close-up on mandibles **E** head in full-face view **F** close-up on petiole in profile.

**Distribution.** Nearctic, Neotropical.

**Galápagos distribution.** Introduced: Fernandina, Floreana, Isabela (CA, SN, VA, VD, VW), San Cristóbal, Santa Cruz (Herrera et al. 2014).

### Genus *Leptogenys* Roger, 1861

#### *Leptogenys santacruzi* Lattke, 2011

Fig. 47

**Remarks.** Cited in Herrera (2015, 2019) and Herrera et al. (2020) [CAS. ICCDRS].

**Taxonomic history.** Lattke (2011) and Bolton (2014).

**Distribution.** Endemic: Isabela (VA), Santa Cruz Islands (Herrera et al. 2020).

#### *Leptogenys* sp. *gorgona* (hh03)

Fig. 48

**Remarks.** Cited in Lattke (2011), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS].

**Distribution.** Native: Santa Cruz.

**New record.** Isabela Island (SN).

### Genus *Odontomachus* Latreille, 1804

#### *Odontomachus bauri* Emery, 1892

Fig. 49

**Remarks.** Cited as *O. bauri* in Emery (1893), as *Odontomachus haematoda bauri* in Wheeler (1919) [CAS], Wheeler (1924), Wheeler (1933) [CAS], Kempf (1972) and *Odontomachus haematoda* in Stitz (1932). *Odontomachus bauri* in Pezzatti et al. (1998), von Aesch and Cherix (2005), Linsley and Usinger (1966), Lubin (1984), Brandão (1991), Brandão and Paiva (1994), de la Vega (1994), von Aesch and Cherix (2005), von Aesch (2006) [ICCDRS], Causton et al. (2006), Dekoninck et al. (2014) [RBINS], Wauters et al. (2014), Herrera (2015, 2019) and Herrera et al. (2020) [ICCDRS, ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Neotropical.

**Galápagos distribution.** Introduced: Floreana, Isabela (CA, SN), San Cristóbal, Santa Cruz (Herrera et al. 2020).

#### *Odontomachus ruginodis* Wheeler, 1908

Fig. 50

**Remarks.** First published record in Herrera et al. (2014), see also Herrera (2015, 2019) and (Herrera et al. 2020) [ICCDRS].

**Taxonomic history.** Bolton (1995, 2014), Bolton et al. (2006).

**Distribution.** Nearctic, Neotropical.

**Galápagos distribution.** Introduced: Santa Cruz (Herrera et al. 2014).

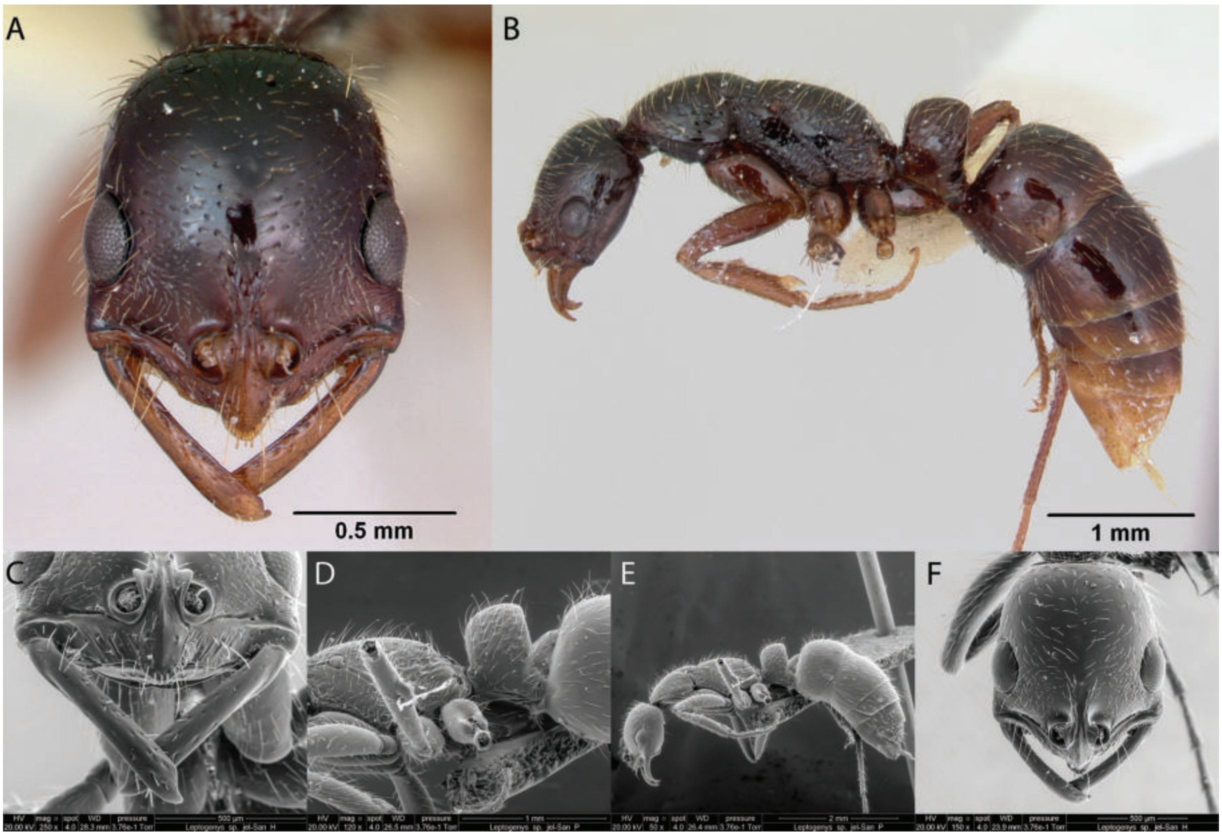

Figure 47. *Leptogenys santacruzi* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on mandibles **D** close-up on petiole in profile **E** view in profile **F** head in full-face view.

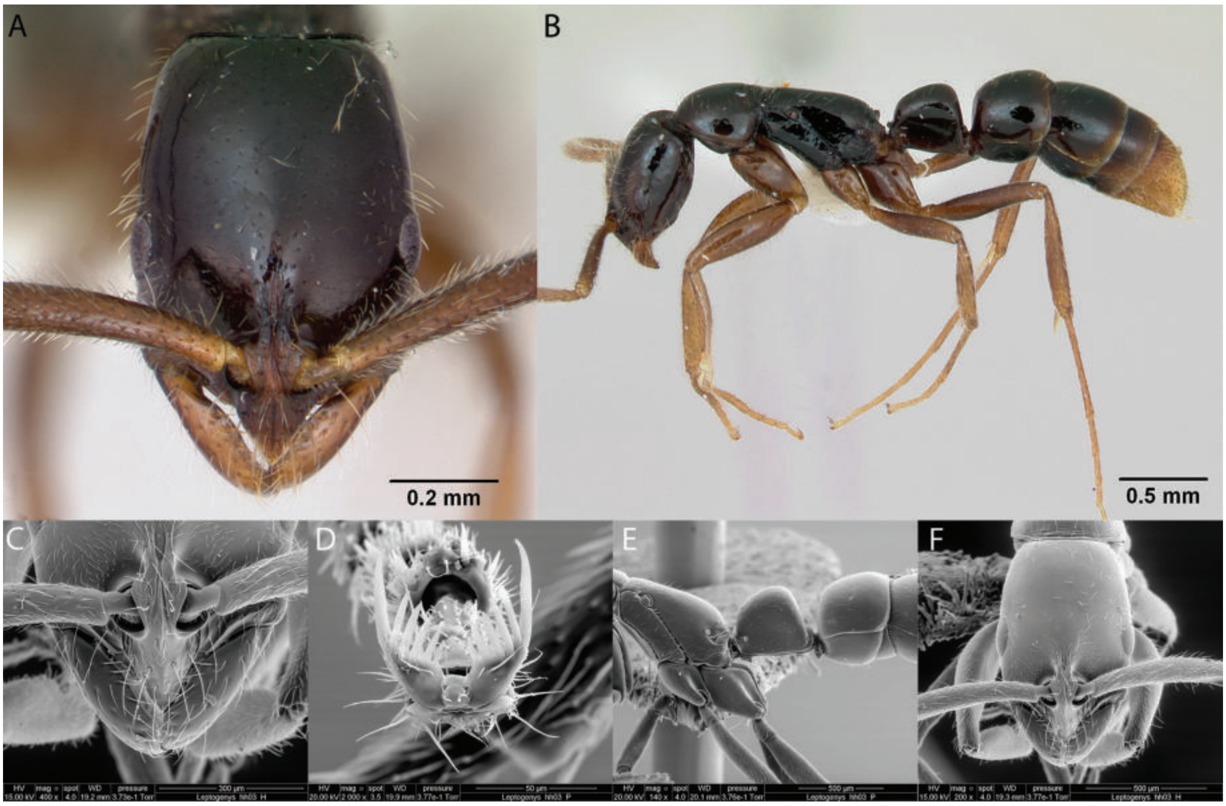

Figure 48. *Leptogenys* cf. *gorgona* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** close-up on clypeus **D** close-up on tarsal claws **E** close-up on petiole in profile **F** head in full-face view.

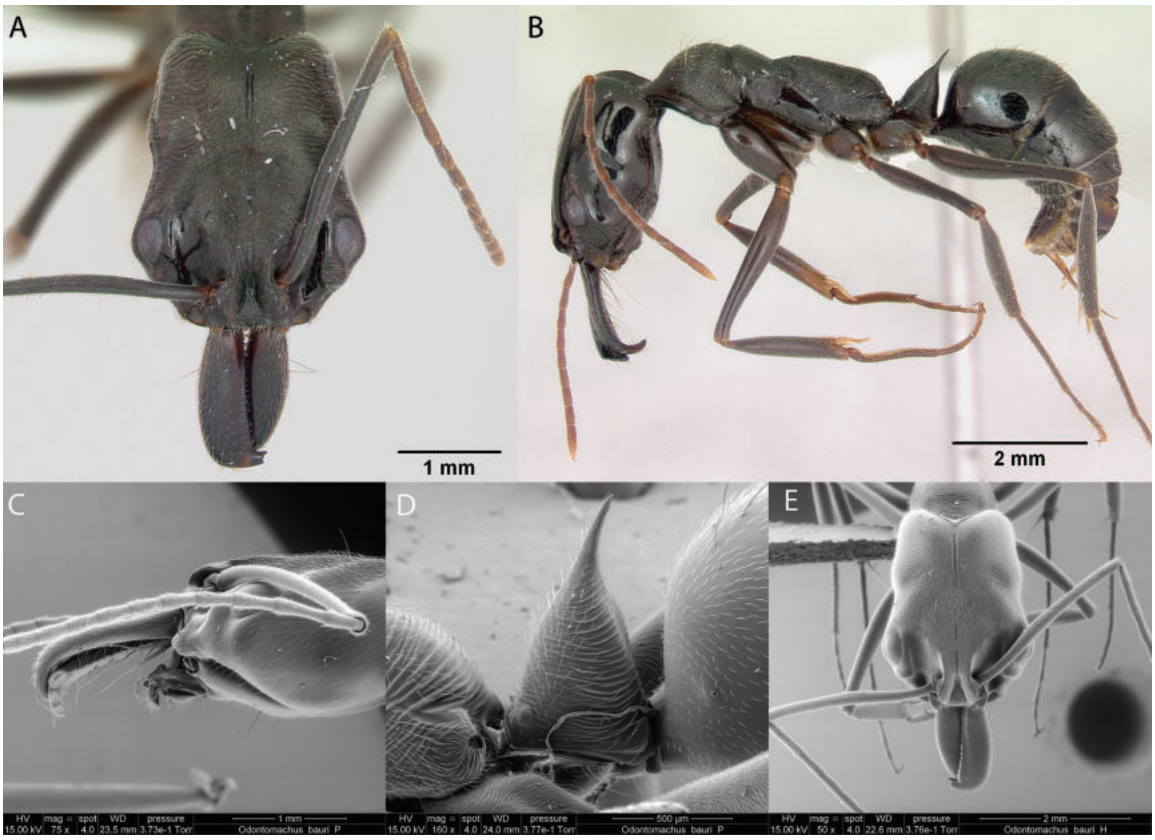

**Figure 49.** *Odontomachus bauri* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in profile **D** close-up on petiole in profile **E** head in full-face view.

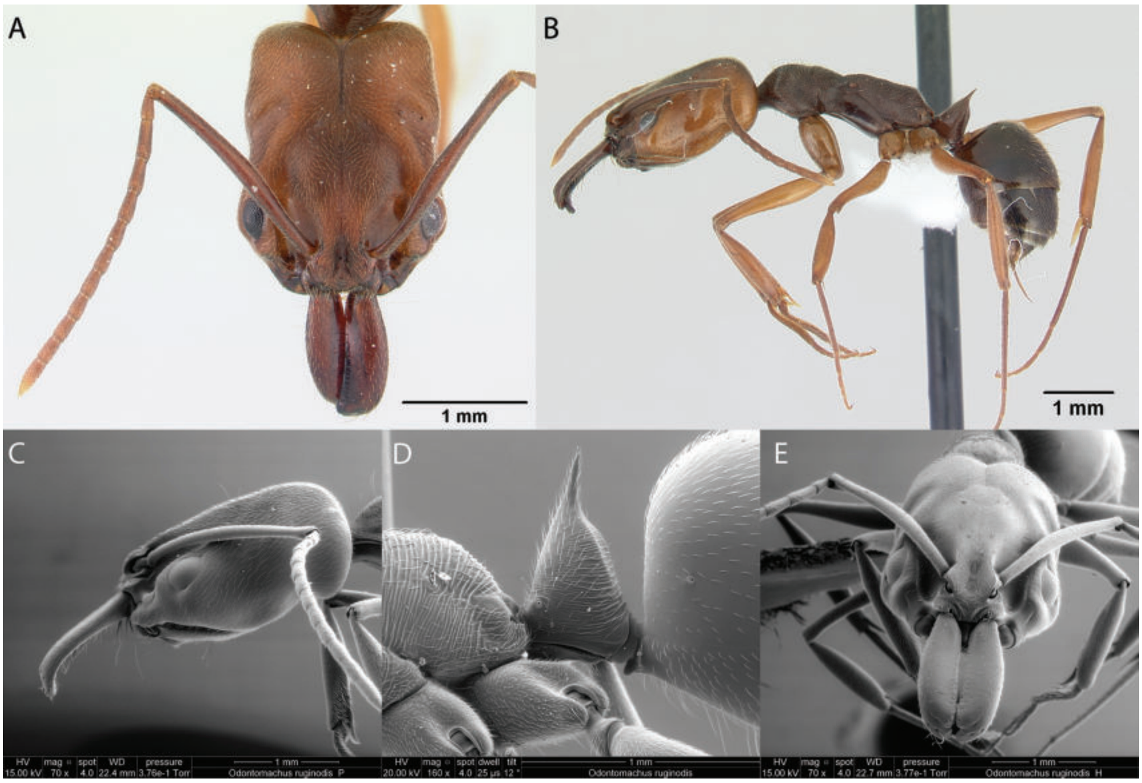

**Figure 50.** *Odontomachus ruginodis* worker micrographs in **A** head in full-face view **B** view in profile, and SEM images of **C** head in profile **D** close-up on petiole in profile **E** head in full-face view.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: HWH, FH, WD. Data curation: MCCT, HWH, GF. Formal analysis: MCCT, GF. Investigation: HWH. Methodology: MCCT, GF. Supervision: HWH. Visualization: GF, MCCT. Writing – original draft: HWH. Writing – review and editing: FH, GF, CEC, WD, MCCT.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# Three new species and two newly recorded species of Tachininae from Tibet, China (Arthropoda, Insecta, Diptera, Tachinidae)

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## Abstract

During our studying of the fauna of Tibet, China, many specimens of the subfamily Tachininae (Diptera, Tachinidae) were collected and examined. Three species are described here as new to science, *Leskia latisurstyla* **sp. nov.**, *Trichoformosomyia cuonaensis* **sp. nov.**, and *Tachina jilongensis* **sp. nov.**, and two species, *Nemoraea javana* (Brauer & Bergenstamm, 1894) and *N. echinata* Mesnil, 1953, are newly recorded from Tibet. In addition to their descriptions, illustrations, and diagnoses, three identification keys are provided. The specimens in this study are kept in the Insect Collection of Shenyang Normal University, China (SYNU).

**Key words:** *Leskia*, *Tachina*, tachinid, taxonomy, *Trichoformosomyia*, western China

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## Introduction

Tibet (=Xizang) Autonomous Region, China (an area of 1,228,400 km$^2$, 26°50'–36°53'N, 78°25'–99°06'E) in western China is located on the main part of the Qinghai-Tibet Plateau (QTP). Zhang et al. (2014) reported that the QTP has an area of 2,542,300 km$^2$ spanning 25°59'37"N to 39°49'33"N and 73°29'56"E to 104°40'20"E, from Pamir in the west to the Hengduan Mountains in the east (about 2800 km) and from the southern edge of the Himalayas in the south to the Kunlun and northern Qilian Mountains in the north (300–1500 km). The average elevation of this plateau is above 4,000 m. QTP has an alpine, low-oxygen environment and is also called the Third Pole of the Earth or the Asian Water Tower. In addition to China (Qinghai, Tibet, southwestern Gansu, western Sichuan, northwestern Yunnan, and southern and southwestern Xinjiang), the QTP is divided among northern Myanmar, Bhutan, northeastern and northwestern India, Nepal, northern Pakistan, Afghanistan, Kyrgyzstan, and Tajikistan. Along its southern and western borders are valleys which are one of the world's 34 "biodiversity hotspots", known as the Himalayan hotspot. Ouyang et al. (2005: 35) reported that QTP is a land of physical and ecological extremes, with the following climatic and biogeographic characteristics: alpine zone, temperate zone, subtropical zone, high Himalayas, and coniferous, valley and montane forests in in southeastern Tibet; shrub grassland in the middle and upper Yar-

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lung Zangbu River valley in southern Tibet; alpine shrub meadow in southeastern Tibet; alpine grassland in central Tibet; mountain desert in western Tibet (Ali region); and arid alpine in northwestern Tibet.

Biogeographically, Tibet is mostly in the Palaearctic Region, but the southern valleys are at the crossroads of the Palaearctic and Oriental regions. Therefore, the tachinid fauna (Diptera, Tachinidae) of Tibet is a combination of eastern Palaearctic, Oriental, and endemic elements. O'Hara et al. (2009) catalogued 1109 valid species in 257 genera, 37 tribes, and four subfamilies of Tachinidae in China. Of these, there are 238 species in 81 genera, 13 tribes and four subfamilies, including 101 species of 22 genera, 10 tribes of Tachininae from Tibet. O'Hara et al. (2020a) listed 2112 species of Palaearctic Tachinidae, including 706 species of Tachininae. O'Hara et al. (2020b) reported 1247 valid tachinid species of 274 genera, 36 tribes, four subfamilies from China, including 269 species of 85 genera, 23 tribes, four subfamilies of Tachinidae with 97 species of 18 genera, eight tribes of Tachininae from Tibet. The phylogenetic position of the family Tachinidae has been partly resolved by Stireman et al. (2019).

During our studying the systematics and diversification of Tachininae (Diptera, Tachinidae) from the Qinghai-Tibetan Plateau, we collected many of specimens of the Tachininae (Diptera, Tachinidae) from Tibet and adjacent northwestern Yunnan in recent years. After careful examination, three species are recognized as new to science, including a species of *Leskia* Robineau-Desvoidy and a species of *Trichoformosomyia* Baranov (both in the tribe Leskiini) and a species of *Tachina* Meigen (tribe Tachinini). Two species of *Nemoraea* Robineau-Desvoidy are newly recorded from Tibet. Descriptions, illustrations, and diagnoses of the above species are given, and keys to the Chinese species of *Leskia* Robineau-Desvoidy and *Tachina* (s.s.) Meigen and of *Trichoformosomyia* Baranov are provided. The keys serve to revise the higher taxonomic classification of Tachininae.

*Leskia* Robineau-Desvoidy is a globally distributed genus with 40 described species, three of which are known to occur in China (O'Hara et al. 2020b; Li et al. 2023): *L. aurea* (Fallén) is widely distributed in the Palaearctic region, *L. flavitegula* Zhang was recently described from Chongqing and Hubei in the Oriental Region, and *L. miranda* Mesnil is distributed in the Palaearctic region of Japan and Russia and was recently found in the Oriental and Palaearctic regions of China (Li et al. 2023). *Trichoformosomyia* Baranov is a small genus with only three known species (Tachi 2013; O'Hara et al. 2020a). *Trichoformosomyia* species are distributed in the Oriental region including Oriental southern China (Guangxi, Sichuan, and Taiwan), Malaysia (Borneo), and Vietnam, and the Palaearctic region including the Russian Far East and Japan (Honshu). Novotna et al. (2009) identified and classified the Western Palaearctic *Tachina* species on the basis of male terminalia and a molecular analysis. O'Hara et al. (2020a) indicated that *Tachina* Meigen has 139 known species of the world, in four subgenera— *Eudoromyia* Bezzi (five species in the Palaearctic), *Nowickia* Wachtl (55 species in the Palaearctic, Oriental, and Nearctic), *Rhachogaster* Townsend (seven species in the Nearctic), *Tachina* Meigen (59 species in the Nearctic, Palaearctic, and Oriental regions)— and 13 species unplaced to subgenus. O'Hara et al. (2020b) reported 67 species of the genus *Tachina* (subgenus *Nowickia* with 15 species and subgenus *Tachina* with 51 species) in China. O'Hara et al. (2020a, b) reported that *Nemoraea* Robineau-Desvoidy has 39 known species in the Afrotropical, Australasian, Palaearctic, and Oriental regions, among which 14 species are known in China.

## Materials and methods

Specimens in the study were collected from Tibet, China. The morphological terminology and measurements used in the descriptions follow Cumming and Wood (2017) and Tschorsnig and Richter (1998). The specimens were examined with Zeiss Stemi SV11 stereomicroscopes. The digital images of heads, abdomens, and bodies of male adults were taken with a Leica 205A microscope and images were blended with Leica Application Suiter v. 4.12.0. Dissections of male terminalia were carried out following the method described by O'Hara (2002), and dissected terminalia were placed in glycerin in a small plastic tube pinned together with the source specimen. The species distribution map was generated with ArcGIS v. 10.2 (ESRI Inc.). The tachinid specimens of this study were deposited in the Insect Collection of Shenyang Normal University, Shenyang (**SYNU**).

## Taxonomy

### Key to Chinese species of *Leskia* Robineau-Desvoidy

1 Abdominal syntergite 1+2 not medially excavate to posterior margin, without median marginal seta, tergite 5 with discal setae. Abdomen covered with some golden- yellow pruinosity. Genal height about 1/7 of eye height. Prementum 3–3.5 times as long as wide .......................... ***L. aurea*** **(Fallén)**

– Abdominal syntergite 1+2 medially excavate to posterior margin, tergites each without discal seta. Abdomen at most covered with grayish-yellow or grayish-white pruinosity. Genal height about 1/4 of eye height. Prementum 3–7 times as long as wide .......................... **2**

2 Prementum 3–5 times as long as wide. Tegula dark or yellow. Postgonite wider at middle in later view .......................... **3**

– Prementum at least 6 times as long as wide. Katepimeron with 4–5 hairs on anterior half. Tegula dark brown except base yellow, costal spine absent or short. Surstylus bluntly rounded apically in caudal view. Postgonite narrower at middle in later view .......................... ***L. latisurstyla*** **sp. nov.**

3 Prementum about 3 times as long as wide. Tegula dark except base brownish yellow, costal spine absent or weak. Surstylus bluntly rounded apically in caudal view .......................... ***L. miranda*** **Mesnil**

– Prementum 4–5 times as long as wide. Tegula yellow, costal spine present, slightly shorter than crossvein r-m. Surstylus pointed apically in caudal view .......................... ***L. flavitegula*** **Zhang**

***Leskia latisurstyla*** **Zhang & Dong, sp. nov.**
https://zoobank.org/12C15996-19EC-42AD-836B-E1BC12BFF7E7
Fig. 1

**Material examined.** ***Holotype*****:** China • ♂ (SYNU-E 19381); Tibet (= Xizang); Linzhi, Bayi Town; 29.7425°N, 94.3189°E; 3000 m elev.; 12.VIII.2013; Q. Wang leg. ***Paratype*****:** 1♂ (SYNU-E 21575; NW Yunnan; Gongshan County, Dimaluo Village; 27.7470°N, 98.6723°E; 1600 m elev.; 19.V.2007; X.Y. Liu leg.

**Etymology.** The specific epithet is derived from the characteristically wide surstylus in caudal view of this species; it is composed from the Latin adjective *lati* and the noun *surstylus*.

**Diagnosis.** This species is similar to *L. flavitegula* Zhang, but it is distinguished from the latter in the height of the gena, which is about 1/4 of eye height, the longer prementum, which is at least 6.5 times as long as wide apical 4/5 of postpedicel dark brown in male, and palpus which is slightly longer than antenna. Discal scutellar setae are slightly shorter than the scutellum length; anepimeral setae 2, katepisternal setae 3; tegula dark brown except for the yellow base. Surstylus wider and bluntly roundedat apex in caudal view, postgonite narrower at middle.

**Description. Male.** Body length 10.0 mm.

Head (Fig. 1C, D). Eye bare. Frontal vitta brownish black, ground colour of fronto-orbital plate, parafacial, and face dark yellow; fronto-orbital plate and parafacial with thin, grayish-yellow pruinosity; face with grayish-white pruinosity. Occiput with grayish-yellow pruinosity. Lunule dark yellow, with grayish-yellow pruinosity. Palpus reddish yellow on apical half and dark on basal half. Prementum gleaming black. Antenna with scape, pedicel, and basal 1/5 of postpedicel reddish yellow; apical 4/5 of postpedicel and basal 4/5 of arista dark brown. Frons slightly widened anteriorly, about 4/7 of eye width at narrowest point; frontal vitta at anterior ocellar point slightly narrower than fronto-orbital plate. In anterior view parafacial at middle about as wide as postpedicel, lower margin of face protruding forward in lateral view, vibrissa at level of lower margin of face. Fronto-orbital plate with fine hairs, parafacial bare. Genal height about 1/4 of eye height; 16–17 pairs of crossed frontal setae, with upper and lower frontal setae smaller than other frontal setae, lowest frontal setae at nearly level with apex of pedicel, 2 to many proclinate ocellar setulae, longest one slightly shorter than upper frontal setae, inner vertical setae strong, crossed, about 0.65 times as long as eye height, outer vertical seta outward, about 0.58 times as long as inner vertical seta, a pair of smaller postocellar setae. Occiput only with 2–3 rows of black hairs below postocular setae except for white hairs, and with a row of subvibrissae below vibrissa, which 0.30–0.35 times as long as vibrissa. Antenna short; scape erect, forming closed angle to pedicel; postpedicel about 3 times as long as wide and about 2.6 times as long as predicel; arista bare, thickened at least on basal 1/5. Palpus longer than antenna. Prementum 6–7 times as long as wide. Proboscis medium-sized.

Thorax (Fig. 1A, B) dark brown, with dense, grayish-yellow pruinosity on dorsum; anterior spiracle yellow; posterior spiracle reddish yellow. Thoracic dorsum with 4 dark longitudinal vittae; broad outer and narrow inner vittae on presutural scutum; distance between inner and outer vittae about 5.5 times as wide as inner vitta; inner vitta extend to scutoscutellar suture. Prosternum bare, about 1.6 times as long as wide; proepisternum bare; 3 postpronotal setae nearly arranged in a straight line; 3 presutural and 2 postsutural acrostichal setae, 3 presutural and 3 postsutural dorsocentral setae, 3 postsutural intra-alar setae, prealar seta about as long as notopleural seta, 2 supra-alar setae, anterior one stronger, 1 upward proepimeral seta, upper anepisternum with 1 shorter and upward seta, a row of 6–7 outward setae behind anepisternum, 2 anepimeral setae, a tuft of fine hairs around it, 3 katepisternal setae, 3 anterior setae set in straight line, katepimeron (= barette) with 4–5 hairs on anterior half, anatergite and katatergite bare.

Scutellum with semi-erect setulae at medialy dorsal surface and 2 discal setae; apical scutellar setae crossed, upward, as long as basal scutellar setae; lateral scutellar setae slender, about 1/2 as long as subscutellar seta.

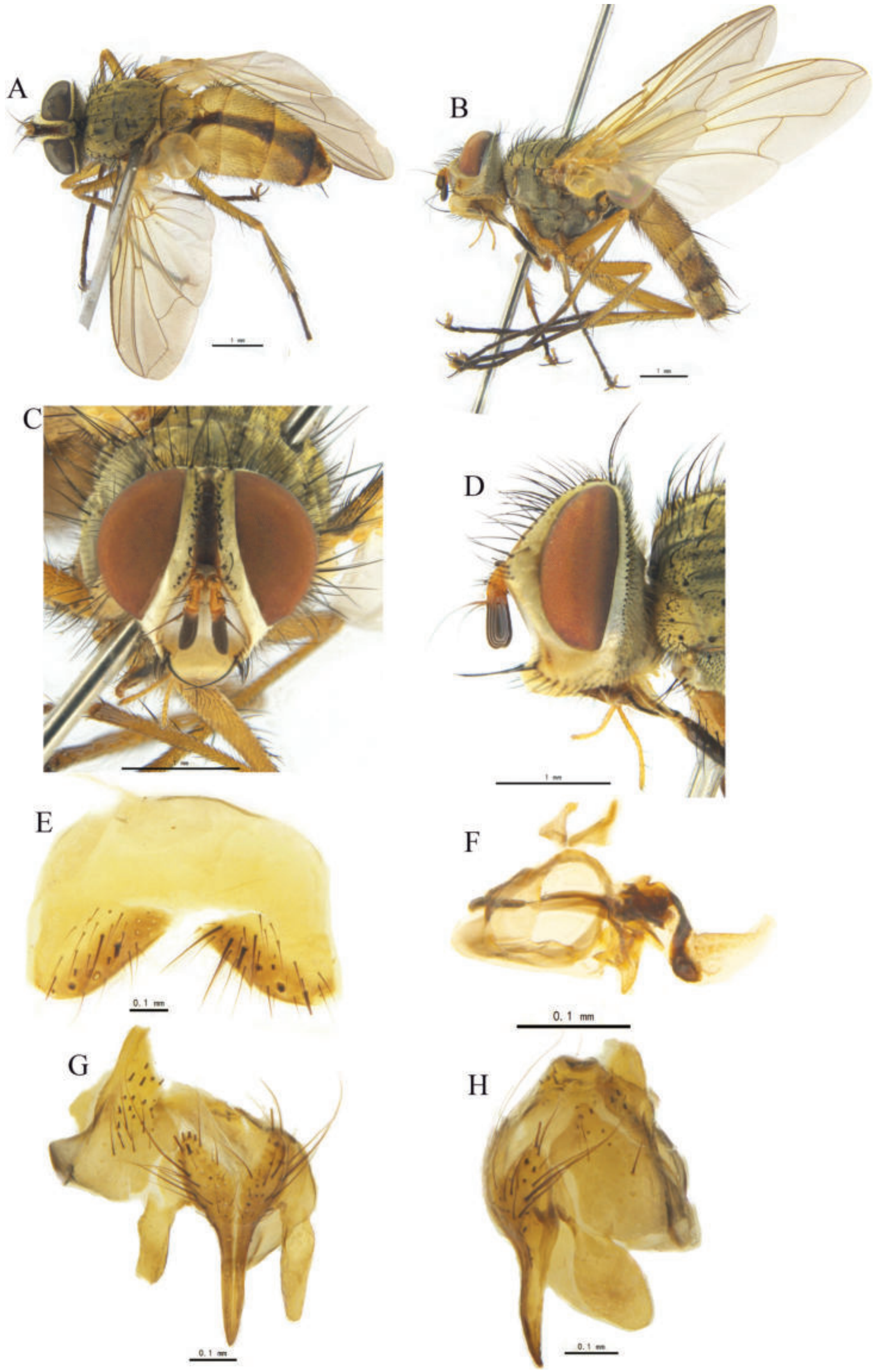

**Figure 1.** *Leskia latisurstyla* sp. nov. **A, B** ♂, bodies, dorsal and lateral views **C, D** ♂, heads, anterior and lateral views **E** sternite 5, ventral view **F** phallus (aedeagal apodeme, hypandrium, pregonite, postgonite, basiphallus and distiphallus) of male, lateral view **G, H** cerci, surstyli and epandrium of male, caudal and lateral views.

Wing pale brownish yellow, hyaline. Tegula dark brown except for yellow base; basicosta yellow. Lower calypter yellowish white, with short fringe on outer margin; halter yellowish white at middle, reddish yellow in both apexes, with 5–7 fine hairs at apical 1/4; costal spine absent or short; vein 1st and 2nd costal sections with fine hairs ventrally; relative lengths of 2nd, 3rd, 4th costal sectors approximately as 1:2:1; base of vein $R_{4+5}$ with 2–3 short setae dorsally and ventrally; vein M from dM-Cu crossvein to its bend about 1.3 times distance between the bend and wing posterior margin; vein M nearly parallel with vein $R_{4+5}$.

Legs slender, yellow to reddish yellow except tarsi black-brown, with thin, grayish-white pruinosity. Fore claw and pulvillus longer than 5th tarsomere, fore tibia with 2 posterior setae, 1 preapical anterodorsal seta, 1 preapical dorsal, and 1 preapical posteroventral setae. Mid tibia with 1 anterodorsal, 1 ventral, and 2 posterior setae. Hind tibia with a complete row of anterodorsal setae, 4–5 posterodorsal setae, and 3 anteroventral setae.

Abdomen long ovate, mostly yellow, with yellowish-gray pruinosity, with a dark-brown, broad, trapezoidal median marking on syntergite 1+2 and tergite 3; tergite 4 with pruinosity on basal 1/5 and dark brown on posterior 4/5; tergite 5 brown. Syntergite 1+2 medially excavate to hind margin and with a pair of lateral marginal setae; tergite 3 with a pair of lateral marginal and 2 median marginal setae; tergite 4 and 5 each with a row of marginal setae; tergites without discal setae. Posterior sternites 2–4 each with 2 posterior setae.

Sternite 5 and male terminalia as Fig. 1E–H. In ventral view, sternite 5 nearly square, V-shaped median cleft about 2/5 of sternite length; lateral lobe bluntly rounded apically. In caudal view, cerci slender and narrowed at apical 2/3 and pointed apically, and surstylus slightly longer and bluntly rounded apically. In lateral view cerci slightly bent ventrally and surstylus wide, bluntly rounded at apex. Distiphallus with some small spines on foot-like membranous part and contacted with sclerotized part. Pregonite long, postgonite short and narrow at middle.

**Female.** Unknown.

**Distribution.** China (Tibet, Yunnan; Fig. 8).

## Key to species of *Trichoformosomyia* Baranov (revised after Tachi 2013)

1 Abdomen with a longitudinal black stripe on mid-dorsal portion of syntergite 1+2–4th tergite; male wing ventrally with many long setae on 1st and 2nd costal sectors and at base of $R_{4+5}$ .................................................................. **2**

– Abdomen without a longitudinal black stripe on mid-dorsal portion; male wing ventrally with short setae on 1st and 2nd costal sectors and 1–3 rather long setae at base of R4+5 ............................................ ***T. abbreviata* Tachi**

2 Abdominal tergites 3 and 4 without median discal setae .......................... **3**

– Abdominal 3 and 4 tergites each with a pair of median discal setae .......... ................................................................................................. ***T. notata* Richter**

3 Postpronotal lobe brown to reddish yellow; basal half of postpedicel reddish yellow on inner surface; coxae and tibiae brown to yellowish; abdominal syntergite 1+2 without median marginal setae ........***T. sauteri* Baranov**

– Postpronotal lobe dark brown; antenna with postpedicel dark brown; coxae and tibiae dark brown; abdominal syntergite 1+2 with 2 median marginal setae....................................................................***T. cuonaensis* sp. nov.**

### *Trichoformosomyia cuonaensis* Zhang & Li, sp. nov.

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Fig. 2

**Materials examined.** ***Holotype*:** China • ♂ (SYNU-XZ 21006); Tibet (= Xizang); Shannan Prefecture, Cuona, Mamamenba Village; 27°52'N, 91°47'E; 2796–2850 m elev.; 3.VIII.2021; C.T. Zhang & X.Y. Li leg. ***Paratype*:** 1♂ (SYNU-XZ 21007); same locality and date as holotype; JJ Li leg.

**Etymology.** The specific epithet is derived from the locality name, Cuona County, southern Tibet, China.

**Diagnosis.** This species is similar to *Trichoformosomyia sauteri* Baranov, which is distributed in Japan, Russia (southern Far East), China (Hunan, Guangxi, Sichuan, and Taiwan), Vietnam, Myanmar. It differs from the latter in having entirely dark-brown antennae and a dark postprontal lobe with gray pruinosity, dark-brown coxae and tibiae, abdominal syntergite 1+2 with 2 median marginal setae.

**Description. Male.** Body length 9.1 mm.

Head (Fig. 2C, D). Frontal vitta linear, fronto-orbital plate, and parafacial with grayish-white pruinosity; occiput with grayish-white pruinosity. Antenna dark brown. Palpi yellow, labella yellow. Frons narrower than postpedicel width, 1/7–1/8 of eye width; genal height 1/8–1/9 of eye height or as wide as postpedicel; lower margin of face protruding forward. Vibrissa inserted at level of lower margin of face. 11–13 frontal setae, upper ones strongest, with a pair of uppermost setae strong and crossed; ocellar setae slender, hair-like. Inner vertical setae slender, hair-like; outer vertical seta hair-like, about as long as postocular setae; postocellar setae 2. Occiput mostly with white hairs except for a row of black hairs below postocular setae. Antenna with postpedicel about 3 times as long as pedicel or about 5 times as long as wide in dorsal view; pedicel with a slender seta on dorsal surface, which about twice as long as pedicel. Arista plumose; longest aristal hairs about as wide as postpedicel. Prementum 4.5–5 times as long as wide.

Thorax (Fig. 2A, B) black, with brownish-gray pruinosity; scutum with 2 broad outer and 2 narrow inner longitudinal vittae; pruinose distance between inner and outer vittae on presutural scutum about 2.5 times as wide as inner vitta; two inner longitudinal vittae on postsutural scutum combined with a broad black longitudinal vittae and extending to level of last posterior dorsocentral seta. Scutellum dark black. Postpronotal lobe black, with gray pruinosity; postalar callus dark brown. Notopleura and pleura with grayish-white pruinosity. Prosternum with hairs on sides. Postpronotal lobe with 3–4 setae arranged in a triangle; anterior 1–2 finer. One presutural and 2–3 postsutural acrostichal setae; 2 presutural and 3 postsutural dorsocentral setae, 3 postsutural intra-alar setae, 3 supra-alar setae, first one distinctly shorter than notopleural seta and first one postsutural intra-alar seta. Scutellum with three pairs of marginal scutellar setae; apical scutellar setae crossed and slightly longer than scutellum and subequal in length to basal scutellar setae; subapical scutellar setae distinctly longer than apical scutellar setae. Proepisternum bare; anepisternum with 2 upper anterior setae and a row of posterior setae; 3 katepisternal setae; anepimeral setae hair-like; katepimeron with 2–3 black hairs; katatergite bare.

Wing pale brownish, distinctly tinged with pale yellow on basal and anterior portion; tegula and basicosta dark brown. Calypters pale yellowish; lower calypter with short fringe on outer margin and not divergent from scutellum. Halter yellow. Relative lengths of 2nd, 3rd, and 4th costal sectors approximately as 1:2.1:1. Base and apex of first costal sector with distinctly long setae; dorsally setulae on $r_{4+5}$ about twice as long as setulae on first and 2nd costal sectors. Base of vein $R_{4+5}$ to vein r-m with a row of setulae ventrally and 3 setae on basal part dorsally. Bend of vein M bluntly angulated; section of M between crossveins R-M and dM-Cu longer than section between dM-Cu and bend of M, the distance between vein M from crossvein dM-Cu to bend about 2.4 times distance between bend to posterior margin of wing, or slightly shorter than distance between bend to apex of M. Crossvein dM-Cu slightly bent anteriorly. Ultimate section of wing vein CuA1 about 1/2 length of crossvein dM-Cu.

Legs coxae dark brown, with grayish pruinosity; trochanters reddish brown; femora, tibiae, and tarsi dark brown. Claws dark brown; pulvillus pale yellow. Fore claw slightly longer than 5th tarsomere; fore tibia slightly longer than head height, with a row of 4–6 short, anterodorsal setae on upper 2/3; 1 posterior seta; 1 preapical dorsal seta distinctly longer than preapical anterodorsal seta; 1 preapical posteroventral seta. Mid femur with 2 anterior setae on middle and 2 preapical posterodorsal setae. Mid tibia with 1 anterodorsal, 2 posterior, and 1 ventral seta; 3 preapical dorsal setae, including 1 dorsal, 1 posterodorsal, and 1 posterior setae; 1 preapical anteroventral and 1 preapical posteroventral setae; 2 preapical posterodorsal setae. Hind femur with a row of posteroventral setae on basal half, a row of complete anterodorsal setae, 1 preapical anteroventral seta. Hind tibia with 4–5 anterodorsal setae, 2 strong, 2–3 posterodorsal setae, 4–5 ventral setae (lowest one strong), 3 preapical dorsal setae, 1 preapical anteroventral seta, without distinct preapical posteroventral seta.

Abdomen long, ovate, reddish yellow; dark brown on middle longitudinal portion of tergites, posterior 2/3 of tergite 4 and entire tergite 5; tergite 5 with grayish-white pruinosity on anterior half. Syntergite 1+2 medially excavate to 2/3–3/4, with 2 median marginal setae, with 1 lateral marginal and 3–4 lateral discal setae. Tergites each with erect hairs; tergite 3 with 2 median marginal setae, 1 lateral discal seta, without median discal seta; tergite 4 with a row of marginal setae, without median discal and lateral discal seta; tergite 5 separately with a row of marginal setae and 2 lateral discal setae. Sternite 1 with black hairs on margin.

Sternite 5 and male terminalia as Fig. 2E–I. In ventral view, sternite 5 nearly square; V-shaped median cleft about 5/9 of the sternite length; apex of lateral lobe slightly blunt and with an inner protruding and pointed apically. In caudal view, syncercus distinctly narrowed and pointed only at apex; surstylus long, thin, slightly blunt at apex. In lateral view apex of syncercus distinctly arc-like and bent ventrally; surstylus long, straight, bluntly rounded at apex; membranous and sclerotized parts of distiphallus long and narrow; pregonite long; ejaculatory apodeme large; postgonite short and arc-like.

**Female.** Unknown.

**Distribution.** China (Tibet; Fig. 8).

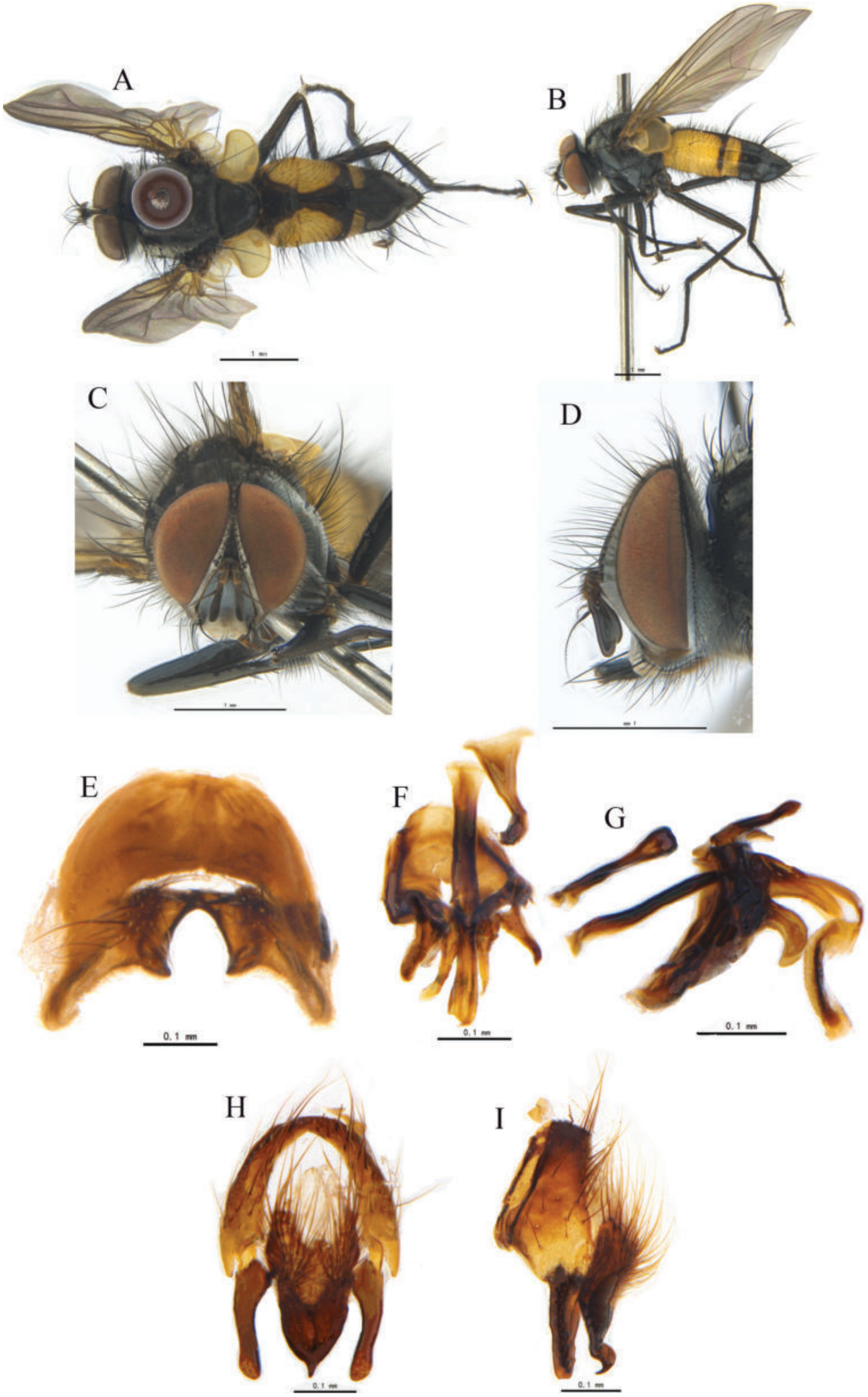

**Figure 2.** *Trichoformosomyia cuonaensis* sp. nov. **A, B** ♂, bodies, dorsal and lateral views **C, D** ♂, heads, anterior and lateral views **E** sternite 5, ventral view **F, G** phallus (ejaculatory apodeme, aedeagal apodeme, hypandrium, pregonite, postgonite, basiphallus and distiphallus) of male, dorsal and lateral views **H, I** cerci, surstyli and epandrium of male, caudal and lateral views.

### Key to Chinese species of *Tachina* (s.s.) Meigen

(revised after Mesnil 1966; Chao et al. 1998; Tschorsnig and Richter 1998; Richter 2004)

1 Hind coxa with one or more setae on posterodorsal margin. Prosternum bare. Eyes bare or nearly bare. Parafacial with hairs or setulae only. Lower margin of face protruding forward. Ocellar seta proclinate, developed. Occiput without black hairs behind postocular seta row. Antenna with broad postpedicel at most as long as narrower pedicel. Arista bare. Prementum at least 4 times as long as wide. Postpronotum with >3 setae, the strongest of them arranged in a triangle. Proepisternum hary. Inner anterior surface of fore coxa bare or predominantly bare. Legs mostly yellow (at least hind tarsi) or black. Abdomen usually reddish yellow, not metallic, syntergite 1+2 medially excavated to its posterior margin ......... .......................................................................................... **2 (*Tachina* Meigen)**

– Hind coxa bare on posterodorsal margin. Prosternum setose .................... ............................................................................................ **other genera**

2 Legs entirely black (Fig. 4A–C). Palpi inflated apically. Cerci nearly rectangular or long triangular, distinctly narrowed on apical half and blunt apex with 1–2 apical spines, and surstylus belt-shaped and bent centrally, its apex with a distinctly pointed, long tooth and without an angular lateral incision in caudal view ..................................... **Subgenus *Nowickia* Wachtl**

– Legs mostly reddish yellow or black, at least hind tarsi reddish yellow. Palpi slender, cylindric. Male terminalia is a hypopygium circumversum, cerci long triangular, distinctly narrowed and pointed at apical half, with an apical spine and surstylus developed, with a distinct angular lateral incision on the apical lobe in caudal view, sternite 5 large, with a V-shaped median mid-incision at posterior margin and bluntly rounded posterior lobes (Fig. 6E–H).................................................... **3 (Subgenus *Tachina* Meigen)**

3 Abdominal syntergite 1+2 without or with 2 median marginal setae (Fig. 5D–F) ...........................................................................................**4**

– Abdominal syntergite 1+2 with 4–12 median marginal setae (Fig. 3).......**5**

4 One presutural and 3 postsutural intra-alar setae, if 1 presutural and 2 postsutural intra-alar setae, then thorax and abdomen without pale hairs...................................................... ***T. grossa* (Linnaeus), *T. punctocincta* (Villeneuve), *T. persica* (Portschinsky), *T. fera* (Linnaeus), *T. corsicana* (Villeneuve), *T. rohdendorfi* Zimin, *T. metatarsa* Chao & Zhou, *T. macropuchia* Chao, *T. magnicornis* (Zetterstedt), *T. nupta* (Rondani) (Fig. 5)**

– One presutural and 2 postsutural intra-alar setae, pleura of thorax with pale hairs................................................................................................................ .... ***T. albidopilosa* (Portschinsky), *T. flavosquama* Chao, *T praeceps* Meigen**

5 Body black, with black hairs. Calypters black............................. ***T. bombidiforma* (Chao), *T. furcipennis* (Chao & Zhou), *T. haemorrhoa* (Mesnil)**

– Body color various. Calypters at least white or yellowish ..........................**6**

6 Parafacial with yellow or yellowish-white hairs. Postocullar setulae usually short, not hair-like.............................................................................**7**

– Parafacial with blending black and pale hairs, or with black hairs on upper 1/2–3/4 and pale hairs on lower 1/4–1/2. Postocullar setulae slender, hair-like.........................................................................................**14**

7 Abdominal tergites 3 and 4 with marginal setae on ventral surface and lateral setae and laterodiscal setae ........................................................ ***T. pubiventris* (Chao), *T. amurensis* (Zimin), *T. tienmushan* Chao & Arnaud, *T. sobria* Walker, *T. gibbiforceps* (Chao), *T. luteola* (Coquillett)**

– Abdominal tergites 3 and 4 without laterodiscal setae and at most tergite 3 with marginal setae on dorsal and ventral surface. Sternite 2–4 mostly with setae........................................................................................**8**

8 Sternite 2–4 without setae (Fig. 3)................................... ***T. zimini* (Chao)**

– Sternite 2–4 with setae..............................................................................**9**

9 A pair of strong apical scutellar setae straight, not crossed....................... ............................................................................ ***T. pingbian* Chao &Arnaud**

– A pair of slender apical scutellar setae inclinated, crossed.....................**10**

10 Abdomen long ovate. Legs reddish yellow................ ***T. longiventris* (Chao)**

– Abdomen ovate (Fig. 3). Femora at least black .......................................**11**

11 Abdomen gleaming black, without pruinosity, at most with pruinosity in anterior margin on tergites 3 and 4, tergites only with brownish red hairs . .................. ***T. breviceps* (Zimin), *T. ursina* Meigen, *T. zaqu* Chao & Arnaud**

– Abdomen wholly covered with pruinosity on dorsal surface or pruinose belts on basal 1/3–3/5 of tergiters 3 to 5 ................................................**12**

12 Tergites 3 to 5 each with distinctly pruinose belt on basal 1/3–3/5 (Fig. 3). Postpedicel about as wide as parafacial .................... ***T. xizangensis* (Chao), *T. aurulenta* (Chao), *T. cheni* (Chao), *T. iota* Chao & Arnaud, *T. stackelbergi* (Zimin), *T. ursinoidea* (Tothill), *T. ardens* (Zimin), *T. jakovlewii* (Portschinsky)**

– Tergites 3–5 entirely or mostly covered with pruinosity, with pruinose markings, without distinctly pruinose belt. Postpedicel narrower than parafacial ..........................................................................................................**13**

13 Three pairs of postsutural dorsocentral setae ............................................ .......... ***T. lateromaculata* (Chao), *T. subcinerea* Walker, *T. ruficauda* (Chao)**

– Four pairs of postsutural dorsocentral setae ............................................... ............................. ***T. luteola* (Coquillett), *T. pulvera* (Chao), *T. chaoi* Mesnil**

14 Body form bombylid fly-like. Basicosta dark black.... ***T. bombylia* (Villeneuve)**

– Body form not bombylid fly-like. Basicosta yellow or yellowish brown ...**15**

15 Abdominal gleaming black, without pruinosity ................ ***T. breviala* (Chao), *T. breviceps* (Zimin), *T. liaoningensis* Zhang & Hao, *T. qingzangensis* (Chao)**

– Abdomen covered with pruinose belt or pruinosity on dorsal surface ....**16**

16 Tergites 3–5 without distinctly pruinose belt, at least with even pruinosity on median surface ............. ***T. spina* (Chao), *T. medogensis* (Chao & Zhou)**

– Tergites 3–5 with distinctly pruinose belts or pruinose markings...........**17**

17 Tergites 4 and 5 each with two grayish-white rectangular lateral pruinose markings ....................................................................... ***T. laterolinea* (Chao)**

– Tergites with complete pruinose belt or absent, or only tergite 4 with two yellowish white lateral pruinose markings................................................**18**

18 Abdomen black with indistinctly dark yellow lateral markings, tergites 4 and 5 with yellowish-white hairs on dorsal surface ..................................... ................. ***T. ursina* Meigen, *T. anguisipennis* (Chao), *T. alticola* (Malloch)**

– Abdomen reddish brown or dark brown with reddish brown on tergites 3 and 4, with broad black median vitta (male), or abdomen completely black except for apex reddish yellow (female). Abdomen only with black hairs on syntergite 1+2 and tergite 3..................................................................**19**

19 Frons of male narrower, 0.4–0.6 of eye width, parafacial wider postpedicel. Apical scutellar setae crossed, Abdominal syntergite 1+2 at most with 8 median marginal setae, tergites 4 and 5 with brownish-red hairs .................................................................................... ***T. rohdendorfiana*** **Chao & Arnaud**

– Frons of male wider, 0.9–1.0 of eye width, or 0.3–0.33 of head width, parafacial of male slightly narrower than postpedicel, scape and pedicel dark brown. Apical scutellar setae parallel, not crossed. Abdominal syntergite 1+2 with 12 median marginal setae, tergite 4 with two yellowish-white pruinose lateral markings and covered with dense, straight, yellowish-white hairs and black hairs on dorsally median portion, only tergite 5 with erect, dense, long, brownish-red hairs (Fig. 6) ..................... ***T. jilongensis*** **sp. nov.**

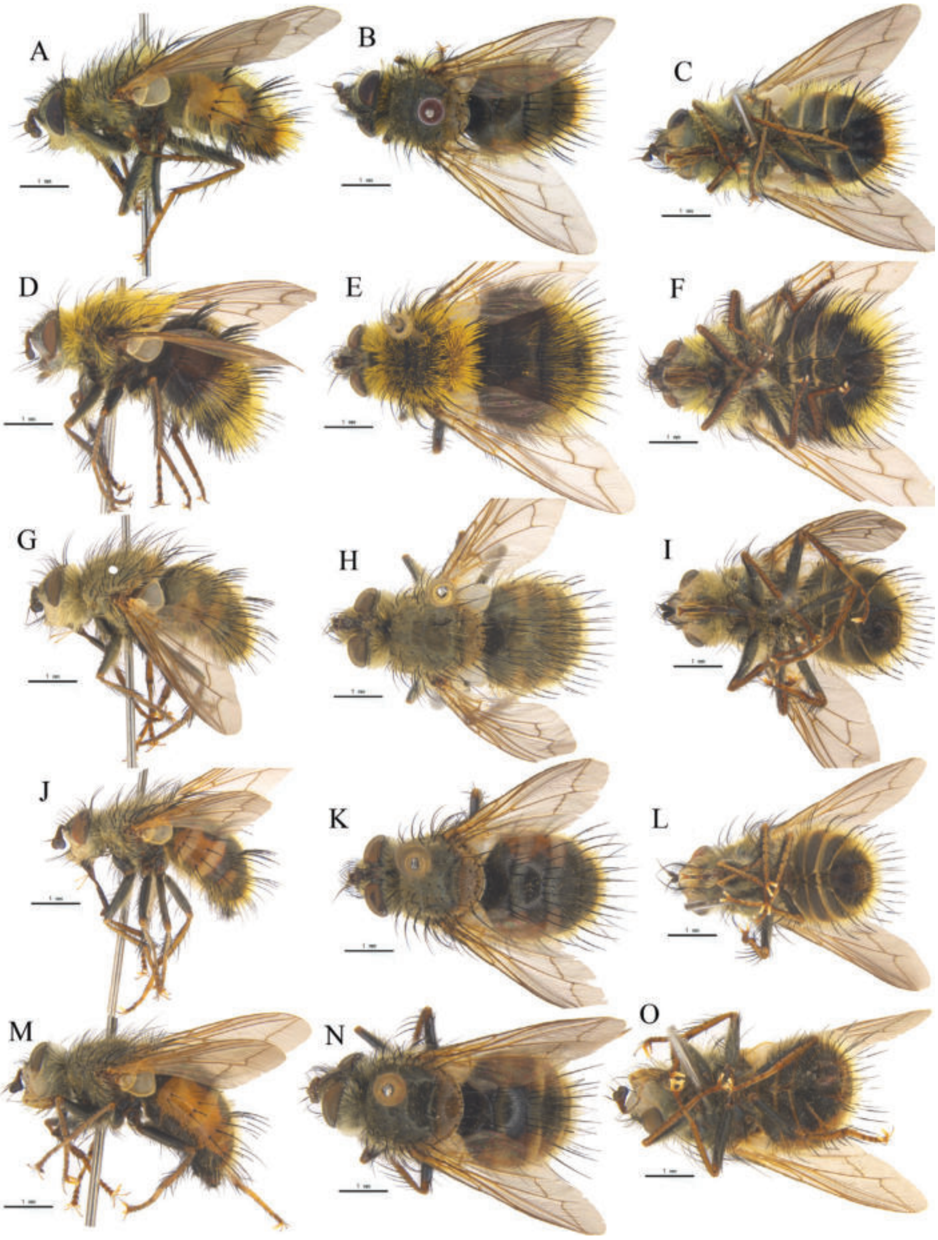

**Figure 3. A–C** *Tachina* (*Tachina*) *anguisipennis* (Chao) from Dingjie, Tibet **D–F** *T.* (*s.s.*) *bombylia* (Villeneuve) from Sichuan **G–I** *T.* (*s.s.*) *cheni* (Chao) from Yaan, Sichuan **J–L** *T.* (*s.s.*) *iota* (Chao & Arnaud) from Lijiang, Yunnan **M–O** *T.* (*s.s.*) *zimini* (Chao) from Pingwu, Sichuan, China **A, D, G, J, M** ♂, bodies in lateral views **B, E, H, K, N,** bodies in dorsal views **C, F, I, L, O** bodies in ventral views.

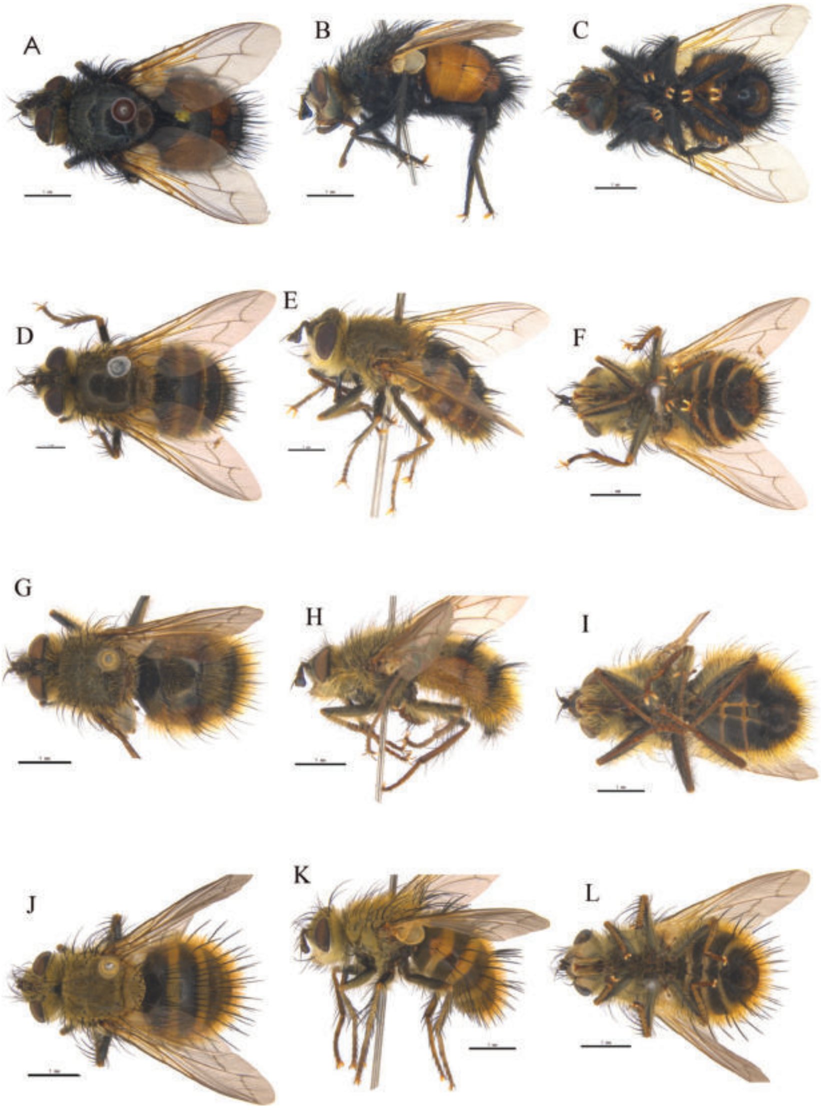

**Figure 4. A–C** *Tachina* (*Nowickia*) *atripalpis* (Robineau-Desvoidy) from Sangzhuzi, Rikaze, Tibet **D–F** *T.* (*s.s.*) *amurensis* (Zimin) from Dingjie, Tibet **G–I** *T.* (*s.s.*) *spina* (Chao) from Xiaojin, Sichuan **J–L** *T.* (*s.s.*) *ursinoidea* (Tothill) from Lijiang, Yunnan **A, D, G, J** ♂, bodies in dorsal views **B, E, H, K,** bodies in lateral views **C, F, I, L,** bodies in ventral views.

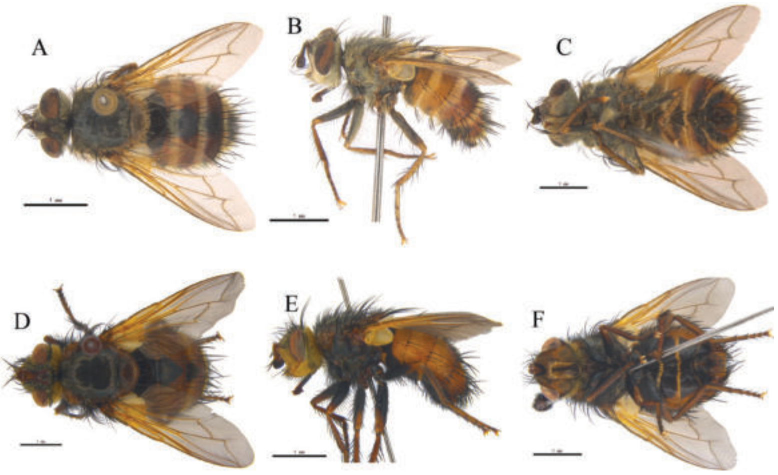

**Figure 5. A–C** *Tachina* (*Tachina*) *sobria* Walker from Yaan, Sichuan **D–F** *T.* (*s.s.*) *nupta* (Rondani) from Weiyuan, Gansu ♂ **A, D,** bodies in dorsal views **B, E,** bodies in lateral views **C, F,** bodies in ventral views.

### *Tachina jilongensis* Zhang & Dong, sp. nov.

https://zoobank.org/1F260668-7797-4BE2-804F-9412BFE40092

Fig. 6

**Materials examined.** ***Holotype*:** China • ♂ (SYNU-XZ 210001); Tibet (=Xizang); Rikaze, Jilong County, Jipu Village, Grand Canyon; 28°22'N, 85°19'E; 2742 m elev.; 21–22.VII.2021; C.T. Zhang & X.Y. Li leg. ***Paratypes*:** 3♂ (SYNU-XZ 210002 to 210004); same data as holotype • 1♂ (SYNU-XZ 210005); Tibet; Rikaze, Jilong County, Langjiu Village, Inspection Station; 28°21'N, 85°20'E; 2578–2902 m elev.; 23.VII.2021; C.T. Zhang & X.Y. Li leg.

**Etymology.** The specific epithet is taken from Jilong County where the type locality of this species is located.

**Diagnosis.** This species is closely similar to *T. rohdendorfiana* Chao & Arnaud, but it is distinguished from the latter in having wider frons and parafacial, narrower postpedicel in male, genal height 0.8–0.9 of eye height, apical scutellar setae parallel, abdomen with black median portion which wider than 1/3 of the tergites 3 and 4, tergites 3 with a pair of large, brownish-yellow lateral markings, tergite 4 covered with two yellowish-white lateral pruinose markings, with dense, straight, yellowish-white hairs on lateral surface and black hairs on median dorsal portion, syntergite 1+2 with 12 median marginal and 3–5 lateral marginal and laterodiscal setae, without ventral marginal seta, with black and some yellowish-white hairs on ventral surface, tergites 3 with a complete row of black marginal setae on dossal surfaces, with 1–3 laterodiscal setae and without ventral marginal seta, with black and some yellowish-white hairs on ventral surface, tergite 4 covered with two yellowish-white pruinose lateral markings, with a complete row of marginal setae and black hairs on dorsal and ventral surfaces and 3–5 laterodiscal setae, only tergite 5 entirely black, with erect, dense, long, brownish-red hairs on dorsal and ventral surface and a row of strong, black, discal setae and a row of black marginal setae on dorsal and ventral surfaces. Sternite 2 with 5–6 setae.

**Description. Male**. Body length 12–14 mm.

Head (Fig. 6C, D). With grayish-white pruinosity; frontal vitta reddish brown to brown, fronto-orbital plate with pale-yellow pruinosity; lunule brown; parafacial and gena with grayish-white pruinosity; occiput with grayish-white pruinosity. Antenna with postpedicel black, with thin, gray pruinosity; pedicel brown to dark brown, with grayish-white pruinosity; base of arista dark brown to brown; palpi yellow; prementum gleaming black. Eye bare. Frons 0.3–0.33 times width of head or slightly narrower than width of eye; frontal vitta widened anteriorly, narrower than fronto-orbital plate width at narrowest point. Parafacial about as wide as postpedicel in anterior view. Genal height 0.8–0.9 of eye height; lower margin of face protruding forward; 5–6 pairs of frontal setae, with lowest setae at level with base of pedicel. Inner vertical setae strong and parallel, slightly longer than eye height; outer vertical seta outward, about 0.67 times as long as inner vertical seta; ocellar seta strong, proclinate, and about as long as upper frontal setae; a pair of smaller postocellar setae upward. Fronto-orbital plate with fine black hairs; parafacial mostly with black hairs and only white hairy on upper portion. Facial ridge with 3 setae inserted above of vibrissa. Vibrissa strong, inserted above level of lower margin of face, equal or longer than postpedicel, with a row of slender subvibrissae below vibrissae. Gena with white hairs. Occiput with long, pale-yellow hairs behind postocular setae. Postpedicel ovate, slightly narrower than parafacial and

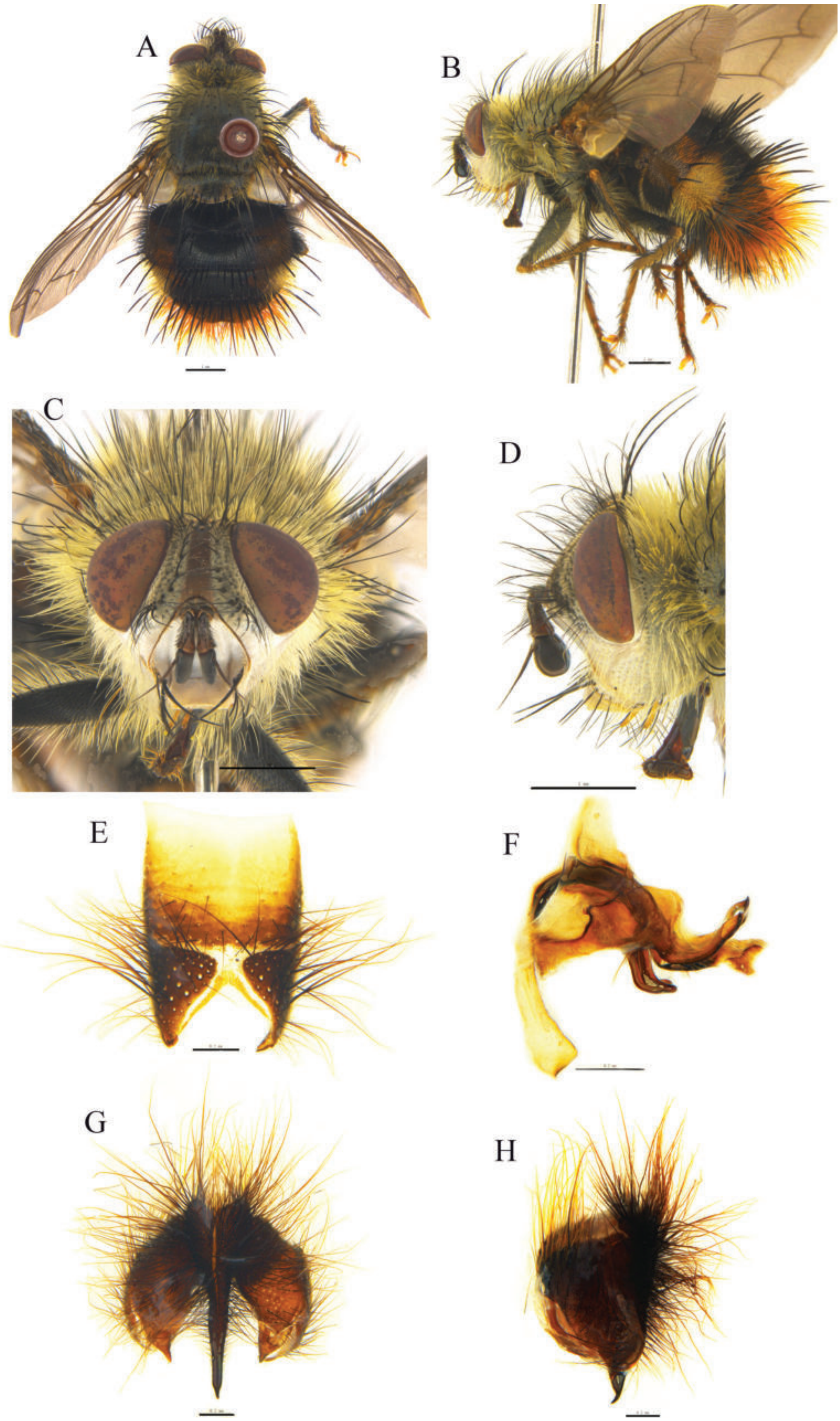

**Figure 6.** *Tachina jilongensis* sp. nov. **A, B** ♂, bodies, dorsal and lateral views **C, D** ♂, heads, anterior and lateral views **E** sternite 5, ventral view **F** phallus (aedeagal apodeme, pregonite, postgonite, basiphallus and distiphallus) of male, lateral view **G, H** cerci, surstyli and epandrium of male, caudal and lateral views.

shorter than pedicel; arista bare, about as long as the combination of pedicel and postpedicel; 2nd aristomere 2–2.5 times as long as its diameter. Palpi slender, longer than antenna or prementum. Prementum 4–5 times as long as wide.

Thorax (Fig. 6A, B) darkly colored, with thin, gray pruinosity; dorsum with 4 dark, longitudinal vittae; outer vittae on anterior 3/5 of postsutural scutum, inter vittae on anterior 2/5 of postsutural scutum; scutellum dark on base, reddish yellow on apical 2/3, with dense, long, yellow hairs. Anterior spiracle brownish yellow, with yellow hairs; posterior spiracle dark yellow. Thoracic dorsum densely covered with yellow fine hairs and mixed with some fine black hairs. Postpronotal lobe with 5–6 setae; 3 strong basal setae set in a triangle, 3–4 presutural and 2 postsutural acrostichal setae, 4 presutural and 4 postsutural dorsocentral setae, 1 presutural and 2 postsutural intra-alar setae, 3 strong supra-alar setae, proepisternum hairy, prosternum bare, 2 notopleural setae, meron with a row of setae, katepimeron (= barette) bare, 3 katepisternal setae. Scutellum reddish yellow except for dark base, with erect, dense, yellowish hairs, 4 pairs of marginal setae, and three pairs of discal setae along margin; apical scutellar setae standing in a straight line, not crossed, about 2 times as long as wide, and as long as subapical scutellar setae.

Wing hyaline, tinged with brownish; tegula dark brown and basicosta brownish yellow. Upper calypter pale brown except whitish anterior half; lower calypter yellowish white. Halter dark brown on apical 1/2, and brown on basal half. Costal spine absent; second costal sector of wing bare ventrally; relative lengths of 2nd, 3rd and 4th costal sectors approximately as 2.5:3.5:1; bend of vein M about right-angled; last section of vein Cu about 2/3 as long as crossvein dM-Cu; base of vein $R_{4+5}$ with 5–6 short, black hairs on dorsal and ventral surfaces; cell $R_{4+5}$ open.

Legs dark brown except for apex of femora reddish brown; tibiae and tarsi reddish yellow; claws reddish yellow except for dark apex; pulvillus pale yellow. Fore claws and pulvillus longer than 4th and 5th tarsomere combined; first tarsomere with dense, short, yellow, brush-like hairs on ventral surface. Fore tibia with a row of anterodorsal and posterodorsal setae; 2 posterior setae; mid femur with 3 anterior setae; mid tibia with a row of strong anterodorsal setae, 5 posteroventral setae, 1 strong ventral seta. Hind femur with a row of anteroventral setae, 3 preapical anterodorsal setae and 3–4 preapical dorsal setae; hind tibia with a row of irregular anterodorsal setae, 4 posterodorsal and 2 ventral setae, and apex with 2 dorsal setae, 1 anterior, 1 anteroventral, and 1 posteroventral seta.

Abdomen ovate, black on base; median depression of syntergite 1+2 extending to posterior margin; tergites 3 and 4 each with a pair of large, brownish-yellow lateral markings, and covered with dense, yellowish-white pruinose markings on tergite 4; tergite 5 gleaming black, with a shallow median depression at posterior portion. Syntergite 1+2 and tergite 3 with dense, straight, black hairs; tergite 4 with two yellowish-white pruinose lateral markings and covered with dense, straight, yellowish-white hairs, black hairs on dorsal-median portion; tergite 5 with dense, fine, brownish-red hairs. Syntergite 1+2 with 12 (6 pairs of) black, median, marginal setae, 3–5 lateral marginal setae, and 2–4 laterodiscal setae; without ventral marginal seta; with black and some yellowish-white hairs on ventral surface; tergite 3 with a complete row of 24–26 black marginal setae on dorsal surface and 1–3 laterodiscal setae, without ventral marginal seta, with black and some yellowish-white hairs on ventral surface; tergite 4 with a complete row of 30–34 marginal setae, black hairs on dorsal and ventral surfaces, and 3–5 laterodiscal setae; tergite 5 with a row of strong, black discal setae and a row of black marginal setae on dorsal and ventral surfaces. Sternite 1 with yellowish hairs; sternite 2 with 5–6 setae; sternite 3 with 6–8 setae; sternite 4 with 8 setae. Sternite 5 and male terminalia as Fig. 6E–H. In ventral view, sternite 5 nearly rectangular, with V-shaped median cleft about 1/3 of the sternite length; lateral lobe slightly pointed at apex. In caudal view, cerci slender and narrowed and pointed apically; surstylus slightly shorter and pointed apically, with a medially deep crevice. In lateral view, cerci slightly bent ventrally and pointed at apex; surstylus broad, bluntly rounded. Distiphallus with some setulae on membranous and sclerotized parts. Pregonite long and pointed apically; postgonite short and blunt apically, bent anteriorly.

**Female.** Unknown.

**Distribution.** China (Tibet; Fig. 8).

## Newly recorded species for Xizang, China

### ***Nemoraea javana*** **(Brauer & Bergenstamm, 1894)**

Fig. 7A, C, E, G

*Prodegeeria javana* Brauer & Bergenstamm, 1894: 617 [also 1895: 81]. Type locality: Indonesia: Jawa, Tengger Mountains.

*Prodegeeria javana*: Crosskey 1976: 198. Chao et al. 1998: 2030. O'Hara et al. 2009: 160. O'Hara et al. 2020a: 741; 2020b: 946.

**Material examined.** China – Tibet (= Xizang) • 2♀ (SYNU-XZ 210021, 210022); Rikaze, Dingjie County, Chentang Town, Xuexiongma; 2426–2600 m elev.; 27°86'N, 87°42'E; 27.VII.2021; C.T. Zhang & X.Y. Li leg.

**Diagnosis.** Eye covered with dense hairs. Parafacial bare; lower margin of face protruding forward; upper part of head usually with only one row of black setulae behind postocular setae. Arista thickened at most on basal 2/5 and aristal hairs at most as long as aristal diameter; first and second aristomere each at most as long as its diameter. Palpus dark brown except yellow apex in female. Thorax with brownish-gray pruinosity. Two katepisternal setae; katepisternum and ventral surface of basal abdomen with white hairs. Wing clouded with brown along veins. Lower calypter with long hairs at least dorsally along outer margin. Inner anterior surface of fore coxa covered with appressed setulae; preapical posteroventral seta on hind tibia distinctly shorter than preapical anteroventral seta. Abdominal tergites 3–4 without median discal seta.

**Distribution.** China (Zhejiang, Hunan, Sichuan, Guizhou, Tibet; Fig. 8), Indonesia.

### ***Nemoraea echinata*** **Mesnil, 1953**

Fig. 7B, D, F, H

*Nemoraea echinata* Mesnil, 1953: 154. Type locality: Myanmar: Kachin, Kambaiti.

*Nemoraea echinata*: Crosskey 1976: 198. Chao et al. 1998: 2028. O'Hara et al. 2009: 159. O'Hara et al. 2020a: 741; 2020b: 946.

**Material examined.** China – Tibet (= Xizang) • 1♀ (SYNU-XZ 210023); Rikaze, Yadong County, Yadong, Gajvsi temple; 3286 m elev.; 27°48'N, 88°90'E; 29.VII.2021; C.T. Zhang & X.Y. Li leg.

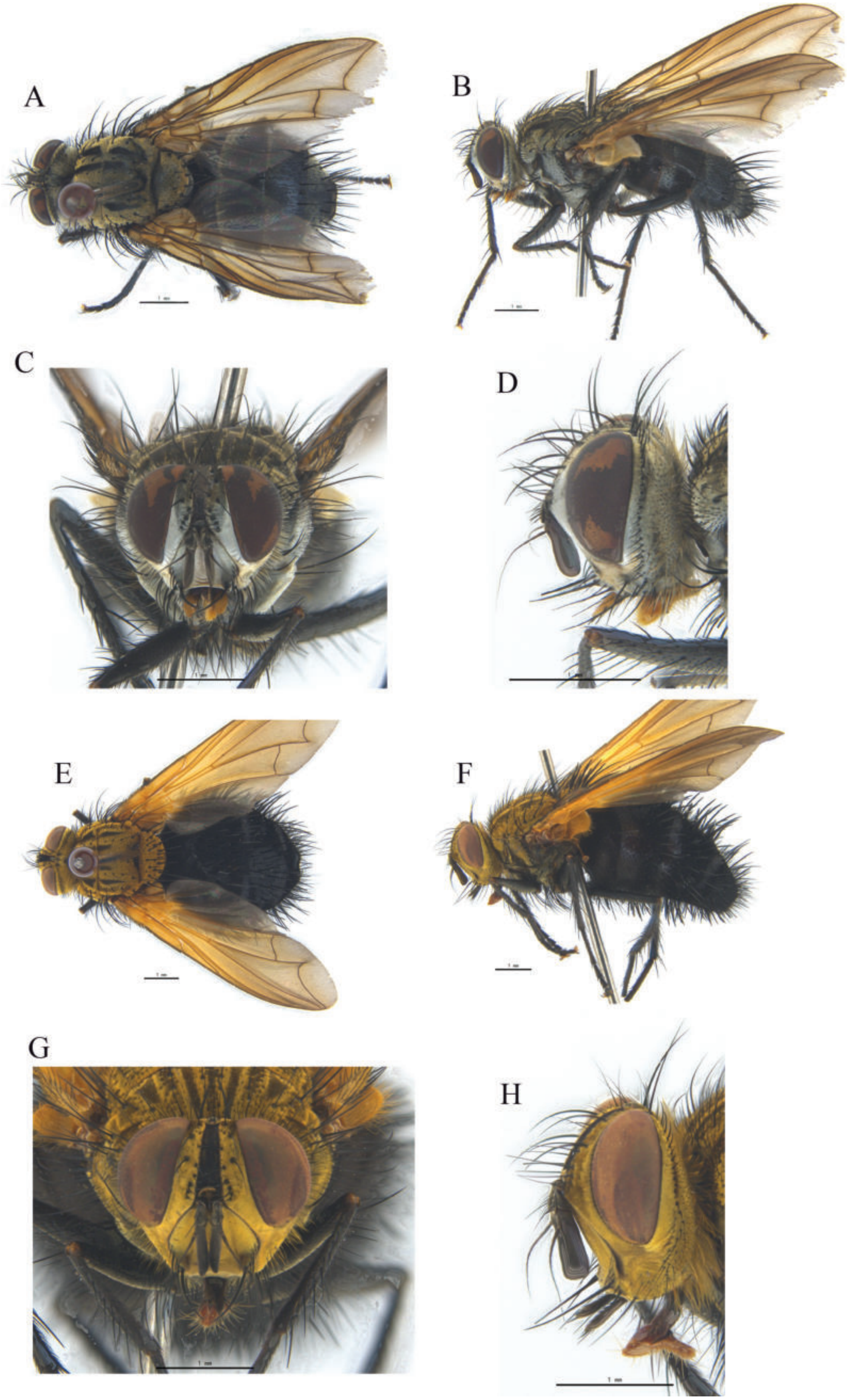

**Figure 7. A–D** *Nemoraea javana* (Brauer & Bergenstamm, 1895) ♀ **E–H** *Nemoraea echinata* Mesnil, 1953 ♀ **A, B, E, F** bodies, dorsal and lateral views **C, D, G, H** heads, anterior and lateral views.

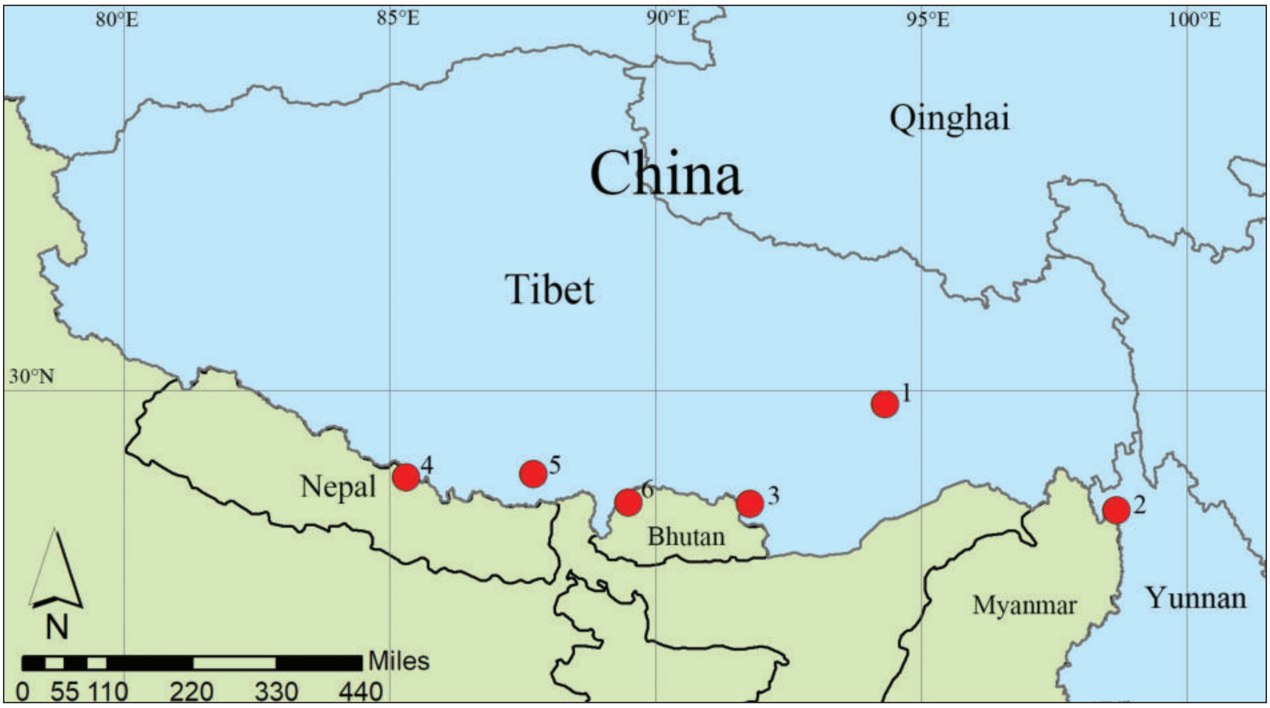

**Figure 8.** New distribution records of Tachininae from Tibet, China. 1, 2 *Leskia latisurstyla* Zhang & Dong, sp. nov. 3 *Trichoformosomyia cuonaensis* Zhang & Li, sp. nov. 4 *Tachina jilongensis* Zhang & Dong, sp. nov. 5 *Nemoraea javana* (Brauer & Bergenstamm, 1895) 6 *Nemoraea echinata* Mesnil, 1953.

**Diagnosis.** Head and thoracic dorsum with golden-yellow pruinosity. Eye covered with dense hairs. Frons of about 0.5 (male) or 0.6 (female) times of eye width; parafacial nearly bare; upper part of head usually with only 1 row of black setulae behind postocular setae. Antenna with postpedicel 4–5 times as long as pedicel; longest aristal hairs at most as long as aristal diameter. Presutural setae 3 and dorsocentral setae 4; apical scutellar seta absent. Lower calypter with long hairs dorsally on posterior half. Legs black. Fore tibia with 2 posterior setae; mid tibia with 5 anterodorsal and 1 ventral setae; hind tibia with 4–5 anterodorsal setae. Abdomen ovate, dark, black, with many erect setae and hairs, densely covered with gray or indistinct pruinosity on tergites. Abdominal syntergite 1+2 medially extending back to hind margin, without median marginal setae.

**Distribution.** China (Shaanxi, Sichuan, Tibet; Fig. 8), India, Myanmar.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: Z-CT, L-JJ. Data curation: Z-CT and D-RQ. Formal analysis: Z-CT, L-JJ. Writing - original draft: Z-CT, D-RQ. Visualization: D-RQ, Y-H. Funding acquisition: Z-CT. Writing - review and editing: Z-CT, L-JJ, D-RQ.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Checklist

# A revised, annotated checklist of Mexican non-biting midges (Diptera, Chironomidae)

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## Abstract

An updated checklist of Mexican non-biting midges (Chironomidae) is presented. A total of 110 species of Chironomidae are known for Mexico: 52 species in 25 genera belong to the subfamily Chironominae, 30 species in 13 genera to Orthocladiinae, 21 species in nine genera to Tanypodinae, five species in two genera to Telmatogetoninae, and two species in one genus to Diamesinae. In addition, 41 genera without identified species are listed. The highest number of species (29) is recorded from the state of Campeche, while 19 species have been found in Veracruz and 15 in Nuevo León. Few or no records exist for states in Central and Northern Mexico, or those on the Pacific coast. The type localities for 34 species are in Mexico; of these, 27 species (25% of the total number of species recorded in the country) are endemic. Twenty-nine species recorded in Mexico have a Neotropical distribution, 15 a Nearctic distribution, and 39 species are distributed in both the Neotropical and Nearctic regions or more widely. It has been suggested that as many as 1000 species might occur in Mexico; so only a little more than 10% of the expected diversity has so far been recorded.

**Key words:** Biodiversity, Nearctic, Neotropical, transition zone

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## Introduction

Mexico is a megadiverse country (Mittermeier et al. 2011; Mendoza-Ponce et al. 2020). Located in the Nearctic-Neotropical transition area, the north to south orientation of numerous warm, low altitude corridors, and the abundance of mountain chains with colder conditions have allowed biota to disperse during past climate change events (Halffter 1987). This high biodiversity results primarily from an accumulation of taxa from other areas and constant changes in the landscape (Priego Santander and Esteve Selma 2017) rather than local diversification (Sundaram et al. 2019; Harvey et al. 2020). However, several of the most species rich and ecologically relevant insect groups are not included in these studies.

Chironomidae have the widest distribution of all free-living groups of holometabolous insects and are likely the most taxonomically and ecologically diverse family of aquatic insects (Cranston 1995; Dijkstra et al. 2014). Reiss (1982) estimated that between 1500–2000 chironomid species might occur in tropical Mexico and Central America, and Andersen et al. (2000) suggested that as many as 1000 species can be expected to occur in Mexico. Spies et al. (2009) compiled an annotated list of the Mexican and Central American genera including a key to the genera known from the region at that time. However, the latest inventory of the Mexican chironomids only included 61 species plus an additional 25 genera without identified species (Andersen et al. 2000).

During the last two decades, several new species have been described based on material from Mexico (Kyerematen et al. 2000; Kyerematen and Andersen 2002; Wang et al. 2006; Vinogradova 2008; Andersen et al. 2010, 2016; Wiedenbrug et al. 2012; Pinho et al. 2013; Acosta et al. 2017; Pinho and Andersen 2021; Andersen 2023). Several species and genera have also been recorded for the first time from Mexico, especially in connection with surveys of particular habitats like the aquatic fauna in spring-fed tropical canyons in the southern Sonora desert (Bogan et al. 2014), or subfossil Chironomidae in surface sediments of the sinkholes of the Yucatan Peninsula (Hamerlík et al. 2018). Several of these studies are based mainly on larvae and the materials are generally not identified beyond genus level.

The Nearctic-Neotropic transition should lead to the existence of chironomid species with different biogeographic affinities. The Nearctic fauna is comparatively well known (Oliver et al. 1990; Oliver and Dillon 1994) and most chironomids in Mexico with this biogeographic affinity can be identified to genus level using the keys to the larvae, pupa and adults of the Holarctic Region (Wiederholm 1986, 1989; Andersen et al. 2013a). The Neotropical chironomids from Mexico are much less studied and more difficult to identify based on available literature.

An updated checklist of Mexican Chironomidae species is presented. The list provides an updated baseline and will facilitate the study of the chironomid fauna in the Nearctic-Neotropical biogeographical transition zone in Mexico. The checklist is based on Andersen et al. (2000), and new records and species published during the last two decades are added. Some ecological information now available for the genera recorded from Mexico are also included.

## Methods

The checklist is based on Andersen et al. (2000); references already given in that list are not repeated here. The checklist includes published records only. Records were compiled from peer reviewed scientific articles, books, and book chapters and, to a lesser extent, unpublished project reports. Specimens of Mexican chironomids are housed in several collections (Contreras-Ramos 2021; Huerta Jiménez 2021; Admin 2022; Bentley and Thomas 2022; European Bioinformatics Institute 2022); and these records can be accessed using “Name search” in GBIF (2023).

Following Ashe and O´Connor (2009) eight major zoogeographical regions are recognized: Antarctic (AN), Neotropical (NT), Nearctic (NE), Palaearctic (PA), Afrotropical (AF), Oriental (OR), Australasian (AU), and Oceanian (OC). Administratively, Mexico is divided in 32 states. Of these the 18 northernmost states are generally regarded as belonging to the Nearctic region, while the remaining 13 southern most states as belonging to the Neotropical region (Ashe and O´Connor 2009). However, the biogeographical zones are not clearly defined and depend to some degree on the group of organisms studied. There are also clearly transition zones between the two regions. Given this, taxa present in Mexico and in Central or South America are considered to be Neotropical, while taxa present in Mexico and in the USA and/or Canada are considered to be Nearctic. The exception is taxa from southern Florida, USA, which is considered to be Neotropical. However, many species are found both in South- and North America or have a wider distribution.

The checklist is arranged alphabetically. Species group names follow the genus and subfamily names. A short outline with information on the number of species, distribution, and larvae habitats is given for each genus. For literature records given as "*Cricotopus* cf. *sylvestris*" or "*Cricotopus sylvestris* group" we assume they are correctly identified to genus level. Following Ashe and O'Connor (2009), two Tanypodinae species originally described as *Macropelopia roblesi* Vargas, 1946 and *Pentaneura marmorata* Johannsen, 1938 are listed as "Generically unplaced valid Macropelopiini" and "Generically unplaced valid Tanypodinae", respectively.

The valid species name is followed by the original combination in parenthesis, with type country (for USA, country and state) in square brackets. When the type locality is situated in Mexico, more specific information is given for the type locality. Synonyms are given if descriptions are based on Mexican material. Mexican records are then given followed by the state(s) from where the species is recorded in square brackets. Finally, the total distribution for a species is given as zoogeographical region(s), followed by the countries from where the species has been recorded. However, this list of countries might not be complete, and for widespread species it is only given as "widespread".

## Citations for species names are arranged as follows

***Cladopelma forcipis* (Rempel, 1939: 211)** (*Chironomus* (*Cryptochironomus*)) [Brazil]. Andersen et al. (2000: 590) [Mexico State; Morelos; Veracruz]; Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]; European Bioinformatics Institute (2022) [Quintana Roo]. NT, NE. Brazil, Colombia, Costa Rica, Guatemala, Mexico, Nicaragua, Panama, USA.

In the checklist, recorded genera lacking identified species are included. Mexican records are listed as e.g.: *Cryptochironomus* sp., followed by the state(s) from where the genus is recorded in square brackets.

Vinogradova and Riss (2007) provided numerous records from the Yucatan Peninsula, but without giving any details on the localities. As Yucatan Peninsula includes partly or totally the territory of three Mexican states; these records are listed as ["Yucatan Peninsula"].

## Results

### Check list

### Subfamily Chironominae

#### Genus *Apedilum* Townes, 1945

A genus with three named species. *A. elachistus* Townes, 1945 is widespread throughout North and South America, *A. subcinctum* Townes, 1945 is distributed in North and Central America, and *A. griseistriatum* (Edwards, 1931) occurs in South America. Larvae are associated with submerged vegetation in ponds, canals, lakes, and slowly running rivers, both in fresh or brackish water (Epler et al. 2013).

***Apedilum elachistus* Townes, 1945: 33** [USA: Texas]. Andersen et al. (2000: 590) [States of Campeche; Puebla; Veracruz]; Contreras-Ramos et al. (2000: 25); Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]. NT, NE. Argentina (Donato et al. 2008a), Brazil, Canada (Giberson et al. 2001), Costa Rica, Guatemala, Mexico, Nicaragua, Uruguay (Donato et al. 2008a), USA.

***Apedilum subcinctum* Townes, 1945: 33** [USA: Nevada]. Andersen et al. (2000: 590) [States of Campeche; Jalisco]; Contreras-Ramos et al. (2000: 25); Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]; Contreras-Ramos (2021). NT, NE. Guatemala, Mexico, USA.

#### Genus *Asheum* Sublette & Sublette, 1983

See: *Polypedilum* Kieffer, 1912.

#### Genus *Axarus* Roback, 1980

A genus of ~ 15 species that occur in the Neotropical, Nearctic, Palaearctic, and the Australasian regions. Ten species are known from South America (Andersen and Mendes 2002a; Andersen et al. 2018; Pinho et al. 2019). Larvae occur in littoral to sublittoral soft sediments in lakes and rivers (Epler et al. 2013).

***Axarus rogersi* (Beck & Beck, 1958: 27)** (*Xenochironomus*) [USA: Florida]. Andersen et al. (2000: 590) [Campeche State]; Contreras-Ramos et al. (2000: 26); Contreras-Ramos (2021). NT, NE. Costa Rica, Mexico, Nicaragua, USA.

#### Genus *Beardius* Reiss & Sublette, 1985

A genus with > 30 named species that occur mainly in tropical areas in the Neotropical region with a few species in the southern parts of the Nearctic region (Jacobsen and Perry 2000; Pinho et al. 2013). The larvae have been found associated with macrophytes or submerged wood in both standing and flowing waters (Epler et al. 2013).

***Beardius aciculatus* Andersen & Sæther, 1996: 40** [COSTA RICA]. Andersen et al. (2000: 590) [States of Campeche; Veracruz]; Contreras-Ramos et al.

(2000: 26); Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]; Contreras-Ramos (2021); Admin (2022). NT. Costa Rica, Mexico.

***Beardius chapala* Pinho, Mendes & Andersen, 2013: 28** [Mexico: Jalisco State, Lake Chapala, El Chante]. Endemic.

***Beardius parcus* Reiss & Sublette, 1985: 183** [Venezuela]. Andersen et al. (2000: 590) [Veracruz State]; Contreras-Ramos et al. (2000: 26) [Campeche State]; Contreras-Ramos (2021). NT. Costa Rica, Mexico, Nicaragua, Venezuela.

### Genus *Caladomyia* Säwedal, 1981

See: *Tanytarsus* Wulp, 1874.

### Genus *Chironomus* Meigen, 1803

One of the most species-rich and common chironomid genera, with ~ 300 described species from all zoogeographical regions except Antarctica. The larvae graze on detritus or are filter-feeders, predominantly in soft sediments of standing water, rarely in flowing water (Epler et al. 2013).

***Chironomus alchichica* Acosta & Prat in Acosta et al. 2017: 53** [Mexico: Puebla State, Lake Alchichica]. Endemic.

***Chironomus stigmaterus* Say, 1823: 15** [USA: Pennsylvania]. Andersen et al. (2000: 590) [States of Durango; Puebla]; Alcocer et al. (2016: 411). NT, NE. Brazil, Cuba, Mexico, USA.

### Genus *Cladopelma* Kieffer, 1921

A genus of ~ 20 described species that occur in all zoogeographical regions except Antarctica and Oceania. The larvae live in streams and larger rivers, lakes, and ponds as well as brackish water and hot springs (Epler et al. 2013).

***Cladopelma forcipis* (Rempel, 1939: 211)** (*Chironomus* (*Cryptochironomus*)) [Brazil]. Andersen et al. (2000: 590) [States of Mexico; Morelos; Veracruz]; Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]; European Bioinformatics Institute (2022) [Quintana Roo State]. NT, NE. Brazil, Colombia, Costa Rica, Guatemala, Mexico, Nicaragua, Panama, USA.

### Genus *Cladotanytarsus* Kieffer, 1921

A genus of ~ 80 described species that occur in all zoogeographical regions except Antarctica and Oceania. No named species are recorded from South America, but larval morphotypes have been recorded from Brazil (Roque et al. 2004). Larvae construct sessile cases of fine detritus and have been found in streams and larger rivers, lakes, and ponds, as well as in brackish water and hot springs (Epler et al. 2013).

***Cladotanytarsus viridiventris* (Malloch, 1915: 491)** (*Tanytarsus*) [USA: Michigan]. Andersen et al. (2000: 590) [Puebla State]. NE. Canada, Mexico, USA.

### Genus *Cryptochironomus* Kieffer, 1918

A genus of ~ 60 named species that occur in all zoogeographical regions, except Antarctica. Four species are described from South America (da Silva et al. 2010). Larvae occur on various substrates in lakes, small streams, and larger rivers (Epler et al. 2013).

***Cryptochironomus* sp.**: Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]; Granados-Ramírez et al. (2017: 45) [Morelos State].

### Genus *Dicrotendipes* Kieffer, 1913

A genus of ~ 85 described species that occur in all zoogeographic regions except Antarctica. The genus was revised by Epler (1988). The larvae inhabit the littoral sediments of standing waters and may be common in lentic habitats (Epler et al. 2013).

***Dicrotendipes aethiops* (Townes, 1945: 107)** (*Tendipes* (*Limnochironomus*)) [USA: New Mexico].
Syn.: *Tendipes* (*Limnochironomus*) *figueroai* Vargas, 1952: 48 [Mexico: Morelos State].
Andersen et al. (2000: 590) [States of Baja California; Mexico; Querétaro]; Huerta-Jiménez (2021) [Morelos State]. NE. Mexico, USA.

***Dicrotendipes californicus* (Johannsen, 1905: 217)** (*Chironomus*) [USA: California]. Andersen et al. (2000: 590) [States of Mexico; Morelos; Oaxaca; Sinaloa]; Bentley and Thomas (2022) [Michoacán State]. NT, NE. Chile, Colombia, Costa Rica, Guatemala, Mexico, Panama, Peru, USA.
**Remark.** Bentley and Thomas (2022) recorded the species from "Cojumatlán, Jalisco". The town of Cojumatlán is located on the shoreline of Lake Chapala in the State of Michoacán. Although close to the border between the two states, the original reference to the State of Jalisco most probably is a mistake.

***Dicrotendipes neomodestus* (Malloch, 1915: 475)** (*Chironomus*) [USA: Illinois]. Andersen et al. (2000: 590) [Puebla State]; Alcocer et al. (2016: 412). NE. Canada, Mexico, USA.

***Dicrotendipes obrienorum* Epler, 1987: 148** [Mexico: Michoacán State, Patzcuaro]. Andersen et al. (2000: 590). Endemic.

***Dicrotendipes sinoposus* Epler, 1987: 152** [Mexico: Hidalgo State, Otongo]. Andersen et al. (2000: 590) [States of Campeche; Hidalgo; Veracruz]; Contreras-Ramos et al. (2000: 26); Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]; Contreras-Ramos (2021). NT. Brazil, Colombia, Costa Rica, Dominica, Mexico, Nicaragua.

### Genus *Einfeldia* Kieffer, 1922

The concept, content and status of *Einfeldia* have been, and to an extent remain, confusing (Cranston et al. 2016a). Narrowly defined, *Einfeldia* contains approximately five species and is distributed in the Neotropical, Nearctic, Palaearctic, Oriental, and Australasian regions. The larvae inhabit standing, predominantly dystrophic waters (Epler et al. 2013).

***Einfeldia* sp.**: Navarrete-Salgado et al. (2004: 157) [México State]; Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"].

### Genus *Endochironomus* Kieffer, 1918

A genus of ~ 20 named species distributed in the Nearctic, Palaearctic, Afrotropical, and Oriental regions. The larvae occur in "Aufwuchs" on living and dead substrata in almost all types of still water; they mine leaves and stems of macrophytes preferentially in small, eutrophic standing waters (Epler et al. 2013).

***Endochironomus subtendens* (Townes, 1945: 65) (***Tanytarsus* (*Endochironomus*)) [USA: New York]. Andersen et al. (2000: 590) [Yucatán State]. NE. Canada, Mexico, USA.

### Genus *Endotribelos* Grodhaus, 1987

A genus of 14 described species, all occurring in the Neotropical and Nearctic regions except one species from China. The Brazilian species were treated by Trivinho-Strixino and Pepinelli (2015). The larvae are associated with aquatic macrophytes, decaying leaves, wood, and fallen fruits in streams (Epler et al. 2013).

***Endotribelos hesperium* (Sublette, 1960: 217)** (*Tendipes* (*Tribelos*)) [USA: California]. Andersen et al. (2000: 590) [Puebla State]. NE. Mexico, USA.

### Genus *Fissimentum* Cranston & Nolte, 1996

A genus with four named species endemic to South America; but larval morphotypes have also been recorded from the Nearctic, Oriental, and Australasian regions (Epler et al. 2013). Larvae are found in fine sediments of lentic and lotic habitats and can tolerate desiccation (Cranston and Nolte 1996).

***Fissimentum* sp.**: Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"].

### Genus *Glyptotendipes* Kieffer, 1913

The taxonomy and nomenclature of the genus have been confusing since its establishment. *Glyptotendipes* now includes ~ 27 species, distributed in the Neartic, Paleartic, Oriental, and Afrotropical regions (Epler et al. 2013; Konar and Majumdar 2021). Three subgenera are recognized, *Glyptotendipes* s. str. (including *Phytotendipes* Goetghebuer, 1937), *Caulochironomus* Heyn, 1992, and *Heynotendipes* Spies & Sæther, 2004 (including *Trichotendipes* Heyn, 1992) (see Spies and Sæther 2004). Larvae occur in detritus-rich littoral sediments of lakes, ponds, small water bodies, and running water (Epler et al. 2013).

***Glyptotendipes* sp.**: Contreras-Ramos and Andersen (1999: 4) [Campeche State]; Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"].

### Genus *Goeldichironomus* Fittkau, 1965

A genus of 15 named species mainly distributed in the Neotropical region (tropical and subtropical Central and South America), but several species reach their northern limits in southeastern USA (Donato and Andersen 2022). The larvae of *Goeldichironomus* are mostly found in sediments, on plants or in floating mats of vegetation in lentic habitats, in fresh to brackish water, and in oligotrophic to hypereutrophic conditions (Epler et al. 2013).

***Goeldichironomus amazonicus* (Fittkau, 1968: 260)** (*Siolimyia*) [BRAZIL]. Andersen et al. (2000: 590) [Veracruz]; Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]. NT. Bahamas, Brazil, Mexico, Nicaragua, Panama, Peru, USA: Florida, Venezuela, Virgin Islands.

***Goeldichironomus carus* (Townes, 1945: 118)** (*Tendipes*) [VENEZUELA]. Vinogradova and Riss (2007: 32) ["Yucatan Peninsula"]. NT, NE. Colombia, Costa Rica, Mexico, Nicaragua, Panama, Venezuela, USA.

***Goeldichironomus holoprasinus* (Goeldi, 1905: 135)** (*Chironomus*) [BRAZIL]. Andersen et al. (2000: 590) [Tabasco]; Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]. NT, NE. Argentina, Brazil, Costa Rica, Ecuador, Mexico, Nicaragua, Panama, Peru, USA, Venezuela, Virgin Islands.

### Genus *Harnischia* Kieffer, 1921

A genus of ~ 20 described species that occur in all zoogeographic regions except the Antarctic, Neotropical, and Oceanian regions. However, unnamed larvae have been recorded from Brazil (Roque et al. 2004). Larvae occur in soft sediments of generally clean lakes and larger rivers (Epler et al. 2013).

***Harnischia* sp.**: Contreras-Ramos et al. (2000: 26) [Campeche State].

### Genus *Hyporhygma* Reiss, 1982

A genus with a single named species, *H. quadripunctatum* (Malloch, 1915), distributed in eastern North America, from Newfoundland to Florida. The larvae mine leaves and stems of *Nuphar* and *Nymphaea* species (Epler et al. 2013).

***Hyporhygma* sp.**: Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"].

### Genus *Kiefferulus* Goetghebuer, 1922

Syn.: *Nilodorum* Kieffer, 1921 (see Cranston et al. 1990).

A genus with at least five species in the Holarctic region. Species previously considered to belong to *Nilodorum* are widespread in the Afrotropical, Oriental, and Australasian regions. The larvae inhabit sediments of small to medium sized waterbodies (Epler et al. 2013).

***Kiefferulus* sp.**: Contreras-Ramos et al. (2000: 26) [Campeche State].

### Genus *Lauterborniella* Thienemann & Bause, 1913

A genus with a single named species, *L. agrayloides* (Kieffer, 1911) distributed in the Neotropical, Nearctic, and Palaearctic regions. Other species referred to as *Lauterborniella* in the literature belong either to *Zavreliella* Kieffer, 1920 or to *Kribiodorum* Kieffer, 1921, or their generic affinities are unclear (Epler et al. 2013). Larvae are mobile amongst submerged vegetation in small bodies of standing water (Epler et al. 2013). In Brazilian streams they have also been found in accumulations of litter attached to stones (Sanseverino and Nessimian 2001).

***Lauterborniella* sp.**: Bogan et al. (2014: 2726) [Sonora State].

### Genus *Microchironomus* Kieffer, 1918

A genus of approximately ten species distributed in the Nearctic, Palaearctic, Afrotropical, and Oriental regions (Yan and Wang 2006). The larvae occur in lakes, rivers, and ditches, including brackish water (Epler et al. 2013).

***Microchironomus nigrovittatus* (Malloch, 1915: 456)** (*Chironomus*) [USA: Illinois]. Andersen et al. (2000: 590) [Veracruz State]. NE. Mexico, USA.

### Genus *Micropsectra* Kieffer, 1909

Based on morphological and molecular data, *Krenopsectra* Reiss, 1969 and *Parapsectra* Reiss, 1969 were recently considered to be junior synonyms of *Micropsectra* (Ekrem et al. 2010). The three genera have a Holarctic distribution with ~ 100 valid species. The larvae have been recorded from a wide range of habitats, including hygropetric situations, thermal springs, moorland pools, and temporary pools. They are often found in muddy deposits in slow flowing stretches of streams and small rivers and in mesotrophic and oligotrophic lakes (Epler et al. 2013).

***Micropsectra* sp.**: Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]; Alcocer et al. (2016: 411) [Puebla State].

**Remarks.** Both records from Mexico appear to be based on larvae only. According to Epler et al. (2013) the larvae of *Micropsectra* can be difficult to separate from *Tanytarsus* larvae.

### Genus *Microtendipes* Kieffer, 1915

A genus of ~ 55 named species that occur in all zoogeographic regions, except Antarctica; Neotropical records are based only on larvae not identified to species level (Roque et al. 2004). Larvae are found in littoral and sublittoral sediments of lakes, and in sediments and submerged mosses in running water (Epler et al. 2013).

***Microtendipes* sp.**: Vinogradova and Riss (2007: 34) ["Yucatan Peninsula"]; Granados-Ramírez et al. (2017: 45) [Mexico State].

### Genus *Nandeva* Wiedenbrug, Reiss & Fittkau, 1998

A genus with seven described species that occur in the Neotropical and Australasian regions (Andersen et al. 2011b). The only described larvae was found in semi-immersed leaf litter packs in a tropical stream in Australia (Cranston 2019).

***Nandeva strixinorum* Sæther & Roque, 2004: 67** [Brazil]. Andersen et al. (2011b: 55) [Campeche State]. NT. Brazil, Mexico.

### Genus *Nilothauma* Kieffer, 1921

A genus with > 60 described species distributed throughout most zoogeographic regions except Antarctica. The Neotropical species were reviewed by Pinho and Andersen (2021). The larvae inhabit littoral and sublittoral soft sediments of lakes, streams, and rivers (Epler et al. 2013).

***Nilothauma maya* Pinho & Andersen, 2021: 103** [Mexico: Campeche State, Calakmul]. Endemic to Mexico.

### Genus *Nimbocera* Reiss, 1972

See: *Tanytarsus* Wulp, 1874.

### Genus *Omisus* Townes, 1945

See: *Zavreliella longiseta* Reiss, 1990.

### Genus *Oukuriella* Epler, 1986

A genus of > 20 species restricted to the Neotropical region. The larvae can be found associated with freshwater sponges or submerged wood in streams and rivers (Fusari et al. 2014). Species associated with sponges were revised by Fusari et al. (2014).

***Oukuriella annamae* Epler, 1996: 4** [Costa Rica]. Andersen et al. (2000: 590) [Campeche State]; Contreras-Ramos et al. (2000: 26). NT. Brazil (Bellodi et al. 2016), Costa Rica, Mexico.

***Oukuriella oliveirai* Messias & Fittkau, 1997: 256** [Brazil]. Bellodi et al. (2016: 191) [Campeche State]. NT. Brazil, Mexico.

***Oukuriella simulatrix* Epler, 1986: 160** [Colombia]. Andersen et al. (2000: 590) [Campeche State]; Contreras-Ramos et al. (2000: 26); Vinogradova and Riss (2007: 33) [“Yucatan Peninsula”]; Bellodi et al. (2016: 193). NT. Colombia, Mexico.

### Genus *Parachironomus* Lenz, 1921

The genus has a worldwide distribution with at least 30 species in the Holarctic region and 20 species in the Neotropical region (Trivinho-Strixino et al.

2010; Epler et al. 2013). The adults of the Neotropical species were revised by Spies et al. (1994). Larvae are found in lentic and lotic water bodies under a wide range of conditions, including leaf miners in submerged macrophytes; they also live in association with Bryozoa or are ectoparasites on other invertebrates (Epler et al. 2013).

***Parachironomus directus* (Dendy & Sublette, 1959: 514)** (*Tendipes* (*Cryptochironomus*)) [USA: Alabama]. Andersen et al. (2000: 590) [Morelos State]; Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]. NT, NE. Mexico, Nicaragua, Panama, USA.

***Parachironomus hazelriggi* Spies, 2000: 133** [USA: California]. Andersen et al. (2000: 590) as *P. monochromus* Wulp, 1874 [States of Querétaro; Mexico]; Spies (2000: 134) [Guanajuato State; Mexico City]. NE, PA. Canada, Mexico, Russia (Orel 2017: 535), USA.

**Remarks.** According to Spies (2000: 129) *P. monochromus* Wulp, 1874 is today considered to be a Palaearctic species and listing from Mexico following Spies & Reiss (1996: 71) must be changed to *P. hazelriggi*.

***Parachironomus tenuicaudatus* (Malloch, 1915: 475)** (*Chironomus*) [USA: Illinois]. Andersen et al. (2000: 590) [Puebla State]. NE, PA. Widespread.

**Remarks.** According to Spies (2000: 133) the record from Puebla is based on Alcocer et al. (1993) and must be considered as uncertain as it appears to be based on immature specimens only.

### Genus *Paracladopelma* Harnisch, 1923

The genus has a predominantly Holarctic distribution, with at least 20 known species; many species are also recorded from the Oriental region (Epler et al. 2013; Yan et al. 2008). The Holartic species were reviewed by Jackson (1977). Larvae inhabit sandy substrata in lakes, streams, and small rivers and the soft profundal sediments of deep lakes (Epler et al. 2013).

***Paracladopelma* sp.**: Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"].

### Genus *Paralauterborniella* Lenz, 1941

A genus with two described species; one of them, *P. nigrohalteralis* (Malloch, 1915), is widely distributed (Tang 2016). The larvae usually occur in littoral soft sediments of lakes (Epler et al. 2013).

***Paralauterborniella* sp.**: Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"].

### Genus *Paratanytarsus* Thienemann & Bause, 1913

A genus of > 60 named species that occur in all zoogeographical regions except Antarctica. The larvae inhabit brackish ponds, cool streams, lakes, rivers, reservoirs, and marshes (Epler et al. 2013).

***Paratanytarsus tolucensis* Reiss, 1972: 62** [Mexico: Mexico State, Nevado de Toluca]. Andersen et al. (2000: 590). Endemic.

### Genus *Paratendipes* Kieffer, 1911

A genus of nearly 40 named species that occur in the Afrotropical and Oriental regions and in the Holarctic realm (Qi et al. 2009). For South America there are only records of unnamed species (Roque et al. 2004; Trivinho-Strixino 2011). Larvae are found in lakes, ponds, small water bodies, bogs, and hot springs and in streams and rivers in soft sediments and sandy bottoms (Epler et al. 2013).

***Paratendipes* sp.**: Contreras-Ramos and Andersen (1999: 4) [Campeche State]; Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]; Bogan et al. (2014: 2726) [Sonora State]; Hamerlík et al. (2018: 217) [Yucatan State].

### Genus *Phaenopsectra* Kieffer, 1921

A genus of more than ten named species that occur in all zoogeographical regions except the Antarctic, Oriental, and Australasian regions. The larvae mainly occur in sandy and muddy sediments of small standing and flowing waters, but also on submerged water plants and hard substrata (Epler et al. 2013).

***Phaenopsectra* sp.**: Navarrete-Salgado et al. (2004: 157) [México State]; Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"].

### Genus *Polypedilum* Kieffer, 1912

#### *Asheum* Sublette & Sublette, 1983, as subgenus

Syn.: *Pedionomus* Sublette, 1964 (see Sæther and Sundal 1999).

The largest genus of Chironomidae, with > 500 described species that occur in all zoogeographical regions except Antarctica. Based on imaginal characters, eight subgenera were recognized by Sæther et al. (2010), namely *Tripedilum* Kieffer, 1921; *Polypedilum* s. str.; *Pentapedilum* Kieffer, 1913; *Tripodura* Townes, 1945; *Uresipedilum* Oyewo & Sæther, 1998; *Cerobregma* Sæther & Sundal, 1999; *Kribionympha* Kieffer, 1921; and *Probolum* Andersen & Sæther, 2010. However, the delimitation of the subgenera within *Polypedilum* was questioned by Yamamoto and Yamamoto (2015) and Cranston et al. (2016b). The position of *Asheum* is unclear but is usually treated as a subgenus within *Polypedilum* (see Pinho and Silva 2020). Larvae of *Polypedilum* occur in virtually all still and flowing waters, except in the Arctic and at high elevation. They are mostly found in sediments, mining water plants or specializing in plant-held waters (phytotelmata) (Epler et al. 2013).

***Polypedilum* (*Asheum*) *beckae* (Sublette, 1964a: 137)** (*Pedionomus*) [USA: Louisiana]. Andersen et al. (2000: 590) [States of Campeche; Veracruz]; Contreras-Ramos et al. (2000: 25). NT, NE. Dominican Republic, Mexico, USA.

***Polypedilum (Asheum) curticaudatum* Rempel, 1939: 214** [Brazil]. Vinogradova and Riss (2007: 33) (as: *Pedionomus curticaudatus*) ["Yucatan Peninsula"]; Pinho and Silva (2020: 184). NT. Brazil, Mexico.

***Polypedilum* (*Polypedilum*) *purus* Bidawid-Kafka, 1996: 216** [Brazil]. Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]. NT. Brazil, Mexico.

***Polypedilum* (*Tripodura*) *bacalar* Vinogradova, 2008: 279** [Mexico: Quintana Roo State, Chetumal, Lake Bacalar]; Zhang et al. (2016: 41). Endemic.

***Polypedilum* (*Tripodura*) *rissi* Vinogradova, 2008: 281** [Mexico: Yucatan State, Lake Punta Laguna]. Vinogradova (2008: 281) [Quinto Roo]; Zhang et al. (2016: 47). NT. Guatemala, Mexico

***Polypedilum* (*Tripodura*) *spiesi* Vinogradova, 2008: 278** [Belize]. Vinogradova (2008: 278) [Quintana Roo State]; Zhang et al. (2016: 48). NT. Belize, Mexico.

***Polypedilum* (*Uresipedilum*) *pedatum* Townes, 1945: 55** [USA: New York & Washington]. Andersen et al. (2000: 590) [Nuevo León State]. NE. Canada, Mexico, USA.

**Remarks.** Townes (1945: 55) described two subspecies, *P. pedatum pedatum* from New York and *P. pedatum excelsius* from Washington. Andersen et al. (2000: 590) recorded the species as *P.* (*Polypedilum*) *pedatum* Townes, while Sæther and Oyewo (2008: 3) placed it in subgenus *Uresipedilum*.

***Polypedilum rohneri* Vinogradova, 2008: 286** [Belize]. Vinogradova (2008: 286) [Yucatan State]. NT. Belize, Guatemala, Mexico.

**Remarks.** The species is not assigned to a subgenus. According to Vinogradova (2008: 288) it might deserve a separate subgenus.

### Genus *Pseudochironomus* Malloch, 1915

A genus with at least 30 species distributed in the Neotropical, Nearctic, and Palaearctic regions. The Brazilian species have recently been treated by Shimabukuro et al. (2017) and Trivinho-Strixino and Shimabukuro (2018). The larvae inhabit sandy or gravelly littoral sediments, primarily in meso- or oligotrophic lakes or in large, slow flowing rivers (Epler et al. 2013).

***Pseudochironomus seipi* Andersen, 2023** [Mexico: Chiapas State, Chintul, Río Chintul]. NT. Costa Rica, Mexico.

### Genus *Rheotanytarsus* Thienemann & Bause, 1913

A genus with ~ 100 species distributed in all zoogeographic regions except Antarctica. The Central American and Mexican species were reviewed by Kyerematen and Andersen (2002); the *Rheotanytarsus pellucidus* group was revised by Kyerematen et al. (2000). Larvae are rheobiontic, occurring in streams, large rivers, and the littoral of lakes where wave action simulates the action of flowing water (Epler et al. 2013).

***Rheotanytarsus calakmulensis* Kyerematen & Andersen, 2002: 33** [Mexico: Campeche State, Calakmul Biosphere Reserve]. Endemic.

***Rheotanytarsus contrerasi* Andersen & Sæther in Kyerematen et al., 2000: 166** [Mexico: Puebla State, Mpio. Progreso, Río San Juan]. Kyerematen et al. (2000: 166) [Nuevo León State]. Endemic.

***Rheotanytarsus foliatus* Kyerematen & Andersen, 2002: 35** [Costa Rica]. Kyerematen and Andersen (2002: 35) [Nuevo León State]. NT. Costa Rica, Mexico.

***Rheotanytarsus hanseni* Kyerematen & Andersen, 2002**: **42** [Mexico: Oaxaca State, Candelaria Loxiela]. Kyerematen and Andersen (2002: 42) [Morelos State]. Endemic.

***Rheotanytarsus kusii* Kyerematen & Andersen, 2002: 37** [Mexico: Nuevo León State, Allende, Río Ramos]. Endemic.

***Rheotanytarsus nuamae* Kyerematen & Andersen, 2002: 38** [Mexico: Nuevo León State, Allende, Río Ramos]. Endemic.

***Rheotanytarsus ramirezae* Kyerematen & Andersen, 2002: 46** [Mexico: Nuevo León State, Santiago, Cola de Caballo]. Endemic.

### Genus *Saetheria* Jackson, 1977

A genus of seven named species that occur in the Neotropical, Nearctic, and Palearctic regions (Orel 2014). Only unnamed larvae have so far been recorded from South America (Roque et al. 2004). Larvae inhabit sandy substrata of lakes and streams (Epler et al. 2013).

***Saetheria* sp.**: Vinogradova and Riss (2007: 33) [“Yucatan Peninsula”].

### Genus *Skutzia* Reiss, 1985

A genus of six species that occur in the Neotropical, Nearctic, and Oriental regions. The genus was revised by Pinho et al. (2009a). The larvae are unknown. However, they can be expected to construct transportable cases of sand grains, small wood or plant remains, as seen in the larvae of other species in the subtribe Zavreliina.

***Skutzia quetzali* Pinho, Mendes & Andersen, 2009a: 204** [Mexico: Campeche State, Calakmul, Ejido Nuevo Becan, El Chorro]. NT. Mexico, Panama.

### Genus *Stempellina* Thienemann & Bause, 1913

A genus of at least 20 species that occur in all zoogeographic regions except Antarctica. The larvae construct long, curved, tapered, transportable cases of fine sand and silt. They are eurytopic, occurring in springs, streams, larger rivers, lakes, brackish water, moorland pools, and in thermal springs (Epler et al. 2013).

***Stempellina* sp.**: Contreras-Ramos and Andersen (1999: 4) [Campeche State]; Vinogradova and Riss (2007: 34) [“Yucatan Peninsula”]; Bogan et al. (2014: 2726) [Sonora State].

### Genus *Stempellinella* Brundin, 1947

A genus of ~ 20 described species that occur in all zoogeographical regions except Antarctica. The larvae construct straight, transportable cases of fine sand and silt, often speckled with detritus; they occur in unpolluted springs and small streams as well as in lakes (Epler et al. 2013).

***Stempellinella* sp.**: Vinogradova and Riss (2007: 34) [“Yucatan Peninsula”]; Bogan et al. (2014: 2726) [Sonora State].

### Genus *Stenochironomus* Kieffer, 1919

A genus of > 100 described species that occur in all zoogeographic regions except Antarctica. The genus was revised by Borkent (1984). South American species were treated by Dantas et al. (2016). Larvae are obligate miners in living or dead vegetation including woody parts of plants, in both lentic and lotic situations (Epler et al. 2013).

***Stenochironomus leptopus* Kieffer, 1906**: **19** [St. Vincent]. Andersen et al. (2000: 590) [Mexico, without specific locality]. NT. Costa Rica, Dominica, Ecuador, Guatemala, Mexico, St. Vincent.

### Genus *Sublettea* Roback, 1975

A small genus with four species distributed in the Neotropical, Nearctic, and Oriental regions (Ashe et al. 1987). The larvae occur in flowing waters including cool, clean, fast flowing, temperate streams and warm, tropical rivers and streams (Epler et al. 2013). The only known larva construct soft, non-transportable cases of fine granules and silk that are attached to the substrate (Roback 1975).

***Sublettea* sp.**: Vinogradova and Riss (2007: 34) [“Yucatan Peninsula”].

### Genus *Tanytarsus* Wulp, 1874

Syn.: *Nimbocera* Reiss, 1972 (see Sanseverino et al. 2010).
Syn.: *Caladomyia* Säwedal, 1981 (see Lin et al. 2018).

A species-rich genus with > 350 described species that occur in all zoogeographic regions except Antarctica. A molecular phylogeny of the genus was presented by Lin et al. (2018), placing *Caladomyia* as a junior synonym of *Tanytarsus*. The larvae are found in all types of freshwaters, with some marine, and at least one terrestrial species. The freshwater species usually construct long, soft tubes that are fixed to the bottom substrate (Epler et al. 2013).

***Tanytarsus hastatus* Sublette & Sasa, 1994: 56** [Guatemala]. Andersen et al. (2000) [Sinaloa State]; Vinogradova and Riss (2007) [“Yucatan Peninsula”]. European Bioinformatics Institute (2022). NT, NE. Brazil, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Peru, USA, Venezuela.

***Tanytarsus pistra*** (**Sublette & Sasa, 1994: 54)** (*Caladomyia*) [Guatemala]. Vinogradova and Riss (2007: 32) [“Yucatan Peninsula”]. NT, NE. Guatemala, Mexico, USA (Lathrop and Mulla 1995).

### Genus *Tribelos* Townes, 1945

A genus with less than 10 named species distributed mainly in the Nearctic and Palaearctic regions. The genus is also recorded from the Neotropical region (Trivinho-Strixino et al. 2000). The larvae occur in littoral sediments of small to large water bodies (Epler et al. 2013).

***Tribelos* sp.**: Contreras-Ramos and Andersen (1999: 4) [Campeche State].

### Genus *Xenochironomus* Kieffer, 1921

A genus with ~ 20 species distributed in the Neotropical, Nearctic, Palaearctic, Oriental, and Australasian regions. The genus was revised by Fusari et al. (2013). The larvae of almost all species are obligate miners in freshwater sponges in standing and flowing waters (Epler et al. 2013).

***Xenochironomus* sp.**: Contreras-Ramos and Andersen (1999: 4) [Campeche State]; Vinogradova and Riss (2007: 33) [“Yucatan Peninsula”].

### Genus *Xestochironomus* Sublette & Wirth, 1972

A genus of more than ten described species that occur only in the Neotropical and Nearctic regions (Pinho and Souza 2013; Bello-González et al. 2016). Known larvae are miners in immersed wood in running waters (Epler et al. 2013).

***Xestochironomus latilobus* Borkent, 1984: 29** [VENEZUELA]. Andersen et al. (2000: 590) [Campeche State]; Contreras-Ramos et al. (2000: 26). NT. Costa Rica, Mexico, Venezuela.

### Genus *Zavreliella* Kieffer, 1920

A genus with ~ 15 species; according to Fusari et al. (2017), 13 of these are known from tropical South America. The genus was revised by Reiss (1990). Larvae build transportable cases and move among submerged vegetation in standing water, but can also be found in sediments in flowing waters (Epler et al. 2013).

***Zavreliella longiseta* Reiss, 1990: 112** [BRAZIL]. Contreras-Ramos and Andersen (1999: 4, as *Omisus* sp.) [Campeche State]; Contreras-Ramos et al. (2000: 26, as *Omisus* sp.); Vinogradova and Riss (2007: 33) [“Yucatan Peninsula”]. NT. Brazil, Costa Rica, Mexico, Panama.

**Remarks.** The genus *Omisus* Townes, 1945 was recorded from Campeche State by Contreras-Ramos and Andersen (1999) and Contreras-Ramos et al. (2000). However, this record is incorrect. At closer examination the specimens belong to *Zavreliella longiseta* Reiss, 1990, a species that lacks dark spots in the wing and has a second, strong, curved spur on the hid tibia. The generic diagnosis given by Reiss (1990) should thus be amended accordingly.

## Subfamily Diamesinae

### Genus *Diamesa* Meigen, 1835

A genus of > 100 named species distributed in the Nearctic, Palaearctic, Afrotropical, and Oriental regions. Larvae of *Diamesa* are generally adapted to cool waters, inhabiting flowing water, springs, and to a lesser extent shallow still water and the hygropetric zone; they can be dominant in the kryon zone of glacier fed streams (Sæther and Andersen 2013a).

***Diamesa mexicana* Serra-Tosio, 1977: 100** [Mexico: Mexico State, Lake Nevado de Toluca]. Andersen et al. (2000: 589); Ashe and O'Connor (2009: 281). Endemic.

***Diamesa reissi* Serra-Tosio, 1977: 99** [Mexico: Mexico State, Lake Nevado de Toluca]. Andersen et al. (2000: 589); Ashe and O'Connor (2009: 283). Endemic.

### Genus *Pseudokiefferiella* Zavřel, 1941

The only included species, *Pseudokeifferiella parva* (Edwards, 1932), is distributed in the Nearctic and Palaearctic regions. The larvae inhabit small streams and the hygropetric zone (Sæther and Andersen 2013a).

***Pseudokiefferiella* sp.**: Bogan et al. (2014: 2726) [Sonora State].

## Subfamily Orthocladiinae

Syn.: Prodiamesinae (see Lin et al. 2022).

### Genus *Allocladius* Kieffer, 1913

A genus of 25 named species that occur in all zoogeographical regions, except Antarctica and Oceania. Andersen et al. (2010) reviewed the South American species; a revision of the genus was given by Ferrington and Sæther (2011). The larvae of *Allocladius* appear to be truly aquatic, as they have been found in ponds, rivers, and streams, including the shores of brackish water bodies and salt marshes, but some are probably able to survive in moist sandy substrata (Andersen et al. 2013b).

***Allocladius nanseni* (Kieffer, 1926: 82)** (*Camptocladius*) [Canada]. Ferrington and Sæther (2011: 66) [Mexico State]; Ashe and O'Connor (2012a: 118). NE, PA. Widespread.

### Genus *Antillocladius* Sæther, 1981

A genus of 30 named species that occur mostly in the Neotropical region, but are also found in the Nearctic, Palaearctic, and Oriental regions (Ashe and O'Connor 2012a; Andersen and Hagenlund 2017). The genus was reviewed by Mendes et al. (2004, 2011) and Mendes and Andersen (2008). Known larvae from South America appear to be terrestrial or semi-terrestrial as they have been collected in moss and lichens on stones and tree trunks; a North American species has been found in seeps near streams and impoundments (Mendes et al. 2004; Andersen et al. 2013b).

***Antillocladius arcuatus* Sæther, 1982: 474** [USA: South Carolina]. Mendes et al. (2004: 29) [Nuevo León State]; Mendes and Andersen (2008: 21); Ashe and O'Connor (2012a: 121). NT, NE. Brazil, Mexico, USA, Venezuela.

***Antillocladius calakmulensis* Mendes, Andersen & Sæther, 2004: 32** [Mexico: Campeche State, Calakmul Biosphere Reserve]. Mendes and Andersen (2008: 28); Ashe and O'Connor (2012a: 122); Admin (2022). Endemic.

***Antillocladius herradurus* Mendes, Andersen & Sæther, 2004: 39** [Mexico: Campeche State, Calakmul Biosphere Reserve]. Mendes and Andersen (2008: 33); Ashe and O'Connor (2012a: 122); Admin (2022). Endemic.

***Antillocladius pluspilalus* Sæther, 1982: 474** [USA: South Carolina]. Mendes et al. (2004: 48) [Campeche State]; Mendes and Andersen (2008: 36); Ashe and O'Connor (2012a: 122). NT, NE. Ecuador, Mexico, Nicaragua, USA.

***Antillocladius zempoalensis* Mendes, Andersen & Sæther, 2004: 57** [Mexico: Morelos State, Lagunas de Zempoala National Park]. Mendes and Andersen (2008: 41); Ashe and O'Connor (2012a: 124). Endemic.

### Genus *Bryophaenocladius* Thienemann, 1934

A species-rich genus with ~ 120 named species that occur in all zoogeographic regions, except Antarctica and Oceania. Neotropical and Mexican species were reviewed by Wang et al. (2006). The larvae of most species are terrestrial or semi-terrestrial, but a few are aquatic (Andersen et al. 2013b).

***Bryophaenocladius digitatus* Sæther, 1973: 55** [USA: South Dakota]. Wang et al. (2006: 23) [Campeche State]; Ashe and O'Connor (2012a: 141). NE. Mexico, USA.

***Bryophaenocladius humerosus* Wang, Andersen & Sæther, 2006: 26 [**Mexico: Morelos State, Lagunas de Zempoala National Park]. Ashe and O'Connor (2012a: 144); Admin (2022). Endemic.

***Bryophaenocladius pichinensis* Wang, Andersen & Sæther, 2006: 28** [Ecuador]. Wang et al. (2006: 28) [States of Nuevo León; Puebla]; Ashe and O'Connor (2012a: 150); Admin (2022). NT. Ecuador, Mexico.

***Bryophaenocladius simplex* Wang, Andersen & Sæther, 2006: 30** [Mexico: Nuevo León State, Allende, Río Ramos]. Wang et al. (2006: 30) [Nuevo León State, Santiago]; Ashe and O'Connor (2012a: 152); Admin (2022). Endemic.

### Genus *Cardiocladius* Kieffer, 1912

A genus of 20 named species that occur in all zoogeographic regions except Antarctica and Oceania. The Neotropical species were reviewed by Andersen et al. (2016). The larvae live in fast-flowing waters and are often associated with the immature stages of blackflies (Simuliidae), on which they are reported to be predaceous (Andersen et al. 2013b).

***Cardiocladius moreloensis* Andersen, Hagenlund & Pinho, 2016: 277** [Mexico: Morelos State, Estación Ceamish]. Endemic.

### Genus *Clunio* Haliday, 1855

A genus of 25 described species that occur in all zoogeographic regions except Antarctica. The larvae are marine and believed to be omnivorous, feeding on algae and dead or dying animals (Andersen et al. 2013b).

***Clunio* sp.:** Sotelo-Casas et al. (2014: 17) [Nayarit State: Marieta Islands].

### Genus *Corynoneura* Winnertz, 1846

A genus of ~ 100 named species that occur in all zoogeographic regions except Antarctica. A review of the Neotropical species was given by Wiedenbrug et al. (2012). Larvae occur in virtually all types of aquatic habitats, from standing waters to fast-flowing streams (Andersen et al. 2013b).

***Corynoneura zempoala* Wiedenbrug, Lamas & Trivinho-Strixino, 2012: 55.** [Mexico: Morelos State, Parque Nacional Lagunas de Zempoala]. Endemic.

### Genus *Cricotopus* Wulp, 1874

Syn.: *Paratrichocladius* Santos Abreu, 1918 (see Cranston and Krosh 2015)

A genus of ~ 270 named species that occur in all zoogeographic regions except Antarctica. Seven subgenera are recognized, namely *Cricotopus* s. str.; *Isocladius* Kieffer, 1909; *Maurius* Lehmann, 1981; *Nostocladius* Ashe & Murray, 1980; *Oliveiriella* Wiedenbrug & Fittkau, 1997; *Paratrichocladius* Santos Abreu, 1918; and *Pseudocricotopus* Nishida, 1987 (see Ashe and O'Connor 2012a; Andersen et al. 2013b; Cranston and Krosch 2015). Larvae inhabit all types of freshwaters including saline coastal waters. They are frequently associated with aquatic plants, including algae, and some mine living parts of aquatic macrophytes (Andersen et al. 2013b).

***Cricotopus* (*Cricotopus*) *bicinctus* (Meigen, 1818: 41)** (*Chironomus*) [Austria]. Andersen et al. (2000: 589) [States of Mexico; Guerrero; Sinaloa]; Ashe and O'Connor (2012a: 209). NT, NE, PA, OR, OC. Widespread.

***Cricotopus* (*Isocladius*) *sylvestris* (Fabricius, 1794: 252)** (*Tipula*) [Germany]. Andersen et al. (2000: 589) [States of Mexico; Guanajuato]; Ashe and O'Connor (2012a: 245). NT, NE, PA. Widespread.

***Cricotopus* (*Cricotopus*) *triannulatus* (Macquart, 1826: 202)** (*Chironomus*) [France]. Andersen et al. (2000: 589) [Puebla State]; Ashe and O'Connor (2012a: 231); Alcocer et al. (2016: 411). NE, PA. Widespread.

### Genus *Diplosmittia* Sæther, 1981

A genus of 10 named species distributed in the Neotropical and Nearctic regions. A review of the genus was provided by Pinho et al. (2009b). Wiedenbrug and Silva (2016) added a species from the Dominican Republic. The immatures are unknown.

***Diplosmittia harrisoni* Sæther, 1981: 30** [St. Lucia]. Pinho et al. (2009b: 177) [Campeche State]; Ashe and O'Connor (2012a: 262). NT. Costa Rica, Mexico, St. Lucia, St. Vincent, Venezuela.

### Genus *Gravatamberus* Mendes & Andersen, 2008

A genus with five named species endemic to the Neotropical region. Larvae have been found in bromeliads (Mendes and Andersen 2008).

***Gravatamberus curtus*** **Mendes & Andersen, 2008: 45** [Mexico: Campeche State, Calakmul Biosphere Reserve]. Ashe & O'Connor (2012a: 293); Admin (2022). NT. Costa Rica, Mexico.

**Remarks.** Epler (2017) recorded *Gravatamberus guatemaltecus* Mendes & Andersen, 2008 from Zurquí de Moravia in Costa Rica and commented on the variation in *G. curtus*.

### Genus *Limnophyes* Eaton, 1875

A genus of > 90 named species that occur in all zoogeographic regions except Oceania. Sæther (1990a, b) revised the Holarctic, Afrotropical, and Neotropical species of the genus. The larvae are eurytopic, including aquatic, semiterrestrial and terrestrial habitats (Andersen et al. 2013b).

***Limnophyes*** **sp.:** Andersen et al. (2000: 591) [Puebla State].

### Genus *Lopescladius* Oliveira, 1967

A genus with eight named species from the Neotropical and Nearctic regions. Two subgenera are recognized, namely *Lopescladius* s. str. and *Cordiella* Coffman & Roback, 1984 (see Ashe and O'Connor 2012a). South American species of *Lopescladius* (*Cordiella*) were described by Hagenlund et al. (2010). Larvae inhabit streams with sandy sediments (Trivinho-Strixino 2011).

***Lopescladius*** **(*Lopescladius*) *verruculosus*** **Sæther, 1983: 289** [Mexico: Michoacán State, Tocuman]. Andersen et al. (2000: 589); Ashe and O'Connor (2012a: 365). NE. Mexico, USA.

### Genus *Mesosmittia* Brundin, 1956

A genus of 18 named species that occur in the Neotropical, Nearctic, Palaearctic, Afrotropical, and Oriental regions. The Neotropical and Mexican species were reviewed by Andersen and Mendes (2002b). The immatures are likely terrestrial (Andersen et al. 2013b).

***Mesosmittia acutistylus*** **Sæther, 1986: 43** [USA: New Mexico]. Andersen & Mendes (2002b: 143) [Campeche State]; Ashe and O'Connor (2012a: 369). NE. Mexico, USA.

***Mesosmittia annae*** **Andersen & Mendes, 2002b: 143** [Guatemala]. Andersen and Mendes (2002b: 143) [Campeche State]; Ashe and O'Connor (2012a: 369); Admin (2022). NT. Guatemala, Mexico.

***Mesosmittia guanajensis*** **Andersen & Mendes, 2002b: 147** [Mexico: Guanajuato State, Acámbaro]. Ashe and O'Connor (2012a: 370); Admin (2022). Endemic.

***Mesosmittia lobiga*** **Sæther, 1986: 45** [USA: New Mexico]. Andersen and Mendes (2002b: 150) [States of Guanajuato; Nuevo León]; Ashe and O'Connor (2012a: 370). NT, NE. Mexico, Puerto Rico, USA.

***Mesosmittia patrihortae*** **Sæther, 1986: 47** [USA: South Carolina]. Andersen and Mendes (2002b: 150) [States of Campeche; Nuevo León; Veracruz]; Ashe and O'Connor (2012a: 371). NT, NE, PA, AF. Widespread.

**Remarks.** Based on material collected in Zurquí, Costa Rica, Epler (2017) could not separate *M. truncata* from *M patrihortae* Sæther, 1986, and considered *M. truncata* to be a junior synonym of *M. patrihortae.*

***Mesosmittia prolixa* Sæther, 1986: 48** [USA: Kansas]. Andersen and Mendes (2002b: 150) [States of Campeche; Nuevo León]; Ashe and O'Connor (2012a: 371). NE. Mexico, USA.

***Mesosmittia tora* Sæther, 1986: 50** [USA: South Dakota]. Andersen and Mendes (2002b: 150) [Nuevo León State]; Ashe and O'Connor (2012a: 371). NE. Mexico, USA.

### Genus *Metriocnemus* Wulp, 1874

A genus of 75 named species that occur in all zoogeographic regions except Antarctica and Oceania. Three subgenera are recognized, namely *Metriocnemus* s. str.; *Crymaleomyia* Ashe & O'Connor, 2000; and *Inermipupa* Langton & Cobo, 1997 (see Ashe and O'Connor 2012a). A review of the genus was given by Sæther (1995). Larvae occur in mosses, phytotelmata, springs, ditches, streams and lakes and a few species are hygropetric (Andersen et al. 2013b).

***Metriocnemus* sp.:** Andersen et al. (2000: 591) [Nuevo León State].

### Genus *Nanocladius* Kieffer, 1913

A genus of 37 named species that occur in all zoogeographic regions except Antarctica. Two subgenera are recognized, namely *Nanocladius* s. str., and *Plecopteracoluthus* Steffan, 1965 (see Ashe and O'Connor 2012a). Neotropical species were treated by Wiedenbrug and Silva (2013). Larvae occur in streams, rivers, lakes, and ponds and some are symphoretic on immature Megaloptera and Ephemeroptera (Andersen et al. 2013b).

***Nanocladius* sp.:** Contreras-Ramos and Andersen (1999: 4) [Campeche State]; Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"].

### Genus *Onconeura* Andersen & Sæther, 2005

A genus of eight named species that occur in the Neotropical and Nearctic regions. A review of the genus was given by Wiedenbrug et al. (2009), and a cladistic analysis of the genus was given by Donato et al. (2012). The larvae inhabit streams and rivers (Andersen et al. 2013b).

***Onconeura semifimbriata* (Sæther, 1981: 32)** (*Thienemanniella*) [St. Vincent]. Andersen and Sæther (2005: 13) [Nuevo León State]; Wiedenbrug et al. (2009: 13); Ashe and O'Connor (2012a: 408). NT. Brazil, Costa Rica, Guatemala, Mexico, St. Vincent.

### Genus *Orthocladius* Wulp, 1874

A genus of ~ 150 named species that occur in the Nearctic, Palaearctic, Afrotropical, and Oriental regions. Six subgenera are recognized, *Orthocladius* s.

str., *Eudactylocladius* Thienemann, 1935; *Euorthocladius* Thienemann, 1935; *Mesorthocladius* Sæther, 2005; *Pogonocladius* Brundin, 1956; and *Symposiocladius* Cranston, 1982 (see Ashe and O'Connor 2012a). The genus is recorded from South America based on unnamed larvae from Argentina belonging to the subgenus *Eudactylocladius* (Wais 1987). The larvae inhabit all types of flowing waters, lakes, ponds, swamps, and moist earth; some species also mine submerged wood (Andersen et al. 2013b).

***Orthocladius* (*Euorthocladius*) sp.:** Andersen et al. (2000: 591) [Mexico State].
***Orthocladius* (*Orthocladius*) sp.:** Andersen et al. (2000: 591) [Mexico State].

### Genus *Paralimnophyes* Brundin, 1956

A genus of five named species that occur in the Nearctic, Palaearctic, Oriental, and Australasian regions. The only species with described larvae inhabits eutrophic lowland pools and ditches (Andersen et al. 2013b).

***Paralimnophyes* sp.:** Andersen et al. (2000: 591) [Puebla State]; Contreras-Ramos et al. (2000: 25) [Campeche State].

### Genus *Parametriocnemus* Goetghbuer, 1932

A genus of 35 named species that occur in all zoogeographic regions except Antarctica and the Neotropical region. The genus is recorded from South America based on unnamed larvae from Brazil, Colombia, Peru, and Venezuela (Roback and Coffman 1983; Ospina-Torres et al. 1999; Trivinho-Strixino 2011). Larvae of *Parametriocnemus* are found in springs and in relatively fast flowing cold streams and rivers (Andersen et al. 2013b).

***Parametriocnemus* sp.:** Contreras-Ramos and Andersen (1999: 4) [Campeche State]; Bogan et al. (2014: 2726) [Sonora State].

### Genus *Paratrichocladius* Santos Abreu, 1918

See: *Cricotopus* Wulp, 1874.

### Genus *Prodiamesa* Kieffer, 1906

A genus of six named species distributed in the Nearctic and Palaearctic regions. Larvae of *Prodiamesa* occur in springs, streams, rivers, ponds, and the littoral zone in lakes (Sæther and Andersen 2013b).

***Prodiamesa* sp.:** Granados-Ramírez et al. (2017: 45) [Morelos State].

### Genus *Psectrocladius* Kieffer, 1906

A genus with > 60 named species that occur in all zoogeographic regions, except Antartica, Australasia, Oceania, and the Neotropical region. Four subgenera are recognized, namely *Psectrocladius* s. str.; *Allopsectrocladius* Wülker, 1956; *Mesopsectrocladius* Laville, 1972; and *Monopsectrocladius* Wülker, 1956 (see Ashe and O'Connor 2012a). The only record from South America is an unnamed larval morphotype from the Peruvian Amazon belonging to subgenus *Psectrocladius* (Roback 1966). The larvae are eurytopic (Andersen et al. 2013b).

***Psectrocladius* sp.:** Andersen et al. (2000: 591) [Puebla State]; Bogan et al. (2014: 2726) [Sonora State].

### Genus *Pseudosmittia* Edwards, 1932

A genus of > 100 described species that occur in all zoogeographic regions, except Antarctica. Andersen et al. (2010) reviewed the Neotropical species, and a revision of the genus was given by Ferrington and Sæther (2011). Most larvae appear to be semiterrestrial to semiaquatic (Andersen et al. 2013b).

***Pseudosmittia forcipata* (Goetghebuer, 1921; 87)** (*Camptocladius*) [Belgium]. Andersen et al. (2010: 39) [States of Campeche; Nuevo León]; Ferrington & Sæther (2011: 297); Ashe and O'Connor (2012a: 545). NT, NE, PA, OR. Widespread.

***Pseudosmittia invirgata* Andersen, Sæther & Mendes, 2010: 43** [Mexico: Campeche State, Calakmul Biosphere Reserve]. Ferrington and Sæther (2011: 288); Ashe and O'Connor (2012a: 547). Endemic.

***Pseudosmittia joaquimvenancioi* (Messias & Oliveira, 2000: 189)** (*Bryophaenocladius*) [Brazil]. Wang et al. (2006: 19); Andersen et al. (2010: 45) [States of Campeche; Veracruz]; Ferrington and Sæther (2011: 184); Ashe and O'Connor (2012a: 547). NT. Brazil, Costa Rica, Mexico, Nicaragua, St. Lucia, St. Vincent, Venezuela.

### Genus *Rheocricotopus* Brundin, 1956

A genus of ~ 75 described species that occur in all zoogeographic regions except Antarctica and Oceania. Two subgenera are recognized, namely *Rheocricotopus* s. str., and *Psilocricotopus* Sæther, 1986 (see Ashe and O'Connor 2012a). The first named species from the Neotropical region, *Rheocricotopus* (*Psilocricotopus*) *sirventorum* Andersen & Mendes, was recently described from Brazil by Andersen and Mendes (2012). Larvae are rheophilic, living on plants and stones in streams and rivers, and are rarely found in the littoral zone of lakes (Andersen et al. 2013b).

***Rheocricotopus* sp.:** Andersen et al. (2000: 589) [Mexico State].

### Genus *Smittia* Holmgren, 1869

A species-rich genus with > 80 named species that occur in all zoogeographic regions except Antarctica. Most larvae are terrestrial, occurring in damp soil, but at least one species is aquatic (Andersen et al. 2013b).

***Smittia* sp.:** Andersen et al. (2000: 591) [Baja California Sur State]; Hamerlík et al. (2018: 217) [Yucatán State].

### Genus *Synorthocladius* Thienemann, 1935

A genus of eight named species that occur in all zoogeographic regions except Antarctica. The larvae inhabit springs, small to large bodies of flowing water and small bodies or shallow parts of still water (Andersen et al. 2013b).

***Synorthocladius semivirens* (Keiffer, 1909: 48)** (*Dactylocladius*) [GERMANY]. Andersen et al. (2000: 589) [Mexico State]; Ashe and O'Connor (2012a: 610). NE, PA, OR. Widespread.

### Genus *Thienemanniella* Kieffer, 1911

A genus of ~ 55 named species that occur in all zoogeographic regions except Antarctica. The Neotropical species were reviewed by Wiedenbrug et al. (2013). The larvae occur in most lotic habitats, from fast-flowing streams to slow-flowing ditches and rivers (Andersen et al. 2013b).

***Thienemanniella* sp.:** Contreras-Ramos and Andersen (1999: 4) [Campeche State]; Bogan et al. (2014: 2726) [Sonora State]; Granados Ramírez et al. (2017: 45) [States of Mexico; Morelos].

### Subfamily Prodiamesinae

See Subfamily Orthocladiinae.

### Subfamily Tanypodinae

### Genus *Ablabesmyia* Johannsen, 1905

A genus of nearly 100 described species that occur in all zoogeographic regions, except Antarctica; it is currently the most speciose genus in Tanypodinae. Four subgenera, *Ablabesmyia* s. str., *Asaya* Roback, 1985, *Karelia* Roback, 1971, and *Sartaia* Roback, 1983 are recognized (see Ashe and O'Connor 2009). Most Neotropical species probably belong in *Ablabesmyia* s. str., but as pointed out by several authors, many South American species cannot be assigned to a subgenus with certainty, as there are inconsistencies in the establishment of these groups (see Neubern et al. 2013). Many of the recently described species are thus not assigned to a subgenus. The Neotropical species were reviewed by Neubern et al. (2013). The larvae occur in a wide variety of habitats, including small and large standing and flowing waters from cold temperate to warm tropical climate zones (Cranston and Epler 2013).

***Ablabesmyia* (*Karelia*) *cinctipes* (Johannsen, 1946: 271)** (*Pentaneura*) [USA: Florida]. Andersen et al. (2000: 589) [States of Chiapas; Guerrero]; Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]; Ashe and O'Connor (2009: 121); Cranston and Epler (2013: 62). NT, NE. Bahamas, Belize, Guatemala, Mexico, St. Vincent, USA.

### Genus *Alotanypus* Roback, 1971

A genus of 11 described species distributed in the Neotropical, Nearctic, Palaearctic, and Australasian regions. Larvae occur in both standing and flowing waters and appear to tolerate a broad range of conditions including very acid waters (Cranston and Epler 2013).

***Alotanypus* sp.:** Andersen et al. (2000: 591) [Nuevo León State].

### Genus *Apsectrotanypus* Fittkau, 1962

A genus of seven named species that occur in all zoogeographic regions except Antarctica and Oceania. In South America unnamed species are recorded from Argentina and Colombia (Donato et al. 2008b; Ruiz-Moreno et al. 2000; Spies and Reiss 1996). The larvae inhabit small, cool, flowing waters (Cranston and Epler 2013).

***Apsectrotanypus* sp.:** Bogan et al. (2014: 2725) [Sonora State].

### Genus *Clinotanypus* Kieffer, 1913

A genus of ~ 45 described species that occur in all zoogeographic regions, except Antarctica. Two subgenera are recognized, *Clinotanypus* s. str. and *Aponteus* Roback, 1971 (see Ashe and O'Connor 2009.) The Neotropical species were reviewed by Neubern et al. (2014). The larvae prefer soft sediments in shallow, warm water bodies including ponds, lakes and slow-flowing streams and rivers (Cranston and Epler 2013).

***Clinotanypus* sp.:** Contreras-Ramos and Andersen (1999: 4) [Campeche State].

### Genus *Coelotanypus* Kieffer, 1913

A genus of ~ 20 described species that occur in the Neotropical, Nearctic, Afrotropical, and Australasian regions. A key to the males of the Neotropical species was given by Paggi and Zilli (2018). The larvae inhabit benthic sediments of lakes, including artificial impoundments, slow flowing reaches of rivers and old riverbeds (Cranston and Epler 2013). The genus can be very abundant in Amazonian flood-plain lakes and in wetlands in southern Brazil (Fonseca Leal et al. 2004; Panatta et al. 2007).

***Coelotanypus atus* Roback, 1971: 37** [USA: Texas]. Andersen et al. (2000: 589) [Mexico, without specific locality]; Ashe and O'Connor (2009: 140). NT, NE. Mexico, Puerto Rico, USA.

***Coelotanypus concinnus* (Coquillett, 1895: 308)** (*Tanypus*) [USA: Texas]. Andersen et al. (2000: 589) [Sonora State]; Ashe and O'Connor (2009: 141). NT, NE. Costa Rica, Mexico, Nicaragua, Puerto Rico, USA.

***Coelotanypus naelis* Roback, 1963: 170** [Surinam]. Andersen et al. (2000: 589) [Veracruz State]; Ashe and O'Connor (2009: 142). NT, NE. Mexico, Panama, Surinam, USA.

***Coelotanypus olmecus*** **Roback, 1965: 33** [Mexico: Veracruz State]. Andersen et al. (2000: 589); Ashe and O'Connor (2009: 142). NT. Mexico, Nicaragua.

***Coelotanypus scapularis*** **(Loew, 1866: 2)** (*Tanypus*) [USA: Washington]. Andersen et al. (2000: 589) [Mexico, without specific locality]; Ashe and O'Connor (2009: 142). NT, NE. Canada, Mexico, Panama, USA.

***Coelotanypus toltecus*** **Roback, 1965: 32** [Mexico: Veracruz State]. Andersen et al. (2000: 589); Ashe and O'Connor (2009: 142). Endemic.

***Coelotanypus tricolor*** **(Loew, 1861: 309)** (*Tanypus*) [USA: New York]. Andersen et al. (2000: 589) [Veracruz State]; Ashe and O'Connor (2009: 143). NT, NE. Costa Rica, Mexico, USA.

### Genus *Djalmabatista* Fittkau, 1968

A genus of 15 described species that occur in all zoogeographic regions except Antarctica and Oceania. The larvae appear to prefer low alkalinity to weakly acid waters, and may be found in lakes, ponds, springs, large and small rivers, as well as in temperate to tropical lentic and lotic depositional habitats (Cranston and Epler 2013).

***Djalmabatista pulchra*** **(Johannsen, 1908: 273)** (*Protenthes*) [USA: New York]. Andersen et al. (2000: 589) [States of Chiapas; Guerrero]; Ashe and O'Connor (2009: 155). NT, NE. Argentina (Oca et al. 2020), Bahamas (Anderson et al. 2014), Brazil, Canada, Costa Rica, Guatemala, Mexico, Nicaragua, USA.

### Genus *Fittkauimyia* Karunakaran, 1969

A genus of eight named species that occur in all zoogeographic regions except Antarctica and Oceania. The larvae inhabit rivers and the littoral zone of lakes, generally in tropical and subtropical regions (Cranston and Epler 2013).

***Fittkauimyia* sp.:** Andersen et al. (2000: 591) [States of Campeche; Nuevo León]; Contreras-Ramos and Andersen (1999: 4); Contreras-Ramos et al. (2000: 25); Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"]; Bogan et al. (2014: 2725) [Sonora State]; Hamerlík et al. (2018: 217) [States of Quintana Roo; Yucatán].

### Genus *Labrundinia* Fittkau, 1962

A genus of ~ 40 named species distributed in the Neotropical, Nearctic, Palaearctic, and Oriental regions. The genus was revised by Silva et al. (2014). The larvae live in small, standing water bodies as well as in streams and rivers (Cranston and Epler 2013).

***Labrundinia fosteri*** **Roback, 1987: 2018** [Colombia]. Vinogradova and Riss (2007 33) ["Yucatan Peninsula"]; Ashe and O'Connor (2009: 164); Silva et al. (2014: 44). NT. Colombia, Mexico.

***Labrundinia longipalpis*** **(Goetghebuer, 1921: 66)** (*Tanypus*) [Belgium].

Syn.: *Labrundinia maculata* Roback, 1971: 278 [USA: California] (Silva et al. 2011: 294).

Andersen et al. (2000: 589) [Coahuila State]; Ashe and O'Connor (2009: 165, 2012b: 127) [Michoacán State]; Silva et al. (2011: 295, 2014: 67). NT, NE, PA. Widespread.

***Labrundinia pilosella* (Loew, 1866: 5)** (*Tanypus*) [USA: District Columbia]. Andersen et al. (2000: 589) [Puebla State]; Ashe and O'Connor (2009: 166); Silva et al. (2014: 127). NT, NE. Canada, Guatemala, Honduras, Mexico, Puerto Rico, Trinidad and Tobago, USA, Venezuela.

### Genus *Larsia* Fittkau, 1962

A genus of ~ 30 named species that occur in all zoogeographic regions except Antarctica. Neubern and Silva (2011) described two new species from the Neotropical region and presented a checklist of the *Larsia* species of the world. In the Southern Hemisphere the larvae are associated with both lotic and lentic warm waters (Cranston and Epler 2013).

***Larsia planensis* (Johannsen, 1946: 284)** (*Pentaneura*) [USA: Texas]. Andersen et al. (2000: 589) [Mexico City and States of Morelos; Oaxaca; Veracruz]; Ashe and O'Connor (2009: 169). NT, NE, OC. Canada, Guatemala, Hawaiian Islands, Mexico, USA.

### Genus *Natarsia* Fittkau, 1962

A genus of six named species distributed in the Nearctic, Palaearctic, and Oriental regions. The larvae of the North American species live in small running waters, perhaps favoring cool water. European species inhabit streams, springs, and the littoral zone of montane or northern lakes and show hygropetric behavior in small, standing waters (Cranston and Epler 2013).

***Natarsia* sp.:** Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"].

### Genus *Nilotanypus* Kieffer, 1923

A genus of 11 named species distributed in all zoogeographical regions except Antarctica and Oceania. Andersen and Pinho (2019) recently described two new species of *Nilotanypus* from Brazil. The larvae inhabit flowing waters, especially areas with sandy beds (Cranston and Epler 2013).

***Nilotanypus* sp.:** Contreras-Ramos and Andersen (1999: 4) [Campeche]; Vinogradova and Riss (2007: 33) ["Yucatan Peninsula"].

### Genus *Paramerina* Fittkau, 1962

See: *Zavrelimyia* Fittkau, 1962.

### Genus *Pentaneura* Philippi, 1866

A genus of eight named species distributed in the Neotropical and Nearctic regions. Silva and Ferrington (2018) recently reviewed the Neotropical species.

The larvae inhabit a variety of aquatic systems, from small streams and ponds to lakes and bays, occasionally the larvae live in shallow water flowing over bedrock covered with moss, algae, and detritus (Silva and Ferrington 2018).

***Pentaneura inconspicua* (Malloch, 1915: 371)** (*Tanypus*) [USA: Illinois]. Andersen et al. (2000: 589) [Mexico City]; Ashe and O'Connor (2009: 195). NE. Canada, Mexico, USA.

### Genus *Procladius* Skuse, 1889

The second most speciose genus of Tanypodinae, with ~ 70 named species that occur in all zoogeographical regions except Antarctica. Four subgenera are recognized, namely *Procladius* s. str., *Holotanypus* Roback, 1982, *Laurotanypus* Oliveira, Messias & Silva-Vasconcellos, 1992, and *Psilotanypus* Kieffer, 1906 (see Ashe and O'Connor 2009; Dantas and Hamada 2018). The larvae prefer muddy substrate of standing or slow-flowing water bodies, especially ponds and small lakes, but a few also inhabit the profundal zone of large, deep lakes (Cranston and Epler 2013).

***Procladius* (*Psilotanypus*) *bellus* (Loew, 1866: 4)** (*Tanypus*) [USA: Washington]. Andersen et al. (2000: 589) [Mexico City]; Ashe and O'Connor (2009: 210); Bentley and Thomas (2022) [Puebla State]. NE, OR. Canada, China, Mexico, USA.

***Procladius* (*Holotanypus*) *culiciformis* (Linnaeus, 1767: 978)** (*Tipula*) [SWEDEN]. Andersen et al. (2000: 589) [Mexico City]; Ashe and O'Connor (2009: 199). NE, PA. Widespread.

**Remarks.** The species was recorded from Campeche State by Mendoza-Arroyo and López-Toledo (2017: 27). This record is doubtful as the specimen was studied using a stereomicroscope with too low magnification to observe morphological details and no experts were involved in the identification of the specimen.

### Genus *Psectrotanypus* Kieffer, 1909

A genus with seven named species that occur in the Nearctic, Palaearctic, Afrotropical, and Oriental regions. The genus was recorded from the Neotropical region by Fittkau and Reiss (1979), but without specifying a country. The larvae occur in ponds, bogs, small bodies of water and slow-flowing streams (Cranston and Epler 2013).

***Psectrotanypus* sp.:** Alcocer et al. (2016: 411) [Puebla State].

### Genus *Tanypus* Meigen, 1803

A genus of > 30 named species that occur in all zoogeographic regions except Antarctica and Oceania. Two subgenera are recognized, namely *Tanypus* s. str. and *Apelopia* Roback, 1971 (see Ashe and O'Connor 2009). The larvae live in sediments in standing and slowly flowing waters, especially in temperate to warm regions, where they can tolerate high salinity (Cranston and Epler 2013).

***Tanypus* (*Tanypus*) *catemaco* (Roback, 1964: 141)** (*Pelopia*) [MEXICO: Veracruz State]. Andersen et al. (2000: 589); Ashe and O'Connor (2009: 227). Endemic.

***Tanypus* (*Apelopia*) *neopunctipennis* Sublette, 1964b: 118** [USA: Illinois]. Andersen et al. (2000: 589) [States of Oaxaca; Veracruz]; Ashe and O'Connor (2009: 226). NT, NE. Bahamas, Cuba (Bello-González and Téllez-Martínez 2012), Mexico, USA.

**Genus *Thienemannimyia* Fittkau, 1957**

A genus of ~ 20 named species occurring in the Nearctic, Palaearctic, Afrotropical, and Oriental regions. Unnamed species were reported from Costa Rica by Watson and Heyn (1993). The larvae are found in both lotic and lentic waters (Cranston and Epler 2013).

***Thienemannimyia* sp.**: Andersen et al. (2000: 591) [Nuevo León State].

**Genus *Zavrelimyia* Fittkau, 1962**

Syn.: *Paramerina* Fittkau, 1962.

Recently Silva and Ekrem (2016) formally placed the genus *Paramerina* Fittkau as a synonym of *Zavrelimyia* Fittkau. The genus now comprises ~ 50 named species that occur in all zoogeographic regions except Antarctica. Larvae of *Zavrelimyia* s. str. are, with few exceptions, more or less cold stenothermic and in temperate regions of the Holarctic primarily inhabitants of sandy or detritus rich sediments of springs and lentic habitats of stream sections close to springs. Larvae of *Zavrelimyia* (*Paramerina*) are eurythermic, living in a variety of standing waters of all sizes, but are also present in small lotic habitats including pools in rivers (Cranston and Epler 2013).

***Zavrelimyia* (*Paramerina*) *smithae* (Sublette, 1964b: 100)** (*Pentaneura* (*Pentaneura*)) [USA: California]. Andersen et al. (2000: 589) [States of Oaxaca; Puebla]; Ashe and O'Connor (2009: 192). NE. Mexico, USA.

## Generically unplaced valid Macropelopiini

***roblesi* Vargas, 1946: 80** (*Macropelopia*) [Mexico: Chiapas State, Mariscal]. Andersen et al. (2000: 589 as *Macropelopia roblesi* Vargas); Ashe and O'Connor (2009: 250, 362). Endemic.

## Generically unplaced valid Tanypodinae

***marmorata* Johannsen, 1938: 219** (*Pentaneura*) [Puerto Rico]. Andersen et al. (2000: 589 as *Pentaneura marmorata* Johannsen) [States of Chiapas; Guerrero; Veracruz]; Ashe and O'Connor (2009: 252). NT. Mexico, Puerto Rico.

**Subfamily Telmatogetoninae**

**Genus *Telmatogeton* Schiner, 1867**

A genus of ~ 30 named species that occur in all zoogeographic regions. Except for a few freshwater species from Hawaii, *Telmatogeton* larvae are marine and live in the intertidal zone where they construct tubes within green algae such as *Enteromorpha* (Cranston and Ashe 2013).

***Telmatogeton alaskensis*** **Coquillett, 1900: 395** [USA: Alaska]. Andersen et al. (2000: 589) [Mexico, without specific locality]; Ashe and O'Connor (2009: 332). NE. Canada, Mexico, USA.

***Telmatogeton latipenne*** **Wirth, 1949: 172** [Mexico: Colima State, Revillagigedo Islands]. Andersen et al. (2000: 589); Ashe and O'Connor (2009: 333). Endemic.

**Genus *Thalassomya* Schiner, 1856**

A genus of 12 named species that occur in all zoogeographic regions except Antarctica. The larvae live in the intertidal marine zone, particularly in the warmer seas of the world (Cranston and Ashe 2013).

***Thalassomya bureni*** **Wirth, 1949: 167** [USA: Florida]. Andersen et al. (2000: 589) [Baja California Sur State]; Ashe and O'Connor (2009: 336). NT, NE. Mexico, USA. According to Wirth (1969) distributed "from Florida to Panama and the West Indies".

***Thalassomya longipes*** **(Johnson, 1924: 86)** (*Galapagomyia*) [Ecuador: Galapagos Islands]. Andersen et al. (2000: 589) [Nayarit State: Tres Marias Islands]; Ashe and O'Connor (2009: 337). NT. Ecuador, Mexico.

***Thalassomya pilipes*** **Edwards, 1928: 60** [American Samoa]. Andersen et al. (2000: 589) [Baja California State; Colima State: Revillagigedo Islands]; Ashe and O'Connor (2009: 338). NT, NE, OR, AU, OC. Widespread.

### Species richness and taxonomic composition

A total of 110 species are listed for Mexico; 52 species in 25 genera belong to the subfamily Chironominae, 30 species in 13 genera to Orthocladiinae, 19 species in nine genera and two valid species that are not placed in a genus to Tanypodinae, five species in two genera to Telmatogetoninae, and two species in one genus to Diamesinae. In addition, there are records of 41 genera without identified species. Of these, 20 genera belong to Chironominae, 12 to Orthocladiinae, eight to Tanypodinae, and one genus to Diamesinae.

## Distribution

The number of species recorded from the different states throughout Mexico is very uneven. More than ten species have only been recorded from six states. From Campeche a total of 29 species are recorded, most of them based on material collected during a project in Calakmul Biosphere Reserve (Contreras Ramos et al. 2000). From Veracruz 19 species have been recorded, from Nuevo León 15 species, from Puebla 13 species, from the State of Mexico 11 species and from Morelos ten species. From the remaining states only five or less species have been recorded. In most of the states in central and northern Mexico, as well as those on the Pacific coast, there are no or only a few records (Fig. 1).

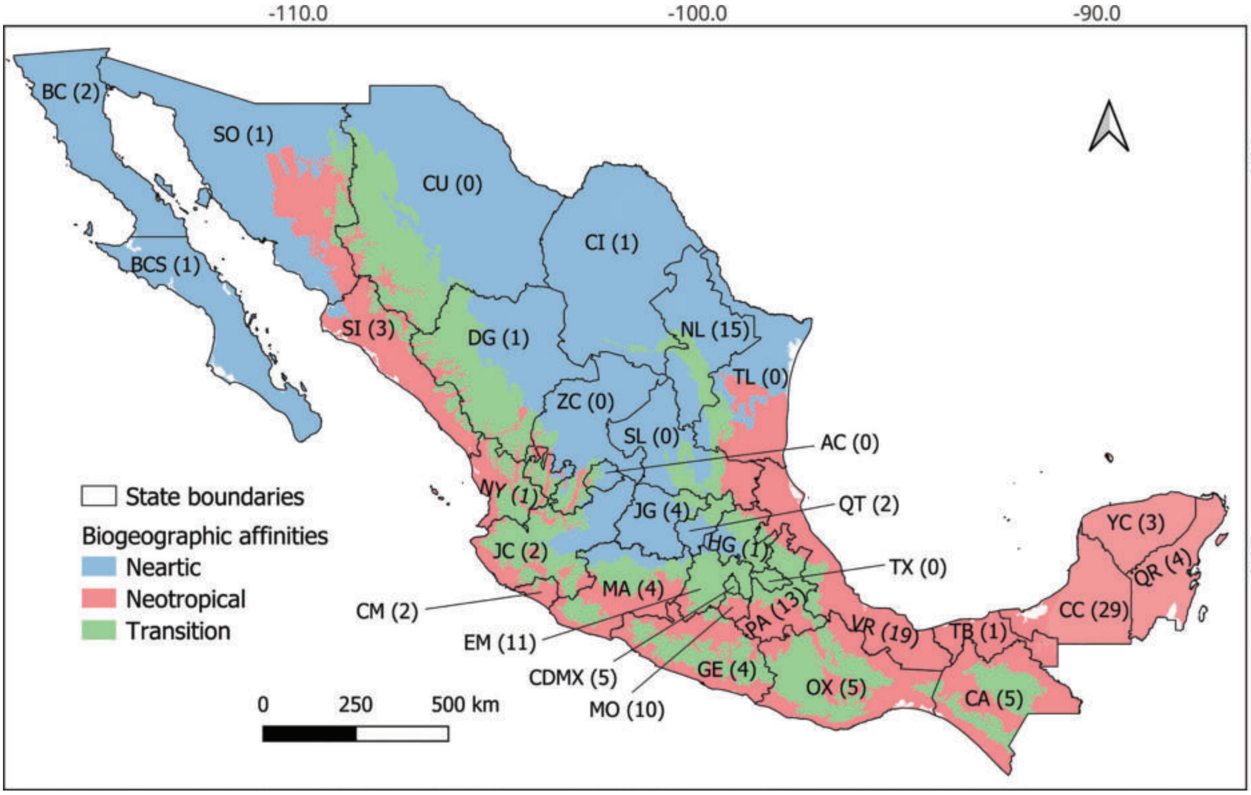

**Figure 1.** Biogeographic affinities and number of chironomid species recorded from each of the 32 Mexican states. Abbreviations: AC: Aguascalientes; BC: Baja California; BCS: Baja California Sur; CA: Chiapas; CC: Campeche; CDMX: Ciudad de México; CI: Coahuila; CM: Colima; CU: Chihuahua; DG: Durango; EM: Estado de México; GE: Guerrero; GJ: Guanajuato; HG: Hidalgo; JC: Jalisco; MA: Michoacán; MO: Morelos; NL: Nuevo León; NY: Nayarit; OX: Oaxaca; PA: Puebla; QR: Quintana Roo; QT: Querétaro; SI: Sinaloa; SL: San Luis Potosí; SO: Sonora; TB: Tabasco; TL: Tamaulipas; TX: Tlaxcala; VR: Veracruz; YC: Yucatán; ZC: Zacatecas.

The type localities for 34 Chironomidae species are in Mexico; of these, 27 species (25% of the total number of recorded species) are endemic. Twenty-nine species have a Neotropical distribution, 15 are Nearctic or Holarctic, while the remaining 39 species are distributed in both the Neotropical and Nearctic regions or are more widely distributed.

## Discussion

In addition to being key to freshwater and riparian ecosystems (e.g., Porinchu and MacDonald 2003; Paetzold et al. 2005), chironomids have been widely used to recreate the environmental history of lakes and rivers (e.g., Plikk et al. 2019), generate typologies (e.g., Schöll and Haybach 2004; Nyman and Korhola 2005), propose biogeographical hypotheses (e.g., Brundin 1966; Krosch et al. 2011), ecotoxicological models (e.g., Beleza et al. 2019; Ferrari et al. 2019), biomonitoring (e.g., Gomes et al. 2018; Molineri et al. 2020) and for the evaluation of taxonomic and functional diversity (e.g., Jyväsjärvi et al. 2018). However, the Mexican Chironomidae fauna needs to be much better studied before it can be useful in such contexts.

In the previous checklist (Andersen et al. 2000), the number of species listed was 61; so, 49 species have been added during the last two decades. Of these, no less than 25 species belong to the subfamily Orthocladiinae, and the number of Orthocladiinae species has thus increased five times from the five species recorded in 2000. In Chironominae the number of species has increased from 29 species in 2000 to 52 species today; while in the subfamilies Tanypodinae, Telmatogetoninae, and Diamesinae no species have been added since 2000.

Comparing the number of Chironomidae species recorded in Mexico with the number in other neighboring, better studied areas, highlights the need for further studies in Mexico. Oliver et al. (1990) and Oliver and Dillon (1994) listed 206 generic and 1065 species names of Nearctic Chironomidae. More than 700 species of chironomids are listed from southeastern USA, including Alabama, Florida, Georgia, North and South Carolina, and Tennessee, which together comprise approximately 41% of the total area of Mexico (Caldwell et al. 1997). For the state of California, bordering Mexico and comprising ~ 22% of the area of Mexico, 245 species of chironomids have been recorded (Spies 1999). More than 400 species have been recorded from the state of Florida, which comprises less than 9% of the total area of Mexico (Epler 2019).

No comprehensive checklist for the Neotropical region has been published since Spies and Reiss (1996). However, in an updated checklist for Brazil (Pinho 2022) 658 species in 99 genera are listed. Mendes and Pinho (2016) recently published a checklist for Colombia listing only 30 species of Chironomidae in 16 genera in three subfamilies. In addition, 32 genera and two subfamilies have been recorded from Colombia based on larva, but without identified species.

The 110 species recovered in the present checklist is far from the 1000 species estimated by Andersen et al. (2000) to occur in Mexico and highlights the need for further studies. Most additional species to be found will undoubtedly belong to the subfamilies Chironominae, Orthocladiinae, and Tanypodinae. Chironominae is the most species rich subfamily of Chironomidae and is found in all biogeographical regions except Antarctica. Additional species will mainly be found in slow flowing streams and rivers, lakes and ponds in lowland habitats, but additional species will also be found in streams, rivers and lakes at higher altitudes. Mexican species of some genera, like e.g. *Rheotanytarsus* Thienemann & Bause, 1913 have been reviewed and new species described. However, there are several species-rich genera in which Mexican material has not or hardly been studied and in genera like *Pseudochironomus* Malloch, 1915, *Tanytarsus* Wulp, 1874, and *Polypedilum* Kieffer, 1912, many more species are likely to be added. The Orthocladiinae is also a very species-rich and widely distributed subfamily that tends to be particularly abundant in streams and rivers in mountainous areas. For some genera, like *Antillocladius* Sæther, 1981, *Bryophaenocladius* Thienemann, 1934 and *Mesosmittia* Brundin, 1956, Mexican material has been included in reviews of the genera, while other species-rich genera like *Corynoneura* Winnertz, 1846 and *Cricotopus* Wulp, 1874, are hardly studied at all. Most additional Tanypodinae species will probably be found in slow flowing streams and rivers, lakes and ponds in lowland habitats. So far only a few genera of Tanypodinae have been studied in detail in Mexico and for several species-rich genera like *Ablabesmyia* Johannsen, 1905 and *Labrundinia* Fittkau, 1962, there are only a few species recorded from Mexico so far.

Particularly in Orthocladiinae, several recently described genera like *Colosmittia* Andersen & Sæther, 1994, *Litocladius* Mendes, Andersen & Sæther, 2004, and *Titimbera* Andersen, Pinho & Mendes, 2015 might also occur in Mexico as they have all been taken in Costa Rica (Andersen et al. 2011a; Mendes et al. 2011; Andersen et al. 2015). There might well be several undescribed genera in the subfamily. Epler (2017) recently recorded no less than 16 undescribed genera of Orthocladiinae from Zurquí in Costa Rica.

Additional species will also likely be found in some of the less species-rich subfamilies. Today, ten extant subfamilies of Chironomidae are recognized. Six subfamilies occur in the Nearctic region, while in the Neotropical region no fewer than nine subfamilies have been encountered. At the subfamily level the Neotropical region is thus the most diverse biogeographical region. Only the monotypic subfamily Usambaromyiinae Andersen & Sæther has not been recorded. In the Neotropical region two of the other subfamilies, Chilonomyiinae Brundin and Aphroteninae Brundin, have only been found in southern Chile and Patagonia and it is unlikely that any species in these two subfamilies occur in Mexico.

However, two subfamilies so far not recorded from Mexico might occur in the country. The subfamily Buchonomyiinae Brundin & Sæther with three included species is found in the Neotropical, Palaearctic, and Oriental regions. It was recorded for the first time from the Neotropical region by Andersen and Sæther (1995) describing *Buchonomyia brundini* Andersen & Sæther, 1995 from a small, shallow, rather fast-flowing river in Costa Rica. The subfamily Podonominae Thienemann & Edwards has a mainly bipolar distribution with five genera and 15 species in North America and Canada, and five genera with altogether 85 species in the southern part of South America. Spies (1999) recorded two species of *Boreochlus* Edwards, 1938 and one species of *Parochlus* Enderlein, 1912 from California. Several species have recently also been described from Brazil, and two genera, *Podonomus* Philippi, 1866 and *Parochlus*, are listed from Colombia based on larvae (Mendes and Pinho 2016; Pinho 2022).

The subfamily Telmatogetoninae with two genera, *Telmatogeton* Schiner, 1867 and *Thalassomya* Schiner, 1856, is marine. Both genera with altogether five species are known from Mexico.

The subfamily Diamesinae has a mainly arctic or alpine distribution with 55 species in ten genera in the Nearctic region and 11 species in five genera in the Neotropical region. Two species of *Diamesa* Meigen, 1835 were described by Serra-Tosio (1977) from a high-altitude lake in the Mexico State. The genus, with 107 species, is known from the Nearctic, Palaearctic, Afrotropical, and Oriental regions. Spies (1999) listed six species of *Diamesa* from California and one species in each of the genera *Pseudodiamesa* Goethgebuer, 1939 and *Sympotthastia* Pagast, 1947. Based on larvae, Mendes and Pinho (2016) listed the genus *Paraheptagyia* Brundin, 1966 from Colombia. *Paraheptagyia*, with five species, is distributed in the southern part of the Neotropical region and two species occur in the Australasian region (Ashe and O´Connor 2009).

The uneven distribution of Chironomidae records throughout the states in Mexico clearly reflects the lack of Chironomidae studies. Some Nematocera groups are better studied than the Chironomidae in Mexico. Consideration of the general distribution patterns of these groups may suggest what can be expected for the chironomids. States like Oaxaca and Chiapas are among the richest when it comes to Culicidae, Simuliidae and Ceratopogonidae (Ibánez-Bernal and Coscarón 1996; Ibánez-Bernal et al. 1996). Bond et al. (2014) also demonstrated that the Pacific slope has a high diversity of aquatic insects. Climatic and topographic heterogeneity in southeastern Mexico leads to high environmental heterogeneity (Rodríguez et al. 2019). The area has a complex geology resulting in barriers such as the Isthmus of Tehuantepec that is responsible for increased diversity in several insect groups (Halffter and

Morrone 2017). It is expected that future studies will show that the increase in the number of Chironomidae species will be particularly striking in Oaxaca and Chiapas.

Mexico is known to have a high proportion of endemic species. In well-studied groups like amphibians, reptiles, and mammals the proportion of endemic species is 60%, 51% and 31%, respectively (Hufnagel and Mics 2021). However, the number of records of chironomids from Mexico is clearly insufficient to appreciate patterns of endemism or clear biogeographic relationships.

To increase the number of species recorded from Mexico, taxonomic studies should be given priority. Even though rearing of larvae is important to associate the immatures with adults, chironomids are generally described based on adult males. To achieve an immediate increase in species numbers, further studies should thus focus on adults rather than on larvae and pupae. Fieldwork should be focused particularly on the states in central and northern Mexico, where the chironomid fauna is poorly known. The southeastern states along the Pacific coast should also be given special attention. Different habitats such as streams, rivers, lakes, and ponds should be visited, and collections should be made at different altitudes. Several chironomid species live in special habitats, like phytotelmata, and many species particularly among the Orthocladiinae, are semiterrestrial or terrestrial.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Orestes C. Bello-González: compilation, updating and analysis of information, taxonomic review, writing of the manuscript, preparation of the figure. Trond Andersen: compilation, updating and analysis of information, taxonomic review, writing of the manuscript. Norman Mercado-Silva: writing of the manuscript.

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## Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# A systematic review of the genus *Bolbelasmus* Boucomont (Coleoptera, Geotrupidae, Bolboceratinae) from Indochina and surrounding areas

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## Abstract

Indochinese species of the genus *Bolbelasmus* (Coleoptera, Geotrupidae, Bolboceratinae) are reviewed. Three new species, *Bolbelasmus chifengi* Wang & Li, **sp. nov.**, *Bolbelasmus concavisuturalis* Li & Wang, **sp. nov.** and *Bolbelasmus yutangi* Li & Wang, **sp. nov.**, are described and illustrated. An annotated checklist and modified key to species of the genus are provided. Information for each species in the checklist includes literature review, synonymy, distribution and type locality.

**Key words:** Checklist, earth-boring beetles, key, natural history, new species, taxonomy

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## Introduction

*Bolbelasmus* Boucomont, 1910 (Coleoptera: Geotrupidae: Bolboceratinae: Bolboceratini) is one of the largest bolboceratine genera, currently consisting of 29 species and two subspecies (Schoolmeesters 2023) (including subgenus *Kolbeus*). Among bolboceratine genera, *Bolbelasmus* has the widest distribution, occurring throughout the Holarctic and Oriental regions (Li et al. 2008; Hillert et al. 2016). Krikken (1977) published the most recent review dealing with eastern and southeastern Asian species and provided a complete checklist and summary of generic affinities and notes of species from the Middle East and North Africa. In that paper, two new species were described including one, *Bolbelasmus meridionalis* Krikken, 1977, from Southeast Asia. Additional distribution data were provided for *B. coreanus* (Kolbe, 1886) in southwestern China, Thailand and India. The Indochinese *Bolbelasmus* species have received little attention since Krikken's (1977) work. Zinchenko (2016) described a new species, *B. korshunovi* Zinchenko, from northern Thailand, the only species described during the past four decades. Currently, ten species are recorded in eastern and southeastern Asia, including the three new species described here based on specimens recently obtained from the Indochinese Peninsula and neighboring areas, including the first record from Myanmar. These collections constitute the basis for further detailed knowledge of the Indochinese bolboceratine fauna.

The natural histories of eastern and southeastern Asian *Bolbelasmus* species are poorly documented. Tsukamoto et al. (2017) reported that two of the Japanese species, *B*. *nativus ishigakiensis* Masumoto and *B*. *shibatai* Masumoto inhabit densely forested montane areas, where adults are nocturnal and fly about 30 cm over the forest floor from late dusk to midnight. Adults of both species can be sporadically attracted to light, as observed with *B. coreanus* (Kolbe) in Taiwan (Li et al. 2008). *Bolbelasmus* specimens can occasionally be collected using baited traps (e.g., Kawai et al. 2005; Li et al. 2008).

In this paper, we review the species of *Bolbelasmus* occurring in the Indochinese Peninsula and neighboring areas, with descriptions of three new species. We also provide an annotated checklist, distributional data for known species in eastern and southeastern Asia, and a modified key.

## Material and methods

The type specimens of the two new species, *B*. *chifengi* and *B*. *yutangi*, were collected by flight interception traps (FIT). The depository of the type specimens is in the following institutions: National Museum of Nature and Science (NSMT, Tsukuba, Japan); Zoological Museum, University of Copenhagen (ZMUC, Copenhagen, Denmark); Taiwan Agriculture Research Institute (TARI, Taichung, Taiwan); and the private collection of Chun-lin Li (CCLI, Nantou, Taiwan). Habitus images of *Bolbelasmus* specimens were taken using a Canon 7D digital camera with a Canon EF 100 mm macro lens and a Canon Macro Twin Lite MT-24EX Flash. Detailed images of specimens, body parts and male genitalia were captured using a Leica M205C stereo microscope equipped with a Leica MC190HD microscope camera or by a Hitachi TM3030 Plus tabletop scanning electron microscope. Color images were processed using Helicon Focus v.8.2.0 to increase depth of field, and all images were edited in Adobe Photoshop v.24.0.0 (background removed, images integrated, numbered and scale bars added). Measurements, treatments, and preservation of specimens and genitalia are based on methods described by Li et al. (2008).

## Taxonomy

### *Bolbelasmus* Boucomont, 1910

**Diagnosis.** Species of *Bolbelasmus* are small to medium-sized (5.6–15.2 mm in body length) and can be recognized by the glossy, unicolored, reddish-brown to black dorsal surface; presence of a conical frontal tubercle with a rounded or bifurcated tip in males; transverse frontal carina present in females; eyes protruding, divided by a canthus anteriorly, canthus with anterior margin smooth; antennal club with first segment glabrous on inner side; pronotum usually quadrituberculate in major males (vestigial or reduced to bituberculate in minor males), females with transverse carina only; first elytral stria terminated by scutellum; parameres usually weakly sclerotized.

## Key to eastern and southeastern Asian *Bolbelasmus* species based on males

(excluding *Bolbelasmus orientalis*)

1 Frontal tubercle located at center of frons (Fig. 15) .................................. **2**
– Frontal tubercle located in junction of clypeofrontal suture (Figs 11–14, 16) .......................................................................................................... **4**
2 Sutural intervals of elytra more convex than other intervals (Figs 25, 26) ..... **3**
– Sutural intervals (Fig. 23, 24, 27, 28) of elytra equally convex as other intervals; pronotal median tubercles well developed, primary punctures moderately distributed throughout disc (Fig. 21) except for a small area near posterior margin impunctate; posterior margin punctate; parameres small, narrowed apically, curved in lateral view ......... ***Bolbelasmus yutangi* sp. nov.**
3 Pronotal median tubercles weakly developed, center of disc typically impunctate, primary punctures moderately distributed at sides of center, posterior margin sparsely punctate at center; parameres small, narrowed apically, flat in lateral view ...................***Bolbelasmus nativus* Krikken, 1979**
– Pronotal median tubercles well developed, disc sparsely punctate, primary punctures sparsely distributed at sides of center (Fig. 20), posterior margin impunctate at center; parameres (Figs 35, 36, 42) moderate in size, trapezoidal, bases swollen in lateral view...................................................... .................................................. ***Bolbelasmus korshunovi* Zinchenko, 2016**
4 Elytral sutural intervals (Fig. 25) distinctly convex..................................... **5**
– Elytral sutural intervals concave (Fig. 23), flat or partially convex (Figs 24, 27, 28) ................................................................................................. **6**
5 Lateral margins of pronotum widely explanate; parameres with tips angulate at anterolateral angles ......... ***Bolbelasmus meridionalis* Krikken, 1979**
– Lateral margins of pronotum narrowly explanate; parameres with tips narrowed anteriorly..................... ***Bolbelasmus minutus* Li & Masumoto, 2008**
6 Elytral sutural intervals completely concave; parameres (Figs 29, 30, 39) small, anteriorly 1/2 curved ventrally in lateral view .................................... .........................................................***Bolbelasmus concavisuturalis* sp. nov.**
– Elytral sutural intervals flat or partially, moderately convex ....................... **7**
7 Elytral sutural intervals partially, moderately convex; parameres with bases contracted in dorsal view, length longer than one-half of basal piece ....... **8**
– Elytral sutural intervals flat; parameres straight, small, length shorter than one-half of basal piece.....................***Bolbelasmus krikkeni* Nikolajev, 1979**
8 Pronotal disc sparsely punctate................................................................... **9**
– Pronotal disc with many primary punctures (Fig. 18); parameres (Figs 31, 32) large with tips acute and vertically curved inward................................ ........................................................................***Bolbelasmus chifengi* sp. nov.**
9 Pronotal disc with primary punctures finer (Fig. 22); elytral intervals (Fig. 28) slightly convex; parameres with inner margins straight and separate, moderately evenly sclerotized .................. ***Bolbelasmus coreanus* (Kolbe, 1886)**
– Pronotal disc with primary punctures coarser; elytral intervals convex; parameres with inner margins broadened basally and overlapping, distinctly sclerotized, partly with median lobe .................................................. ...................................................... ***Bolbelasmus shibatai* Masumoto, 1984**

## Checklist of species of *Bolbelasmus* Boucomont from eastern and southeastern Asia

***Bolbelasmus chifengi*** **Wang & Li, sp. nov.**
https://zoobank.org/624857C3-4224-46EF-80FA-FDD3E4B1F169
Figs 3, 4, 12, 18, 24, 31, 32, 40, 46, 47

**Type materials. *Holotype* male.** "China: Yunnan, Bangdashan (邦達山), 16.IX.2015. leg. Y.-T. Wang." (glued on label, TARI), Taichung, Taiwan. ***Paratypes*.** 3♂♂, 1♀(TARI). same collecting data as the holotype. 1♀ (TARI). "China: Yunnan, Wudian (武甸), 17.IX.2014. leg. Y.-T. Wang". 1♂, 2♀♀(TARI). "China: Yunnan, CCCC, Nabang (那邦), 21.VI.2017. leg. Y.-T. Wang". 1♀ (CCLI). "China: Yunnan, Banggunjianshan (邦棍尖山), 19.IX.2015. leg. Y.-T. Wang". 1♂ (CCLI). "China: Yunnan, Bangdashan (邦達山), 01.IX.2015. leg. Y.-T. Wang". 2♂♂, 1♀(CCLI). "China: Yunnan, Ruili (瑞麗), 01.IX.2014. leg. Y.-T. Wang".

**Description. Holotype male** (Figs 3, 4). Body length 9.7 mm; width across humeri 6.0 mm. Dorsum moderately shiny. Head, pronotum and scutellum dark brown with elytra reddish brown. ***Head*** (Fig. 12): labrum with anterior margin crenulate, disc transversally rugose. Clypeus trapezoidal, surface densely rugopunctate; protrusion at basal angle moderately developed. Clypeofrontal suture well defined, distinctly curved in front of frontal tubercle. Frons with surface sparsely punctate, punctures fine, frontal tubercle vertically located in junction of suture, right-triangle in shape in lateral view. Eye prominent, canthus simple, not exceeding eye. ***Thorax:*** pronotum (Fig. 18) quadrituberculate, tubercles placed in a line, lateral tubercle greatly reduced in size; anterior face of median tubercles almost perpendicular to plane of pronotum; primary punctures coarse, moderately distributed on disc and intermixed with impunctate area, punctures between lateral margins of pronotum and fovea bigger and denser, posterior area between elytral humeri and suture impunctate except for four coarse punctures in front of scutellum, secondary punctures tiny, evenly scattered throughout surface of pronotum; frontal and lateral margins beaded, posterior margin beaded only in front of elytral humeri. Scutellum elongate, secondary punctures sparse throughout surface with a coarse puncture at center. ***Elytron*** (Fig. 24): elytral striae shallow, punctures mostly spaced 2–3 times diameters of punctures. Intervals slightly convex including sutural one, surface with scattered secondary punctures. Male genitalia (Figs 31, 32, 40).

**Female** (Figs 46, 47). Body length 7.7–10.0 mm; width across humeri 5.4–6.5 mm. Similar to male with minor differences in the form of strongly wrinkled surface of clypeus, transverse frontal carina trilobed, central lobe more prominent than lateral lobes, punctures on frons and vertex rugose, transverse pronotal carina feebly bilobed with lobes broadly developed, punctures on pronotal disc coarser and denser than males.

**Variation in male.** Dorsum brown, smaller body size, 6.6 mm in length and 5.2 mm in width across humeri, frontal tubercle less developed and not in junction of clypeofrontal suture, pronotal tubercles feebly convex, and number of coarse punctures arranged at pronotal posterior margin variable.

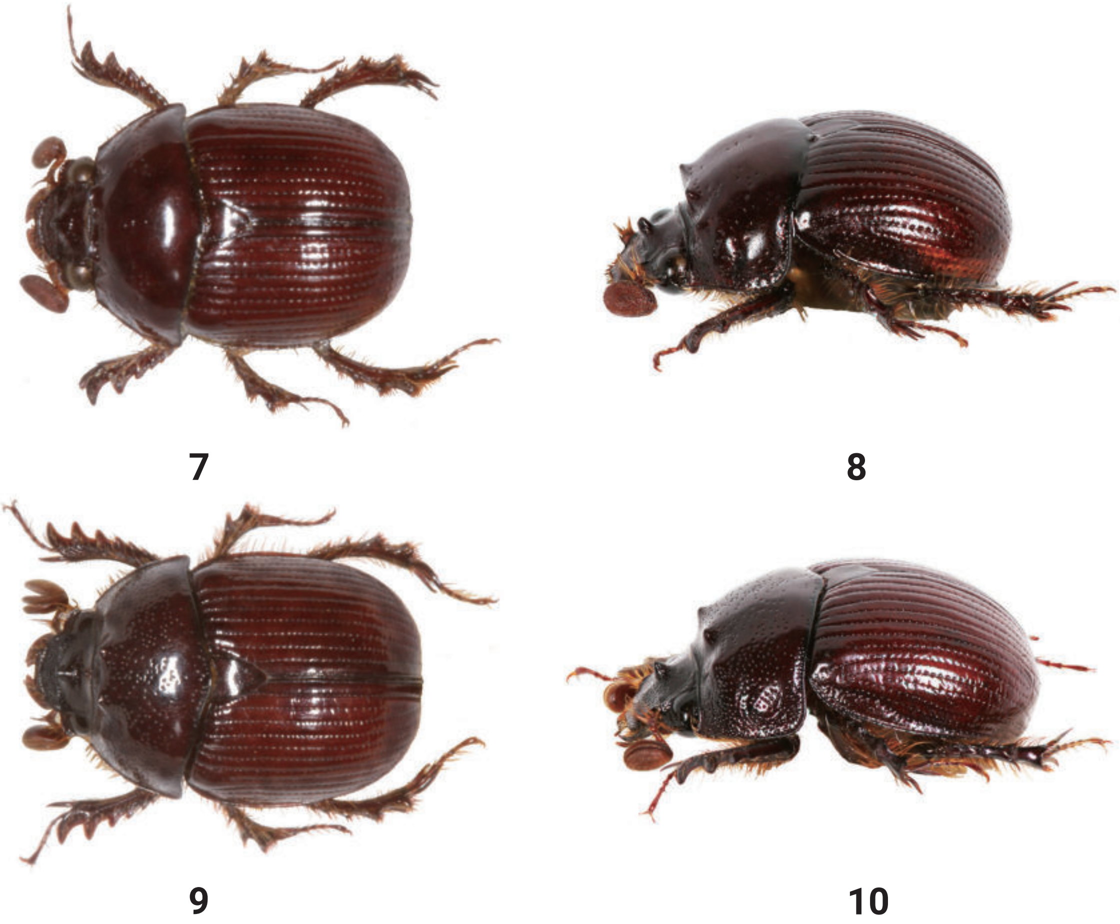
**Diagnosis.** *Bolbelasmus chifengi* is morphologically similar to *B. concavisuturalis*, but can be distinguished from the latter by the coarser and denser primary punctures on the pronotal disc (finer and scattered in *B. concavisuturalis*), elytral

**Figures 1–6.** Dorsal and lateral views of male *Bolbelasmus* spp. **1, 2** *B. concavisuturalis* sp. nov.sp. nov., holotype **3, 4** *B. chifengi* sp. nov., holotype **5, 6** *B. meridionalis*.

intervals evenly convex (elytral intervals flat with sutural interval concave in *B. concavisuturalis*) and by the longer parameres (shorter in *B. concavisuturalis*).

**Distribution.** Southern Yunnan, China (Fig. 52).

**Etymology.** *Bolbelasmus chifengi* sp. nov. is named after Dr Chi-feng Lee, the curator of the Department of Applied Zoology, Taiwan Agriculture Research Institute, Taichung, Taiwan, who kindly provided materials used in this study.



**Figures 7–10.** Dorsal and lateral views of male *Bolbelasmus* spp. **7, 8** *B. korshunovi* **9, 10** *B. yutangi* sp. nov., holotype.

### *Bolbelasmus concavisuturalis* Li & Wang, sp. nov.

https://zoobank.org/B3BDDA3C-0CE3-4ACF-9470-E2750D968B93
Figs 1, 2, 11, 17, 23, 29, 30, 39, 44, 45

**Type materials. *Holotype* male.** "Mon-Angget, near Chiangmai, North Thailand, 31-V-1990, K. Masumoto leg." (glued on label, NSMT). ***Paratypes*.** 1♂ (ZMUC) "Northern Thailand, Doi Sutep, 21.6.1958, B. Degerbøl leg., Pr. 548 (1.7.59)". 1♀ (NSMT) "Doi Suthep, Chiang Mai, Thailand, 15-VIII-1989, Y. MANIT leg."

**Description. Holotype male** (Figs 1, 2). Body length 10.2 mm; width across humeri 6.3 mm. Dorsum distinctly shiny. Head, pronotum and scutellum reddish brown with elytra brown in color. ***Head*** (Fig. 11): labrum with anterior margin crenulate, disc transversally rugose. Clypeus trapezoidal, surface densely rugopunctate; protrusion at basal angle reduced. Clypeofrontal suture well defined, distinctly curved in front of frontal tubercle. Frons with surface sparsely punctate, punctures fine, frontal tubercle vertically located in junction of suture, triangular in lateral view. Eye prominent, canthus simple, not exceeding eye. ***Thorax:*** pronotum (Fig. 17) quadrituberculate, tubercles situated in a line, lateral tubercle smaller; anterior face of median tubercles almost perpendicular to surface of pronotum; primary punctures weakly defined, sparse on disc except between lateral margin of pronotum and fovea, these coarser and denser, line in front of scutellum with a coarse puncture, secondary punctures tiny, evenly scattered on surface of pronotum; frontal and lateral margins beaded, posterior margin beaded only anterior to humeri of elytra. Scutellum elongate, secondary punctures sparsely distributed. ***Elytron*** (Fig. 23): elytral striae shallowly impressed, punctures mostly spaced 2–3 times diameters of punctures. Intervals flat, with sutural interval weakly concave, surface scattered with secondary punctures. Male genitalia (Figs 29, 30, 39).

**Female paratype** (Figs 44, 45). Body length 9.8 mm; width across humeri 5.8 mm. Similar to male with minor differences in the form of strongly wrinkled surface of clypeus, transverse frontal carina trilobed, central lobe more prominent than lateral lobes, punctures on frons and vertex rugose, transverse pronotal carina feebly bilobed, lobes broad, punctures on pronotal disc coarser and denser than those of males.

**Male paratype.** The single male paratype is smaller in body size, 9.4 mm in length and 5.1 mm in width across humeri, frontal tubercle less developed and with three coarse punctures along pronotal posterior margin in front of scutellum.

**Diagnosis.** *Bolbelasmus concavisuturalis* sp. nov. is morphologically similar to *B. coreanus*, but can be distinguished from the latter by having denser punctures along the midline of the pronotum (Fig. 17) (sparser punctures in *B. coreanus* (Fig. 22)), punctures in elytral striae moderately developed (Fig. 23) (punctures weakly developed in *B. coreanus* (Fig. 28)) and ventrally curved parameres (straight in *B. coreanus*).

**Distribution.** Northern Thailand (Fig. 52).

**Etymology.** *Concavi-* (L.) = concave, *-suturalis* (L.) = suture. In reference to the concave sutural intervals of the elytra.

### *Bolbelasmus coreanus* (Kolbe, 1886)

*Bolboceras coreanus* Kolbe, 1886: 188. Original combination (type locality: Seoul, Korea, female type in the Museum für Naturkunde, Berlin, Germany).

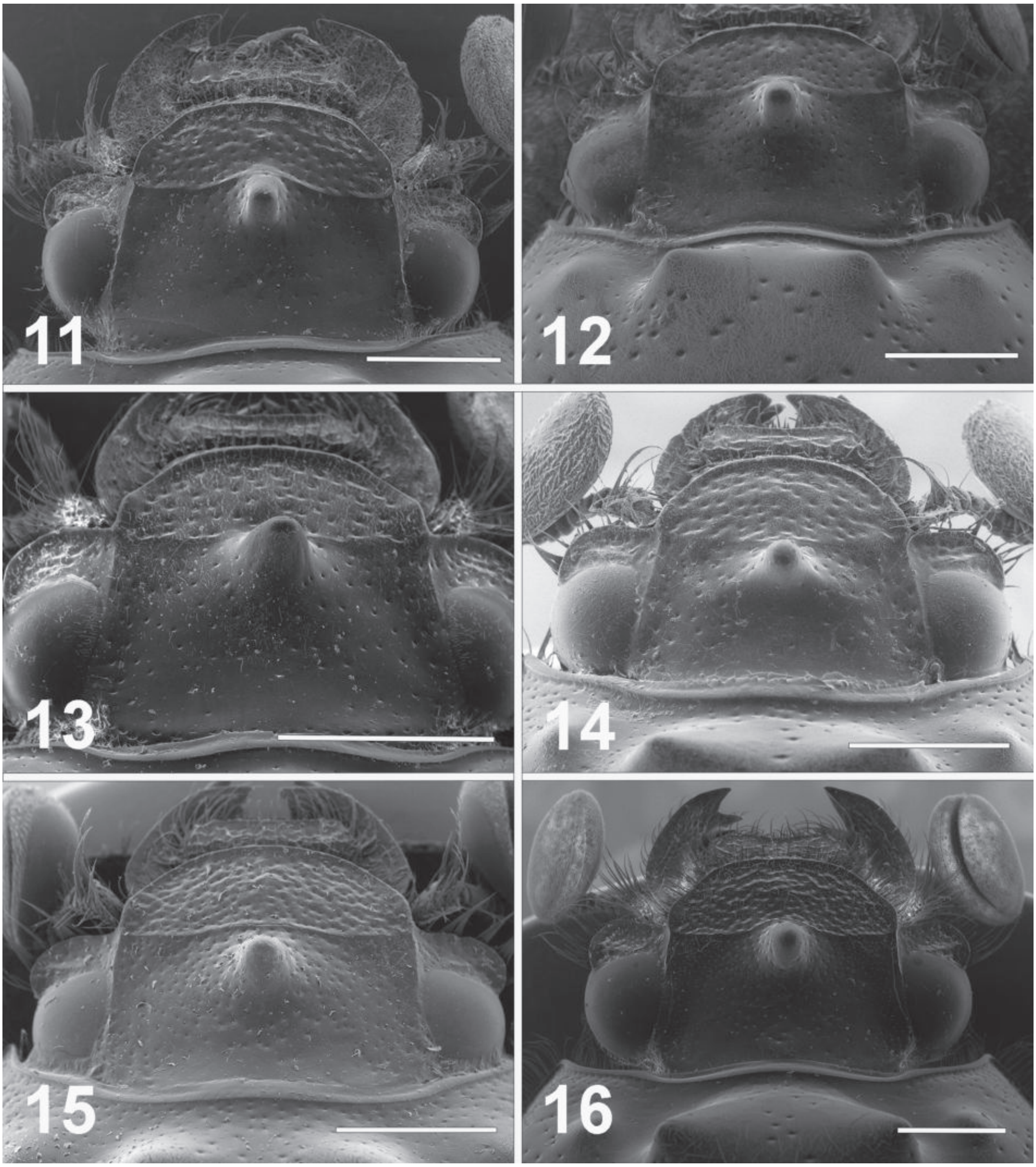
*Bolbelasmus coreanus* (Kolbe, 1886): Cartwright 1953: 97 (generic combination); Krikken 1977: 288 (notes; diagnosis; illustration); Kim 2000: 45 (diagnosis; collecting records); Li et al. 2008: 480 (redescription, illustrations, collecting records, distribution, remarks); Král, Löbl and Nikolajev 2006: 83 (catalog, subgenus *Kolbeus*); Nikolajev, Král and Bezděk 2016: 33 (catalog, subgenus *Kolbeus*).

*Kolbeus coreanus* (Kolbe, 1886): Boucomont 1911: 335 (generic combination); Boucomont 1912: 17 (catalog); Boucomont and Gillet 1921: 72 (record to Taiwan; diagnosis); Miwa 1930: 164 (catalog); Miwa 1931: 276 (catalog); Miwa and Chûjô 1939: 30 (catalog); Paulian 1945: 42 (diagnosis; figures; distribution).

*Bolbelasmus kurosawai* Masumoto, 1984: 76; Li et al. 2008: 481 (junior synonym).

*Bolboceras conicifrons* Fairmaire, 1896: 82; Boucomont and Gillet 1921: 72 (junior synonym).

**Distribution.** Korean Peninsula; China (Anhui, Zhejiang, Kweichow, Szechuan, Yunnan); Taiwan.



**Figures 11–16.** Scanning electron micrographs of heads of male *Bolbelasmus* spp. **11** *B. concavisuturalis* sp. nov. **12** *B. chifengi* sp. nov. **13** *B. meridionalis* **14** *B. korshunovi* **15** *B. yutangi* sp. nov. **16** *B. coreanus*. Scale bar: 1 mm.

**Remarks.** The detailed distribution of *B. coreanus* in China requires further investigation, particularly those from southwestern areas. Based on a large number of *Bolbelasmus* specimens recently collected from Yunnan and neighboring areas, we found no representatives of *B. coreanus* among them. Therefore, we reserve a decision about whether *B. coreanus* occurs in Yunnan, Thailand and India, as recorded by Krikken (1977). Voucher specimens from the areas mentioned above are required.

### ***Bolbelasmus korshunovi*** **Zinchenko, 2016**

Figs 7, 8, 14, 20, 26, 35, 36, 42

*Bolbelasmus korshunovi* Zinchenko, 2016: 328. Original combination (type locality: Nong Bun Nak, Nakhon Prov., Thailand).

**Material examined.** (5♂♂). 2♂♂ (ZMUC). Thailand: Loei Province, Phu Luang Wildlife Sanctuary, 8.–14.x.1984, 700–900 m, Karsholt, Lomboldt & Nielsen leg., Pral Siaw, 1923-9-33, Paūl Fogh/ Coll. Roseberg. 3♂♂ (NSMT). Sansai, Chiang Mai, Thailand, 17. VI. 1993.

**Diagnosis.** Body length, males, 6.8–9.0 mm, greatest width at pronotal base 4.4–5.7 mm; females, 7.1–8.7 mm in length, 4.3–5.6 mm in width (Zinchenko 2016). *Bolbelasmus korshunovi* is distinguished from the other Oriental *Bolbelasmus* species by elytral sutural intervals that are moderately convex, primary punctures sparsely distributed either side of the center of the pronotum, and shapes of the parameres.

**Notes.** Thirteen type specimens were designated in the original description of the species (Zinchenko 2016), 12 of them collected from June to August, and the holotype during November. Accordingly, the temporal activity of adults is likely at least half the year during both rainy and dry seasons. This is identical to the sympatric species, *B. meridionalis*.

**Distribution.** Northern Thailand.

**Remarks.** *Bolbelasmus korshunovi* inhabits plains to low-elevational montane areas and occurs sympatrically with *B. meridionalis* in northern Thailand.

### ***Bolbelasmus krikkeni*** **Nikolajev, 1979**

*Bolbelasmus krikkeni* Nikolajev, 1979: 225. Original combination (type locality: Gopaldhara, Sikkim, India); Král, Löbl and Nikolajev 2006: 83 (catalog, in subgenus *Kolbeus*); Nikolajev, Král and Bezděk 2016: 33 (catalog, subgenus *Kolbeus*).

**Distribution.** Northern India.

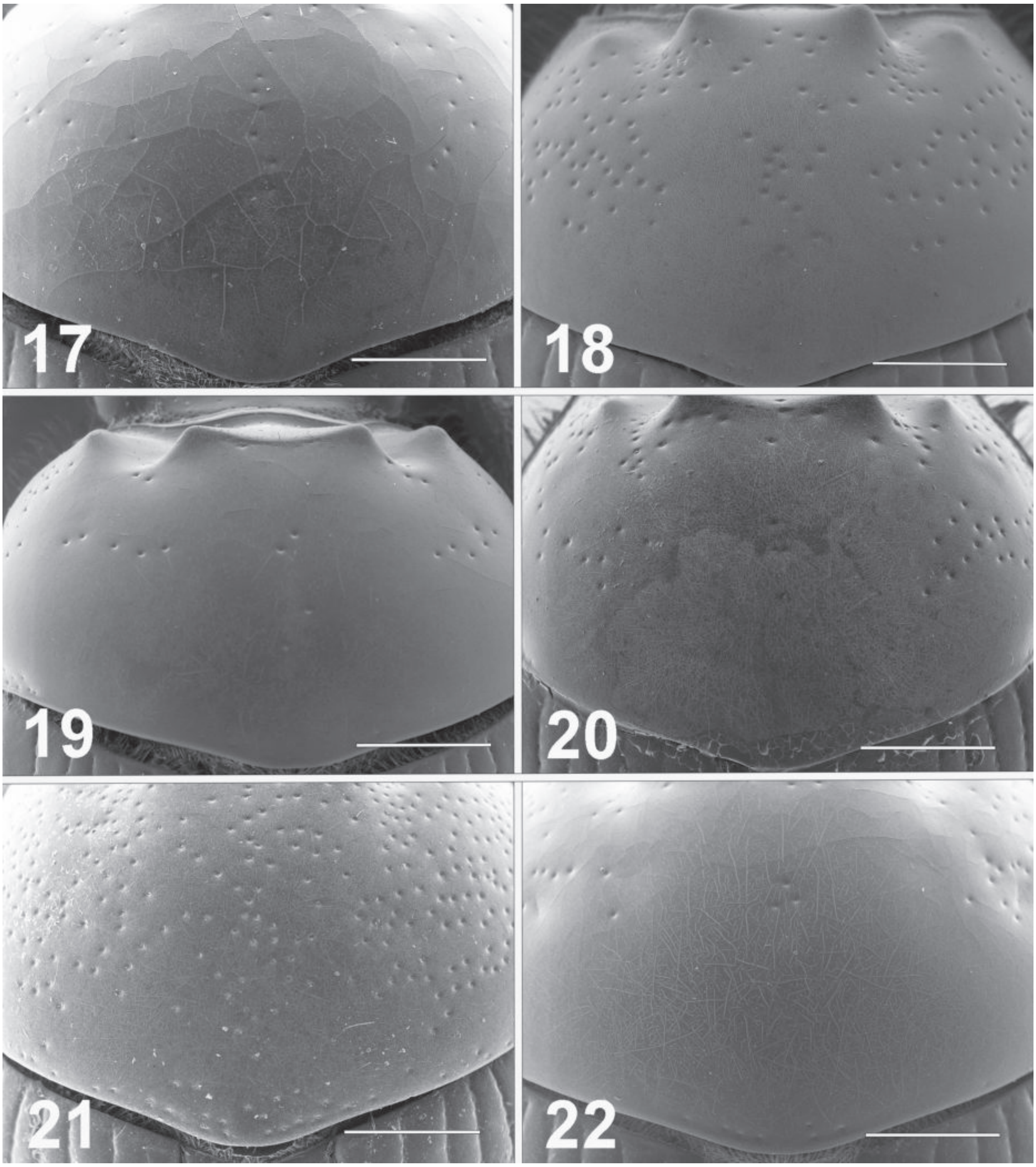
**Remarks.** Based on the collecting data from the monotypic specimen, *B. krikkeni* occurs in mid-elevation forests above 1000 m and is unique compared to its congeners that usually inhabit plains to low-elevation montane areas in the region. No additional specimens have been recorded since the publication of the original description.

### ***Bolbelasmus meridionalis*** **Krikken, 1977**

Figs 5, 6, 13, 19, 25, 33, 34, 41, 48, 49

*Bolbelasmus meridionalis* Krikken, 1977: 285. Original combination (type locality: Java, Indonesia); Král, Löbl and Nikolajev 2006: 83 (catalog, subgenus *Kolbeus*); Nikolajev, Král and Bezděk 2016: 33 (catalog, subgenus *Kolbeus*).

**Material examined.** (11♂♂, 8♀♀). 1♂ (NSMT). Thailand: Sansai, Chiang Mai, 17. VI. 1993 (1 male at NSMT). 9♂♂, 7♀♀ (NSMT); same locality, 12-V-1996.



**Figures 17–22.** Scanning electron micrographs of pronota of male *Bolbelasmus* spp. **17** *B. concavisuturalis* sp. nov. **18** *B. chifengi* sp. nov. **19** *B. meridionalis* **20** *B. korshunovi* **21** *B. yutangi* sp. nov. **22** *B. coreanus*. Scale bar: 1 mm.

1♀ (NSMT); near Chiang Mai, N Thailand, VII-1996, native collector. 1♂ (NSMT). Taiwan: Formosa, Heito, 10-VII-1941, H. Kondo/Sizumu Nomura Bequest, 1981.

**Diagnosis.** Body length, males, 6.1–8.2 mm, greatest width at pronotal base, 3.7–5.0 mm; females, 5.6–8.2 mm in length, 3.3–5.2 mm in width. Both *B. meridionalis* and *B. minutus* constitute a distinctive group among southeastern Asian congeners based on sharing the distinctly convex elytral sutural intervals and the tips of the parameres acute and curved ventrally in lateral view. Due to a lack of further material being available of the later species, *B. meridionalis* and *B. minutus* can only be separated by the shape of male genitalia and the lateral margin of the pronotum in *B. meridionalis*, which is more widely explanate than that of *B. minutus*.

**Chinese name.** 脊背厚角金龜

**Notes.** Li et al. (2008) excluded *B. meridionalis* from the registered Taiwan fauna due to the lack of verified records. During the present study, we examined a male *B. meridionalis* specimen housed in NSMT bearing identical labels as the paratype of the species collected in Heito (now Pingtung) by the late Japanese coleopterist, Yushiro Miwa. We therefore confirm the record of *B. meridionalis* in Taiwan, though it has been lacking in reports of the genus for 90 years. Consequently, the conservation status of *B. meridionalis* in Taiwan is in urgent need of study, along with that of *B. minutus* Li & Masumoto, 2008 and *Bolbotrypes davidis* (Fairmaire, 1891). These species are restricted to habitats in highly urbanized areas and/or intensively farmed plains of Taiwan.

**Distribution.** Indonesia (Java); eastern China; Thailand; Vietnam; Taiwan.

**Remarks.** *Bolbelasmus meridionalis* has the widest known distribution among congeners in the region in eastern and southeastern Asia. Also, the records from Java for the holotype and paratypes indicated that it is the only member from the Sunda Islands of the genus.

### *Bolbelasmus minutus* Li & Masumoto, 2008

*Bolbelasmus minutus* Li & Masumoto, 2008: 482. Original combination (type locality: Heito (presently Pingtung), Taiwan); Nikolajev, Král and Bezděk 2016: 33 (catalog, subgenus *Kolbeus*).

**Distribution.** Taiwan.

**Remarks.** *Bolbelasmus minutus* was described from a pair of specimens collected during 1931, and no further records of the species have been recorded. This species occurs sympatrically with *B. meridionalis* and *B. nativus* in the plains of southern Taiwan.

### *Bolbelasmus nativus nativus* Krikken, 1977

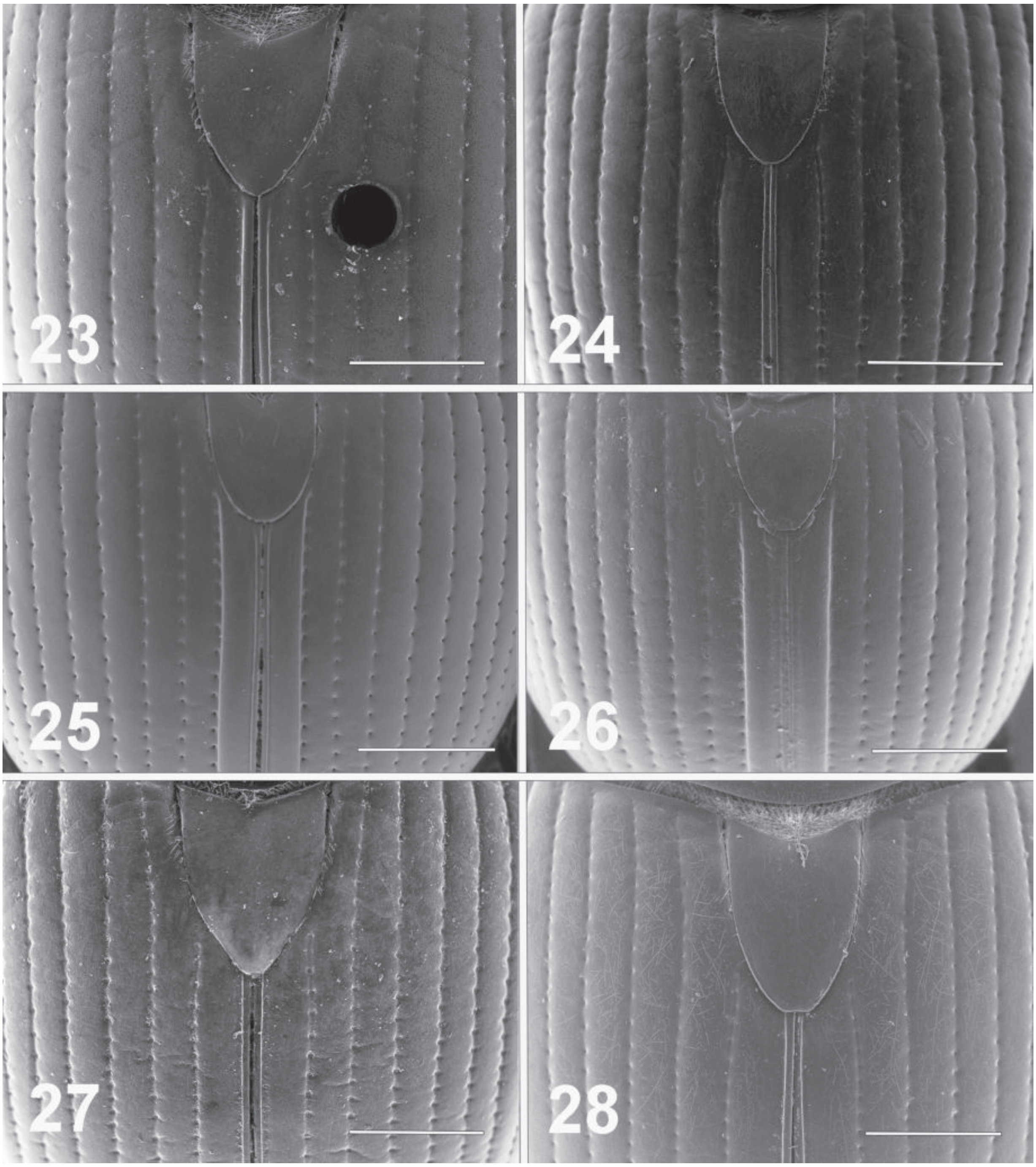
*Bolbelasmus nativus* Krikken, 1977: 287. Original combination (type locality: Heito (presently Pingtung), Taiwan); Nikolajev, Král and Bezděk 2016: 33 (catalog, in nominate subgenus *Bolbelasmus*).

*B. n. ishigakiensis* ssp. Masumoto, 1984.

*Bolbelasmus ishigakiensis* Masumoto, 1984: 73. Original combination (type locality: Ishigaki island, Okinawa, Japan); Král, Löbl and Nikolajev 2006: 83 (catalog, subgenus *Kolbeus*); Ochi and Masumoto 2005: 244 (as subspecies of *B. nativus*); Nikolajev, Král and Bezděk 2016: 33 (catalog, subgenus *Kolbeus*).

**Distribution.** Taiwan (southern areas and Lanyu island); Japan (Iriomote, Ishigaki and Tarama islands, Okinawa Prefecture).

**Remarks.** *Bolbelasmus nativus* was originally described based on a single male from Taiwan. Ochi and Masumoto (2005) treated the population distributed on a few small islands near Taiwan as a subspecies, *B. nativus ishigakiensis*.



**Figures 23–28.** Scanning electron micrographs of elytra of male *Bolbelasmus* spp. **23** *B*. *concavisuturalis* sp. nov. **24** *B*. *chifengi* sp. nov. **25** *B*. *meridionalis* **26** *B*. *korshunovi* **27** *B*. *yutangi* sp. nov. **28** *B*. *coreanus*. Scale bar: 1 mm.

### *Bolbelasmus shibatai* Masumoto, 1984

*Bolbelasmus shibatai* Masumoto, 1984: 75. Original combination (type locality: Amami Oshima Island, Japan); Nikolajev, Král and Bezděk 2016: 33 (catalog).

**Distribution.** Japan (Amami oshima and Okinawa island).

**Remarks.** Populations of *B*. *shibatai* are restricted to a few small islands in the southwestern archipelagos of Japan. Males possess strongly sclerotized parts of the parameres that can be distinguished from the similar species, *B*. *coreanus*.

### ***Bolbelasmus yutangi*** **Li & Wang, sp. nov.**

https://zoobank.org/A57879F9-F8A6-4D40-B922-DF3429C8BA4D
Figs 9, 10, 15, 21, 27, 37, 38, 43, 50, 51

**Type materials. *Holotype* male.** "Myanmar: Bago Region, Moe Yin Gyi, CCCC, 21.V.2017. leg. Y.-T. Wang." (glued on label, TARI). ***Paratypes.*** 1♀(TARI). data as the holotype. **5**♂♂ (TARI). "China: Yunnan, Wudian (武甸), 17.IX.2014. leg. Y.-T. Wang". 1♀ (CCLI) "China: Yunnan, Banggunjianshan (邦棍尖山), 18.IX.2015. leg. Y.-T. Wang". 6♂♂ (CCLI). "China: Yunnan, Bangdashan (邦達山), 01.IX.2015. leg. Y.-T. Wang". 1♂ (CCLI). "China: Yunnan, Ruili (瑞麗), 15.IX.2014. leg. Y.-T. Wang". 1♂ (NSMT). "Doi Saket, Chiang Mai, THAILAND, 12-X-1989, Y. MANIT leg". 1♂ (NSMT). "Doi Mon Unggate, Samoeng Distr., Chiang Mai Prov., THAILAND, 18-VII-1989, Y. MANIT leg".

**Description. Holotype male** (Figs 9, 10). Body length 9.3 mm; width across humeri 5.9 mm. Dorsum moderately shiny. Head, pronotum and scutellum dark brown with elytra reddish brown. ***Head*** (Fig. 15): labrum with anterior margin crenulate, disc transversally rugose. Clypeus trapezoidal, surface densely rugopunctate; protrusion at basal angle moderately developed. Clypeofrontal suture well defined, slightly curved in front of frontal tubercle. Frons with surface moderately punctate, punctures coarse, frontal tubercle vertically located at center of disc, triangular when viewed laterally. Eye prominent, canthus simple, not exceeding eye. ***Thorax:*** pronotum (Fig. 21) quadrituberculate, tubercles placed in a line, lateral tubercle greatly reduced in size; anterior face of median tubercles almost perpendicular to plane of pronotum; primary punctures coarse, dense on disc with small impunctate area in front of middle of posterior margin, punctures between lateral margins of pronotum and fovea bigger and denser, scattered coarse punctures distributed along posterior margin with seven punctures in front of scutellum, secondary punctures tiny, evenly scattered on surface of pronotum; frontal and lateral margins beaded, posterior margin beaded only in front of elytral humeri. Scutellum elongate, fine punctures sparsely distributed on surface. ***Elytron*** (Fig. 27): elytral striae shallowly impressed, punctures mostly spaced by 1–3 times diameters of punctures. Intervals slightly convex, including sutural interval, surface with scattered secondary punctures. Male genitalia. Figs 37, 38, 43.

**Female** (Figs 50, 51). Body length 8.4–8.7 mm; width across humeri 5.1–5.3 mm. Similar to male with minor differences in the form of strongly wrinkled surface of clypeus, transverse frontal carina trilobed, central lobe more prominent than lateral lobes, punctures on frons and vertex rugose, transverse pronotal carina feebly bilobed, with lobes broadly developed to reduced, bigger punctures on pronotal disc denser than those of males and scutellum with 1 or 2 bigger punctures.

**Variation in male.** Male paratypes differ from the holotype in the following respects: smaller body size, 6.6 mm in body length and 5.2 mm in width across humeri, frontal tubercle less developed and not in junction of clypeofrontal suture, pronotal tubercle feebly convex, reduced, and number of coarse punctures along pronotal posterior margin variable.

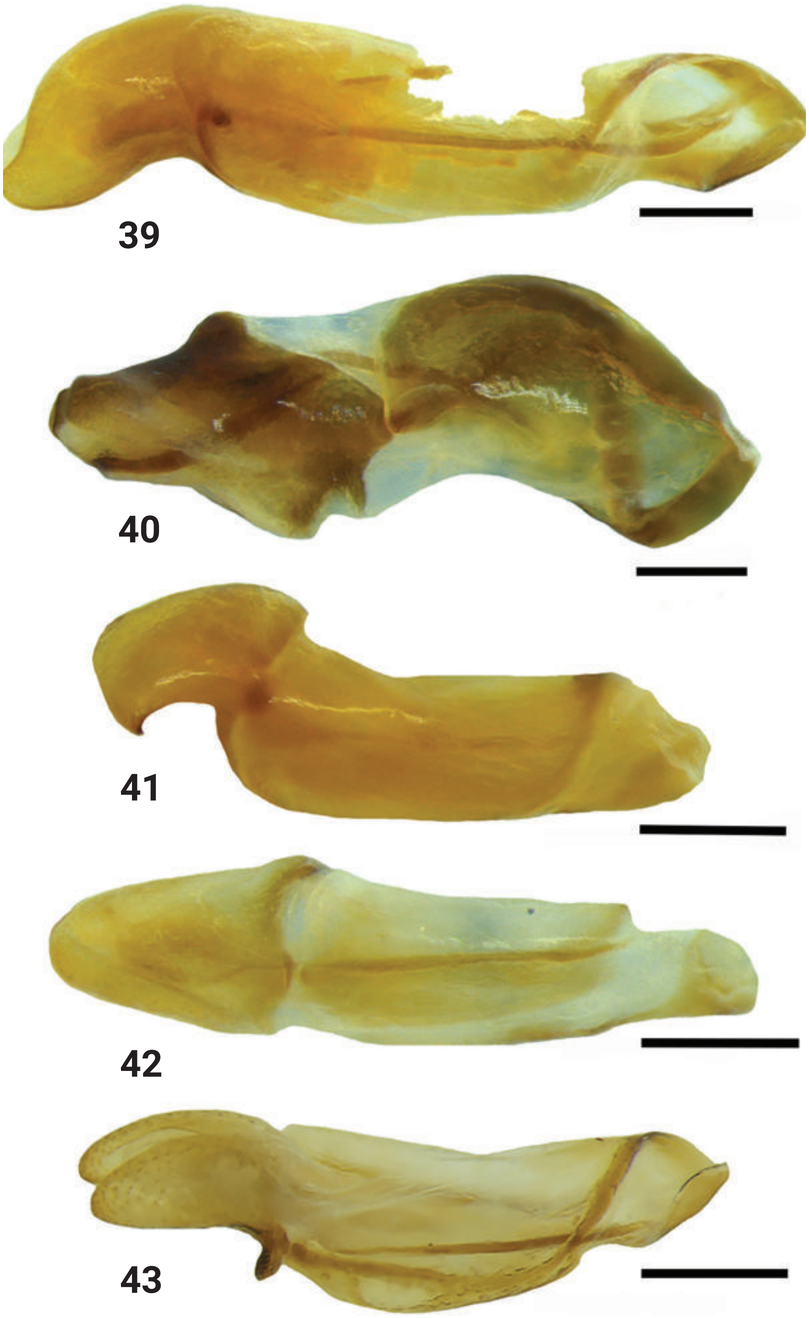
**Diagnosis.** *Bolbelasmus yutangi* is similar to *B. nativus* in sharing the frontal tubercle location at the center of the frons as well as having smaller parameres. It can be distinguished from the latter by the weakly convex basal angle of the

**Figures 29–38.** Male genitalia of *Bolbelasmus* spp. (29, 31, 33, 35, 37, dorsal views; 30, 32, 34, 36, 38, ventral views) **29, 30** *B. concavisuturalis* sp. nov. **31, 32** *B. chifengi* sp. nov. **33, 34** *B. meridionalis* **35, 36** *B. korshunovi* **37, 38** *B. yutangi* sp. nov. Scale bar: 0.3 mm.

clypeus (distinctly bulging in *B. nativus*), primary punctures densely distributed on the disc (almost impunctate along the middle of disc in *B. nativus*), sutural interval convex, similar to discal intervals (distinctly more convex than discal intervals in *B. nativus*) and parameres with the tips tapered (parameres broader at tips in *B. nativus*).

**Distribution.** Eastern Myanmar, northern Thailand and western Yunnan, China (Fig. 52).

**Etymology.** *Bolbelasmus yutangi* sp. nov. is named after Mr Yu-tang Wang, a beetle enthusiast of Taiwan, who collected most of the material used in this study.



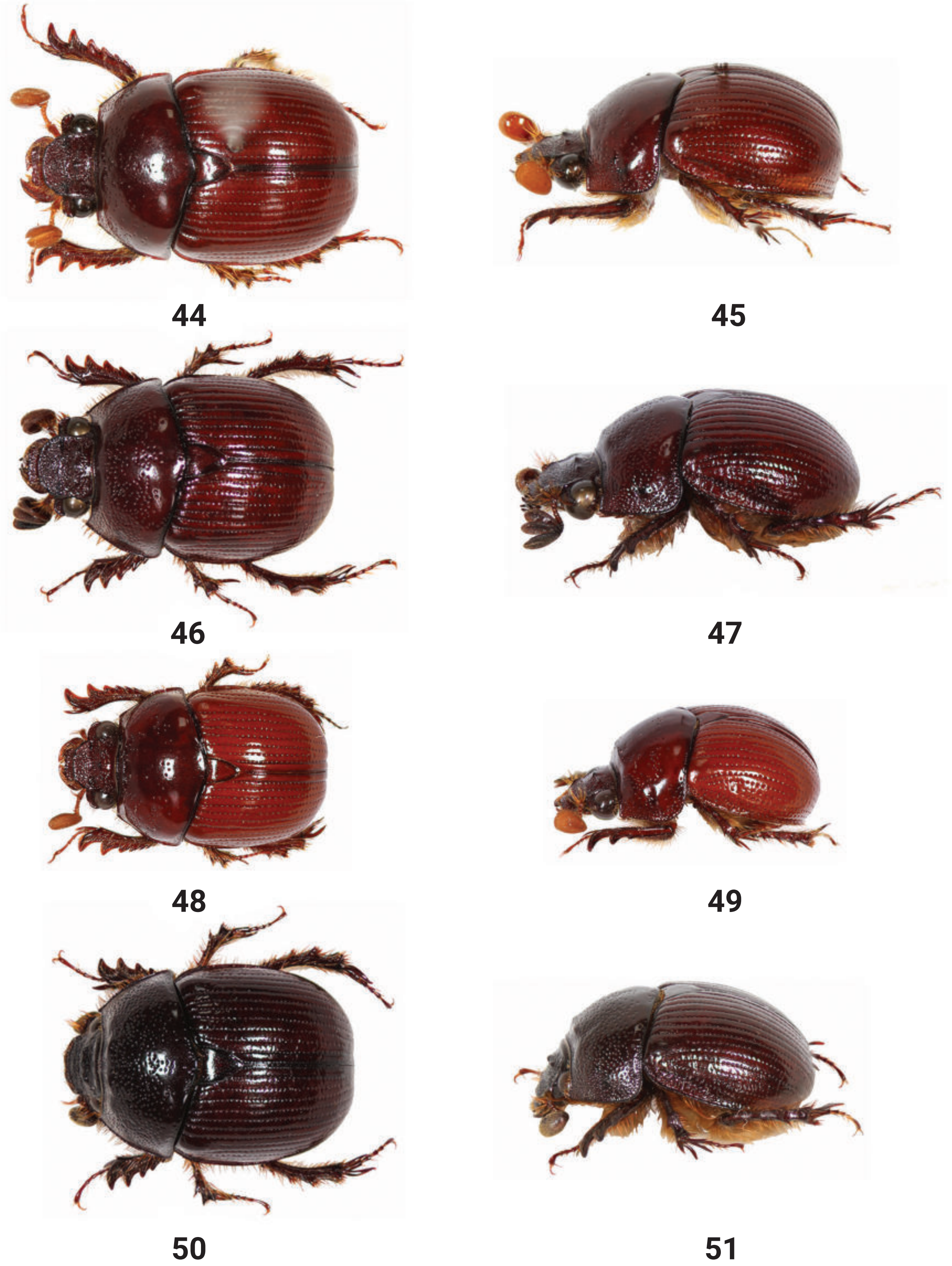
**Figures 39–43.** Male genitalia of *Bolbelasmus* spp., lateral views **39** *B. concavisuturalis* sp. nov. **40** *B. chifengi* sp. nov. **41** *B. meridionalis* **42** *B. korshunovi* **43** *B. yutangi* sp. nov. Scale bar: 0.2 mm.

## Species with doubtful locality record

### ***Bolbelasmus orientalis* Petrovitz, 1968**

*Bolbelasmus orientalis* Petrovitz, 1968: 185. Original combination (type locality: Wladiwostok [Vladivostok], Primorskii Territory, Russia); Krikken 1977: 289 (notes; diagnosis; illustration); Nikolajev, Král and Bezděk 2016: 33 (catalog).

**Distribution.** Described from Vladivostok, Russian Far East.



**Figures 44–51.** Dorsal and lateral views of female *Bolbelasmus* spp. **44, 45** *B. concavisuturalis* sp. nov., paratype **46, 47** *B. chifengi* sp. nov., paratype **48, 49** *B. meridionalis* **50, 51** *B. yutangi* sp. nov., paratype.

**Remarks.** *Bolbelasmus orientalis* was described from one male and one female. Krikken (1977) examined both type specimens and found that the female allotype to be a minor male. Also, he noted that the species has no direct

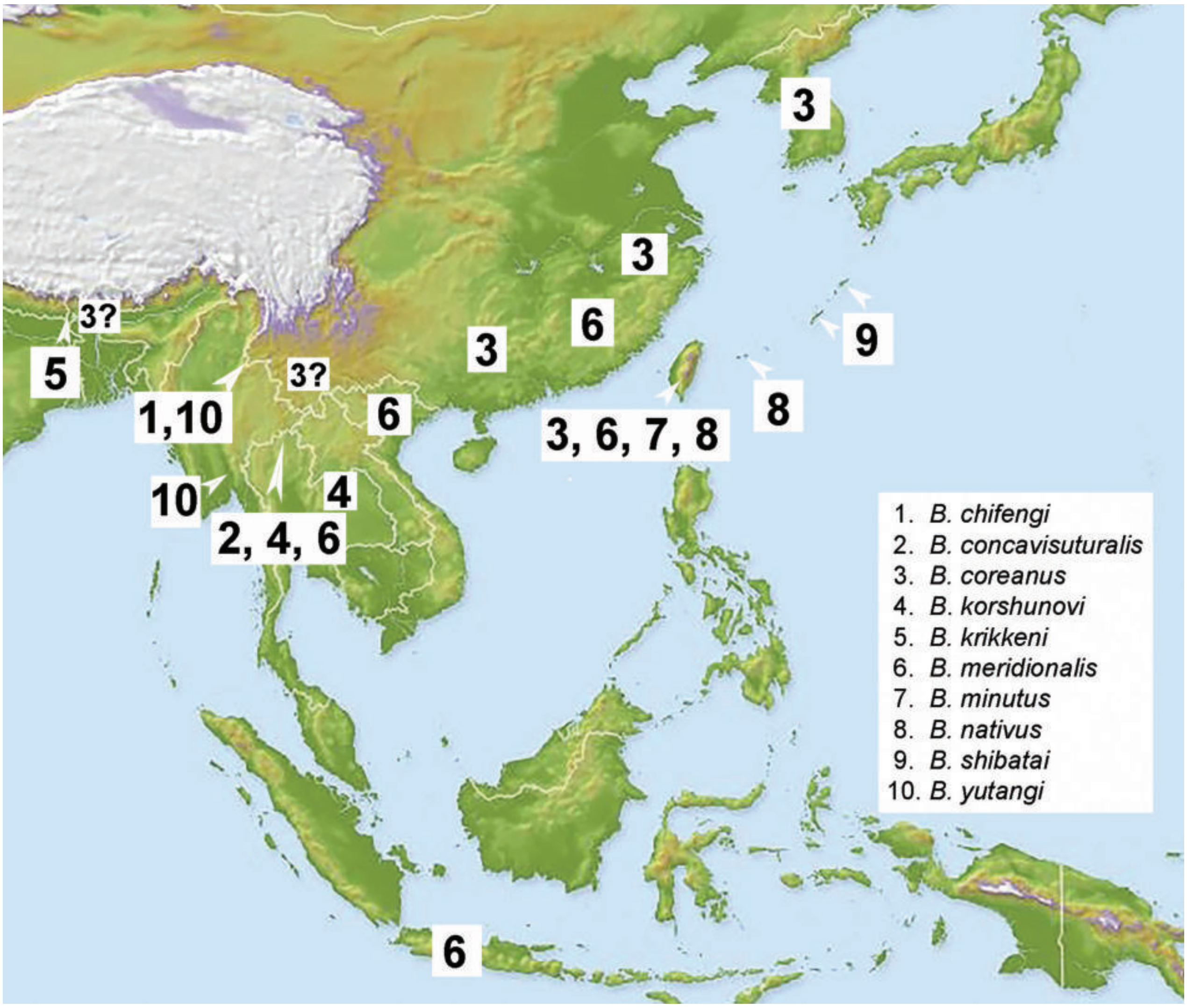


**Figure 52.** Distribution map of the eastern and southeastern Asian *Bolbelasmus* species. Question marks indicate doubtful distributional records.

affinity with three congeners, *B. coreanus*, *B meridionalis* and *B. nativus*, which are geographically close to *B. orientalis* but are allied to the western Palaearctic *B. unicornis*. Bezborodov and Koshkin (2014) doubted the locality label attached to the type specimens because there were no additional records of the species documented in Russia or nearby territories other than that of type specimens. We, therefore, exclude *B. orientalis* from the *Bolbelasmus* fauna in the eastern Palaearctic and the Oriental regions.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Funding acquisition: CLL. Investigation: CLL. Methodology: CLL. Supervision: CCW. Writing – original draft: CLL. Writing – review and editing: CCW.

### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# A new genus and species of oceanic planktonic Tisbidae (Crustacea, Copepoda, Harpacticoida) with enlarged modified eyes

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## Abstract

Both sexes of a new monotypic genus of Tisbidae (Copepoda, Harpacticoida) are described from the epi- or mesopelagic zone in the Kuroshio region, Japan. *Gyorome guttatum* **gen. et sp. nov.** belongs to a monophyletic lineage of deepwater holoplanktonic genera defined by a suite of characters. Within this clade, *Gyorome* **gen. nov.** appears most closely related to *Neotisbella* Boxshall, 1979. The most distinguishable feature of *G. guttatum* **gen. et sp. nov.** is the presence of large, paired, frontal modified eyes, each consisting of a baculiform ocellus, a globular (Gicklhorn's?) organ, and a semi-parabolic plate. The taxonomic position of *Tisbe spinulosa* Bradford & Wells, 1983 is discussed and a key to the six meso- and bathypelagic tisbid species is provided. Confusion surrounding earlier literature reports of supernumerary elements on the caudal ramus in some harpacticoid taxa is clarified. Secondary modifications of ocellar components of the typical naupliar eye in the Harpacticoida are reviewed. It is suggested that the development of specialized eyes in *G. guttatum* **gen. et sp. nov.** may provide a means for detecting bioluminescent food particles in oligotrophic pelagic environments. The large, vaulted prosome indicates the species is an opportunistic macrophage that has adopted gorging as a feeding strategy.

**Key words:** Caudal ramus, ecological radiation, Gicklhorn's organ, key to species, Kuroshio, mesopelagic, taxonomy, zooplankton

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## Introduction

Lang's (1944, 1948) revision of the family Tisbidae Stebbing, 1910 (Crustacea, Copepoda, Harpacticoida) assigned the 12 genera recognized at the time to two subfamilies. In the Tisbinae he placed *Tisbe* Lilljeborg, 1853 (type genus), *Scutellidium* Claus, 1866, *Cholidya* Farran, 1914, *Sacodiscus* Wilson, 1924, and *Tisbella* Gurney, 1927. The new subfamily Idyanthinae was proposed by Lang (1944) to accommodate *Zosime* Boeck, 1873, *Idyella* Sars, 1905, *Idyanthe* Sars, 1909a, *Tachidiella* Sars, 1909b, *Pseudozosime* Scott, 1912 and *Idyellopsis* Lang, 1948, in addition to *Tachidiopsis* Sars, 1911 which was classified as *incertae sedis*. A third subfamily, the Cholidyinae, was proposed by Boxshall (1979) for

*Cholidya*, a parasite of cephalopods (Humes and Voight 1997), but no proper justification was provided for this course of action.

The Idyanthinae was raised to family rank by Seifried (2003) to which the following genera have been added since: *Dactylopia* Becker, 1974; *Styracothorax* Huys, 1993; *Aspinothorax* Moura & Martínez Arbizu, 2003; *Meteorina* George, 2004; *Nematovorax* Bröhldick, 2005 and *Pseudometeorina* George & Wiest, 2015 (as genus incertae sedis but see George 2023). A new family, the Zosimeidae [for correct spelling see Huys and Clark (2009) and Anonymous (2010)], was established to accommodate *Zosime*, *Pseudozosime* and *Peresime* Dinet, 1974 while *Tachidiopsis* was transferred to the Neobradyidae (Seifried 2003).

The Tisbinae saw the addition of *Paraidya* Sewell, 1940 (an unavailable name subsequently validated by Huys (2009) under his authorship) and *Tisbintra* Sewell, 1940, both genera were not considered by Lang (1944, 1948), and *Neoscutellidium* Zwerner, 1967. Boxshall (1979) discussed the relationships between the tisbinid genera, reinstated *Bathyidya* Farran, 1926 (previously a junior subjective synonym of *Tisbe*; see also Volkmann 1979b), and added two new genera, *Neotisbella* Boxshall, 1979 and *Volkmannia* Boxshall, 1979. Itô (1976) had previously reinstated *Scutellopsis* Wiborg, 1964 from the synonymy of *Scutellidium* while Dahms & Dieckmann, (1987) proposed *Drescheriella* Dahms & Dieckmann, 1987 as a new addition to the Tisbinae. Moura and Martínez Arbizu (2003) postulated that the family Porcellidiidae is nested within the Tisbidae, most likely as the sistergroup of *Sacodiscus*, but this hypothesis did not gain any acceptance (Wells 2007).

Following Boxshall's (1979) proposal of the Cholidyinae, Avdeev (1982, 1983, 1986) subsequently described five new genera associated with deep water octopodans but created taxonomic confusion by placing three of them in the Cholidyinae (*Cholidyella* Avdeev, 1982; *Brescianiana* Avdeev, 1982; *Tripartisoma* Avdeev, 1983) and the remaining two in the Tisbinae (*Yunona* Avdeev, 1983; *Octopinella* Avdeev, 1986). This subfamilial assignment, effectively implying a dual colonization of cephalopod mollusks by two sister lineages, was uncritically adopted by most authors (Bresciani and Lützen 1994; Humes and Voight 1997; López-González et al. 2000; Wells 2007) while the more parsimonious alternative involving a single colonization event was favored by Huys (2016) who also considered *Neoscutellidium* (parasitic on fish) a member of the same monophyletic lineage. In this scenario, the Tisbinae, as currently defined, constitute a paraphyletic group at the exclusion of the Cholidyinae, implying that the current subfamilial division of the Tisbidae is meaningless and must be abandoned. With the addition of *Avdeevia* Bresciani & Lützen, 1994, *Genesis* López-González, Bresciani & Huys in López-González et al. 2000 and *Amplipedicola* Avdeev, 2010 (all of which parasitize cephalopod hosts) the current number of genera in the Tisbidae stands at 21.

Members of the family Tisbidae exhibit a variety of lifestyles ranging from free-living to obligatory parasitic. Although all species are exclusively marine, the family as a whole serves as a typical example illustrating the complex ecological radiation that characterizes the evolutionary history of harpacticoid copepods. Tisbids, in particular species of the genera *Tisbe* and *Scutellidium*, show a universal occurrence of parallelism in phytal habitats (Hicks 1980, 1985), either as associates of the sediments trapped by algae when the fronds and holdfasts are heavily loaded with silt-clay or detritus, or as genuine algae-dwelling forms (Hicks and Coull 1983). In most cases a critical experimental verification of their trophic dependence on the algae does not exist. Others, such as members of *Tisbintra* and *Tisbella* are commonly found in surface plankton samples or mangrove ecosystems (Willey 1930; Sewell 1940; Ummerkutty 1961; Volkmann 1979a; Gómez and Fuentes-Reines 2017; Fuentes-Reinés and Suárez Morales 2019) and coastal marine (Coull 1970; Coull and Herman 1970; Fleeger and Shirley 1990; Franz and Friedman 2002) and brackish water habitats (Gurney 1927; Wilson 1932; Yeatman 1963, 1983; Reid and Hribar 2006; Morales-Serna and Gómez 2008). An increasing volume of literature has demonstrated that members of *Drescheriella* are sympagic (sea-ice inhabiting) and are often associated with microalgae colonizing the cracks in the sea ice (e.g., Giesbrecht 1902; Dahms and Dieckmann 1987; Dahms et al. 1990; Dahms and Schminke 1992; Schnack-Schiel et al. 1998, 2001a, b, 2004, 2008; Swadling et al. 2000; Kiko et al. 2008; Loots et al. 2009; Kramer et al. 2011; Wallis et al. 2016; Makabe et al. 2022).

In the Tisbidae, twenty-five species have entered into symbiotic associations with metazoan hosts (mollusks, echinoderms, crustaceans and teleost fish), representing ten independent colonization events (Huys 2016). Three of those events involve mollusk hosts, including cephalopods, bivalves, and gastropods. Most members of the “Cholidyinae” utilize deep water octopuses as hosts and complete the entire copepodid phase inside the tissues of the cephalopod while the free-swimming phase is presumably reduced to the naupliar and adult stages (López-González et al. 2000). Two species of *Tisbe* have been reported from the mantle cavity of mussels (*Mytilus* spp.) in both North and South America (Humes 1954; Huys and Song 2004; Cremonte et al. 2015; Huys 2016), representing the only records of tisbids associated with bivalved mollusks. The only association between marine gastropods and harpacticoid copepods was reported by Branch (1974) who found large numbers of all developmental stages of *Scutellidium patellarum* Branch, 1974, in the pallial cavity of five species of *Patella* L. in South Africa. Huys (2016) documented four independent associations between tisbids and crustacean hosts. *Sacodiscus ovalis* (Wilson, 1944) lives as an ectosymbiont on the exoskeleton of the American lobster *Homarus americanus* H. Milne Edwards, 1837 in North America (Wilson 1944; Humes 1960). *Tisbe elongata* (A. Scott, 1896) spends most of its life cycle in the gill chamber of the European lobster *Homarus gammarus* (Linnaeus, 1758) in British waters (Gooding 1957; Bruce et al. 1963; Holmes and O’Connor 1990; Gotto 1993; Gurney 1933). An undescribed species of *Tisbe* was recorded from the gills of the red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), in the Barents Sea (Haugen et al. 1998; Jansen et al. 1998; Dvoretsky and Dvoretsky 2013, 2023). The three known species of *Paraidya* are exclusively associated with Indo-Pacific diogenid anomuran crabs of the genus *Dardanus* Paul’son, 1875 (Humes and Ho 1969; Humes 1981; Innocenti 2009). Two tisbid species are known to live in associations with echinoderm hosts (Huys 2016). *Tisbe japonica* Ho, 1982 is an associate of the blue bat star *Patiria pectinifera* (Müller & Troschel, 1842) in the Sea of Japan and the only harpacticoid known to utilize starfish hosts (Ho 1982). Stock (1960) recovered *Sacodiscus humesi* Stock, 1960 from washings of *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1791 collected in the Bay of Banyuls, France but this association requires confirmation (Huys 2016). Finally, *Neoscutellidium yeatmani* Zwerner, 1967 occurs on the gills of the bathydemersal Antarctic eelpout, *Lycodichthys dearborni* (DeWitt, 1962), and is the only confirmed record of a harpacticoid utilizing a fish host (Zwerner 1967).

Only few harpacticoid families have secondarily colonized open oceanic waters (Boxshall 1979; Huys and Böttger-Schnack 1994; Huys and Conroy-Dalton 2000) and their evolutionary success in terms of diversification in the oceanic realm has generally remained limited. The Tisbidae contains a monophyletic clade uniting three genera (*Bathyidia*, *Neotisbella*, *Volkmannia*) that are exclusively found in the meso- and bathypelagic zones of the Atlantic Ocean (Farran 1926; Deevey and Brooks 1977; Boxshall 1979; Khodami et al. 2017). Here we describe a new genus and species of oceanic planktonic Tisbidae from the epi- or mesopelagic zone of the Kuroshio region, Japan, compare its unique morphological features and discuss its relationships with other deepwater genera in the family.

## Material and methods

The copepods were collected in the Kuroshio region, Japan (33°10'N, 136°00'E) in the daytime (1423–1650) on 28 November 2018 during the 1828 research cruise by the TRV SEISUI-MARU of Mie University. An oblique tow (sampling depth 0–935 m) at speed of 2 knots was performed using an ORI net (diameter 160 cm, mesh size 330 µm; cf. Omori 1965). Specimens were fixed in 10% neutralized formalin seawater immediately after capture, cleared in lactophenol, and dissected under an Olympus SZX stereo microscope. Illustrations were drawn using an Olympus BX53 compound microscope equipped with a drawing tube. The descriptive terminology is adopted from Huys and Boxshall (1991) and Huys et al. (1996). Abbreviations used in the text are ae, aesthetasc; P1–P6, for legs 1–6; exp, enp for exopod and endopod, respectively; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segments of a ramus. Type specimens (NMST-Cr 31562–31565) were deposited in the National Museum of Nature and Science (NSMT; Tsukuba, Ibaraki Prefecture, Japan).

## Systematics

### Order Harpacticoida Sars, 1903
### Family Tisbidae Stebbing, 1910

### Genus *Gyorome* gen. nov.

https://zoobank.org/D0C2FE57-C793-4EEA-A36A-609F05494255

**Diagnosis.** Tisbidae. Body cyclopiform, large (> 1 mm); genital and first abdominal somites completely fused in ♀, forming genital double-somite. Sexual dimorphism in prosomal ornamentation, antennule, maxilliped, P2 endopod, P5, P6 and urosomal segmentation. Prosome capacious and vaulted; dorsal surface pustulate (covered by dense pattern of denticles); posterior margin of cephalothorax with middorsal protrusion in ♀, absent in ♂. Cephalic region with large, paired, modified eyes, each comprising a baculiform ocellus, a globular

(Gicklhorn's?) organ and a semi-parabolic plate. Caudal ramus with seven setae and paired multi-branched tube-pores along posterior margin, displacing setae III–VI towards inner distal corner.

Antennule short, relatively compact and 8-segmented in ♀, with aesthetasc on segment 4; slender, 8-segmented and haplocer in ♂, with geniculation between segments 6 and 7, and aesthetasc on segment 4 and elongate digitiform segment 8. Antenna without seta on basis and proximal endopodal segment; exopod 4-segmented with armature [2, 1, 1, 3]. Mandible with unarmed basis and 1-segmented rami; exopod with one lateral and two terminal setae; endopod with two lateral and four terminal setae. Maxillule 3-segmented, comprising praecoxa, endopod, and compound segment representing fused coxa, basis and exopod. Maxilla 2-segmented, comprising syncoxa and allobasis; syncoxa with small coxal endite bearing one plumose seta; allobasis produced into curved claw with fine pinnules along outer margin and short plumose seta just over halfway claw length. Maxilliped ♀ 3-segmented, comprising short syncoxa articulating with subcylindrical pedestal, unarmed elongate basis, and small endopod with one unipinnate lateral seta and long, slender, distal claw accompanied at base by plumose seta. Maxilliped ♂ with modified basis (distal palmar margin produced into lobate spinular expansion) and endopod (with unguiform projection along medial margin).

P1–P4 with 3-segmented exopods and endopods; with dense pattern of minute spinules on anterior surface of protopod and rami. P1 outer spines on exp-2 and -3 without spinular combs; exp-2 not markedly longer than other exopodal segments. P1 endopod non-prehensile; indistinctly 3-segmented with transverse surface suture marking original segmentation between enp-2 and -3; enp-1 expanded in distal half forming lobate extension along medial margin; enp-3 small. P2 enp-1 inner seta modified in ♂, displaying pinnate ornamentation along distal half of outer margin (instead of plumose in ♀). Armature formula of P1–P4 as follows (Roman and Arabic numerals indicate spines and setae, respectively):

| | Coxa | Basis | Exopod | | | Endopod | | |
|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 1 | 2 | 3 |
| Leg 1 (P1) | 0–0 | I–I | I–0 | I–1 | I+5 | 0–1 | 0–1 | 3 |
| Leg 2 (P2) | 0–0 | 1–0 | I–1 | I–1 | III, I+1, 2 | 0–1 | 0–2 | I, 2, 2 |
| Leg 3 (P3) | 0–0 | 1–0 | I–1 | I–1 | III, I+1, 3 | 0–1 | 0–2 | I, 2, 3 |
| Leg 4 (P4) | 0–0 | 1–0 | I–1 | I–1 | III, I+1, 3 | 0–1 | 0–2 | I, 2, 2 |

P5 2-segmented in both sexes, comprising baseoendopod and elongate exopod; obsolete endopodal lobe represented by one seta (minute in ♂); exopod with one outer, one inner and two terminal well developed setae. P6 with two minute setae in ♀; sixth pair of legs symmetrical in ♂, each with three well developed setae.

**Type species.** *Gyorome guttatum* gen. et sp. nov. (by original designation).

**Etymology.** The generic name is based on the Japanese word "Gyorome", meaning "bulging eyes" and refers to the large ocelli in the cephalosome of the type species. Gender neuter.

### *Gyorome guttatum* gen. et sp. nov.

https://zoobank.org/20C65F2B-C974-40F9-B6E8-E7167EB00802
Figs 1–7

**Type locality.** Japan, Kuroshio region (Off Mie Prefecture, 33°10'N, 136°00'E), epi- or mesopelagic zone (0–935 m depth).

**Type material. *Holotype*:** Undissected ♀ (1.80 mm) in vial (NSMT-Cr 31562). ***Allotype*:** ♂ (1.47 mm), dissected prosome, urosome and appendages mounted on glass slide (NSMT-Cr 31563). ***Paratypes*:** One dissected ♀ (1.77 mm) mounted on glass slide (NSMT-Cr 31564), one undissected ♀ (1.64 mm) preserved in 10% neutralized formalin-seawater solution in vial (NSMT-Cr 31565).

**Description of adult female.** Total body length ranging from 1.64–1.80 mm (*n* = 3). ***Habitus*** (Figs 1, 2A, B) cyclopiform and yellowish. Prosome (Fig. 2A, B) significantly expanded bilaterally, ovoid in dorsal aspect producing vaulted appearance; integument of cephalothorax (except anterior portion) and somites bearing legs 2–4 with dense pattern of minute surface denticles (Fig. 2A). Cephalosome completely fused to first pedigerous somite, forming cephalothorax; ventral surface between maxilliped and leg 1 with distinct protuberance; posterodorsal margin with semicircular lobate extension covering anterior third of leg 2-bearing somite. Anterior part of cephalosome with middorsal pair of baculiform ocelli (BO in Fig. 2A, B) and one pair of globular organs (GO in Fig. 2A, B) each surrounded by thin semi-parabolic plate (SP in Fig. 2A, B) either side of baculiform ocelli; lipid droplets (LD in Fig. 2B) filling up space between and posterior to semi-parabolic plates; ovaries (OV in Fig. 2B) occupying larger part of posterior half of cephalothorax. Rostrum (Fig. 2C) small and triangular, pointing downwards; labrum (LB in Fig. 2D) a rounded lobe with spinules around distal margin; paragnaths (PG in Fig. 2D) represented by semicircular lobes fringed with setulae posteriorly and laterally.

Pedigerous somites bearing legs 2–4 completely separated (Fig. 2A, B); with well-developed pleurotergites, gradually decreasing in width; pleural areas of somites bearing legs 3 and 4 protruding posteriorly.

***Urosome*** (Fig. 3A, B) cylindrical, comprising fifth pedigerous somite, genital double-somite, and three free abdominal somites; all somites with dense pattern of minute surface denticles (Fig. 2A). Leg 5-bearing somite with lateral setular tufts in anterior half. Original segmentation of genital double-somite marked by transverse suture and accompanying spinules dorsally and dorsolaterally; posterior margin with spinules all around; copulatory pore small, located midventrally, immediately posterior to genital slit; copulatory duct well developed, with slight bilateral constriction halfway down its length. Genital double-somite and free abdominal somites with numerous minute tubercles laterally; fourth and fifth urosomites with continuous row of spinules around posterior margin; anal somite with setulae posteromedially and with paired rows of spinules near bases of caudal rami.

***Caudal ramus*** (Fig. 3C, D) ~ 3.3× as long as wide (measured in dorsal aspect); with seven setae, setae I–III and VII slender and naked, setae IV–V broken, represented in all specimens by short basal parts, setae VI slender and pinnate; seta I longer than caudal ramus, originating laterally in proximal third of ramus; seta II arising from outer distal corner; bases of setae IV and V positioned slightly ventral to that of seta VI; seta VI long (Fig. 3A, B), ~ 2.5× length of ramus length; seta VII located dorsally near inner margin at ~ 70% of ramus

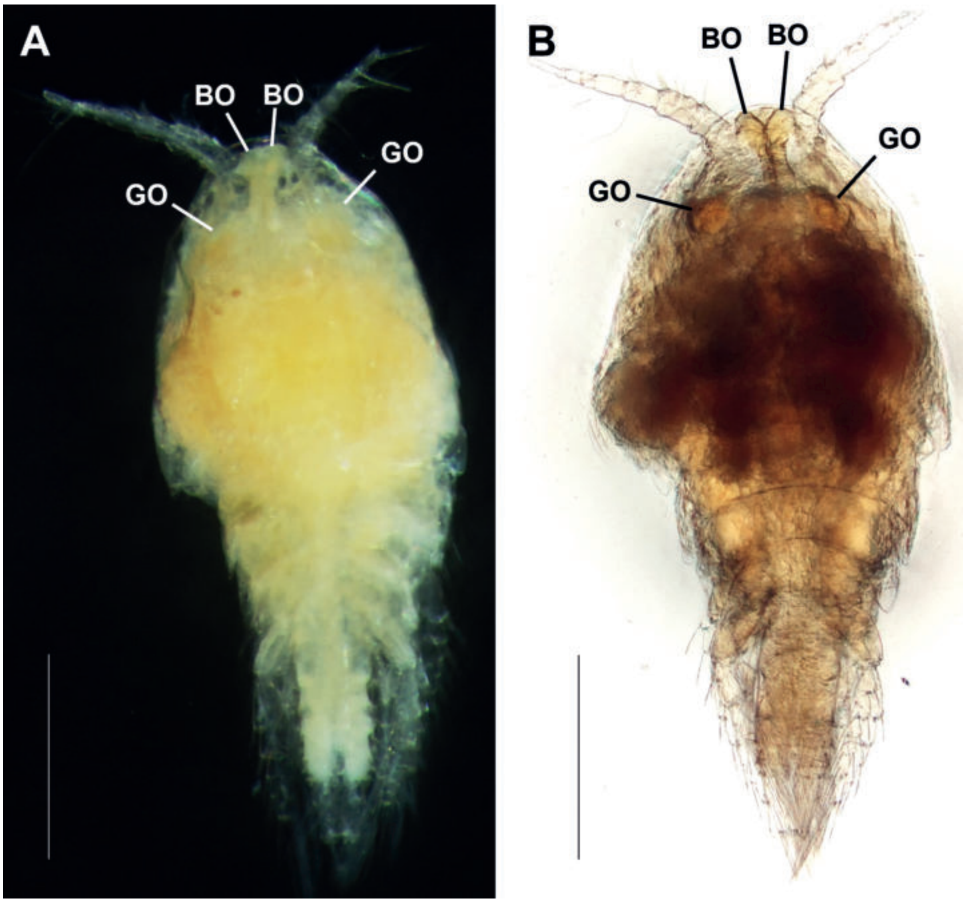

**Figure 1.** Focus stacked micrographs of *Gyorome guttatum* gen. et sp. nov., adult female, holotype, using **A** reflected (incident) light microscopy and **B** transmitted light microscopy. Abbreviations: BO, baculiform ocelli; GO, globular organs. Scale bars: 0.5 mm.

length; dorsal posterior margin of ramus with two elongate, branching tube-pores (inner one distinctly longer than outer one), covering bases of setae III–VI; ornamentation consisting of spinules on ventral surface of ramus and around bases of setae I–III and, to a lesser extent, VII.

***Antennule*** (Fig. 4A) 8-segmented, ~ 0.25× as long as body length; armature as follows: 1-(1), 2-(15), 3-(4), 4-(3 + ae), 5-(2), 6-(3), 7-(1), 8-(5); all setae naked; segment 1 with inner spinules; aesthetasc on segment 4 well-developed and 0.8× as long as antennule; segments 7 and 8 incompletely fused, original segmentation indicated by transverse surface suture.

***Antenna*** (Fig. 4B, B’) without ornamentation on coxa. Basis unarmed, with setules on posterior surface. Endopod 2-segmented; proximal segment unarmed, with setules along abexopodal margin; distal segment with one minute and two well developed elements laterally and six setae apically, inner margin with short spinules proximally and outer margin with longer spinules in proximal half. Exopod 4-segmented; segments 1–3 with one lateral seta; segment 4 with three apical setae and spinules along inner and outer margins.

***Mandible*** (Fig. 4C). Gnathobase with three well developed bicuspid teeth, three smaller teeth with terminal setular tuft, one hirsute dorsal seta, and transverse row of fine, densely arranged setules. Basis unarmed. Endopod unsegmented, with two proximal setae along inner margin and four distal setae; outer margin with row of setules. Exopod unsegmented, with one inner and two distal setae.

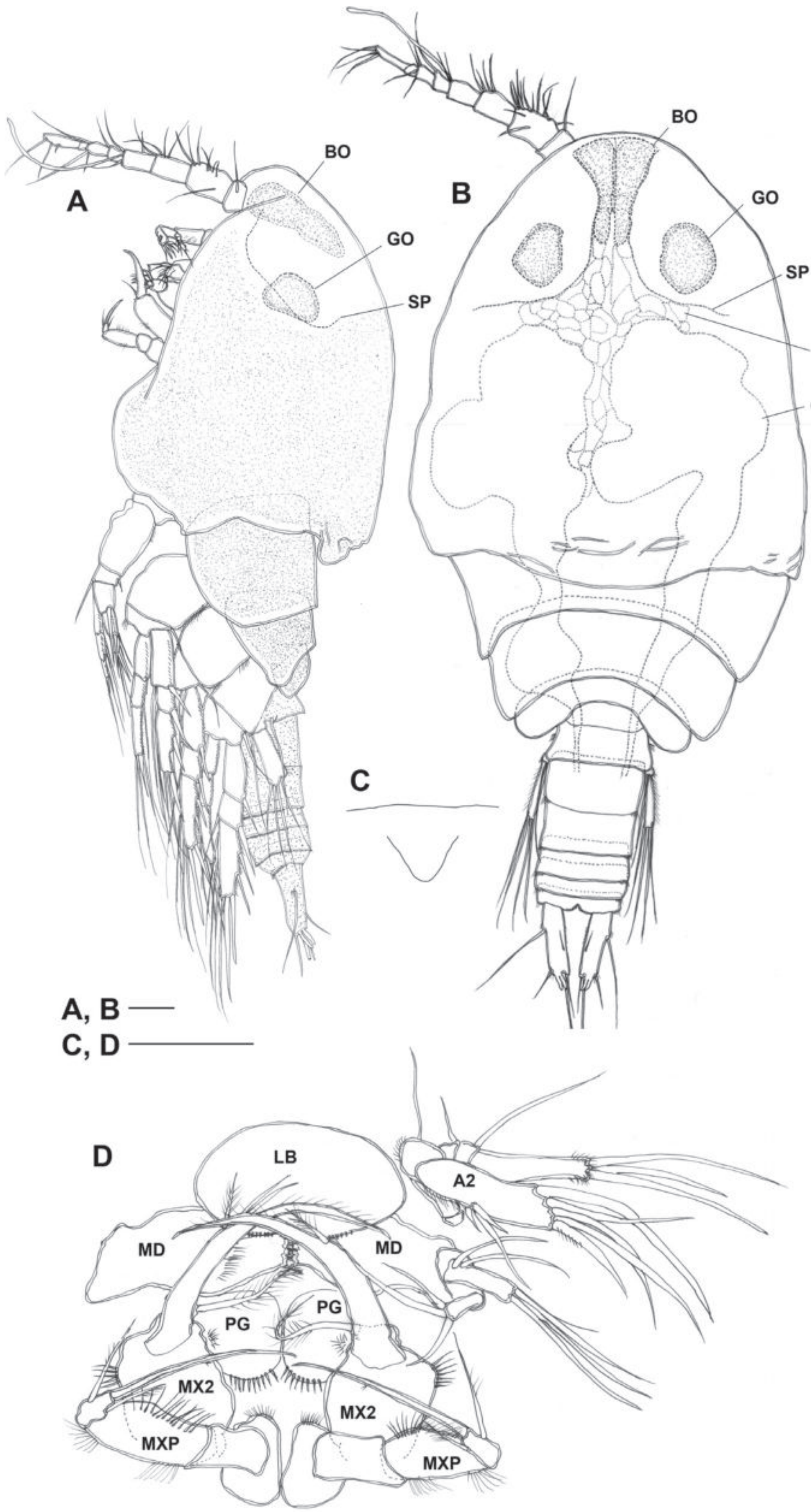

**Figure 2.** *Gyorome guttatum* gen. et sp. nov., adult female, holotype **A** habitus, internal structures omitted **B** habitus, dorsal view, surface ornamentation omitted **C** rostrum, ventral view **D** mouthparts, ventral view, right antenna, right mandibular palp, and both maxillules omitted. Abbreviations: A2, antenna; BO, baculiform ocellus; LB, labrum; LD, lipid droplets; MD, mandible; MX2, maxilla; MXP, maxilliped; OV, ovary; PG, paragnath; GO, globular organ; SP, semi-parabolic plate. Scale bars: 0.1 mm.

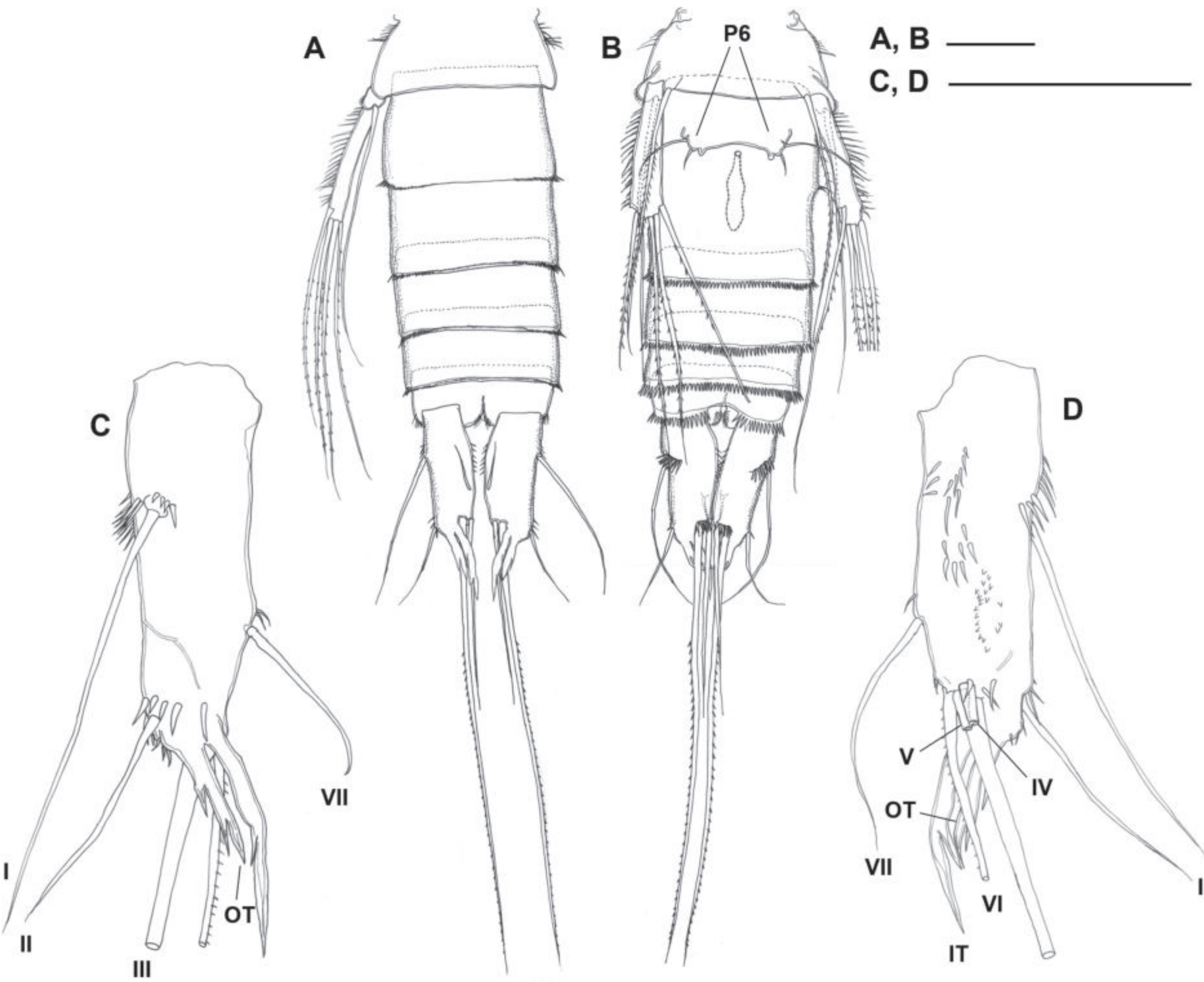

**Figure 3.** *Gyorome guttatum* gen. et sp. nov., adult female, paratype **A, B** urosome, dorsal and ventral views, respectively (surface denticles partly omitted to reveal other structures) **C, D** left caudal ramus, dorsal and ventral views, respectively (surface denticles omitted). Abbreviations: P6, sixth pair of legs; I–VII, caudal ramus setae I–VII; IT, inner branching tube-pore; OT, outer branching tube-pore. Scale bars: 0.1 mm.

***Maxillule*** (Fig. 4D) 3-segmented, comprising praecoxa, endopod, and compound segment representing fused coxa, basis and exopod. Praecoxal arthrite with two naked setae on anterior surface; medial margin with one plumose seta; distal margin with two naked and three pinnate spines (fused at base to arthrite). Compound segment with few spinules along inner margin; coxa represented by subcylindrical endite with two setae; basal endites with three setae; exopod completely incorporated in segment, represented by single seta. Endopod distinct, with two setae.

***Maxilla*** (Fig. 4E) 2-segmented, comprising syncoxa and allobasis. Syncoxa with setules along outer margin; medial margin with proximal protuberance bearing spinular row; coxal endite represented by small process with one plumose apical seta. Allobasis produced into curved claw with fine pinnules along outer margin and short plumose seta just over halfway claw length.

***Maxilliped*** (Fig. 4F) 3-segmented, comprising syncoxa, basis and endopod. Syncoxa small, articulating with subcylindrical pedestal bearing long spinules at outer distal corner; with few spinules along medial margin. Basis elongate,

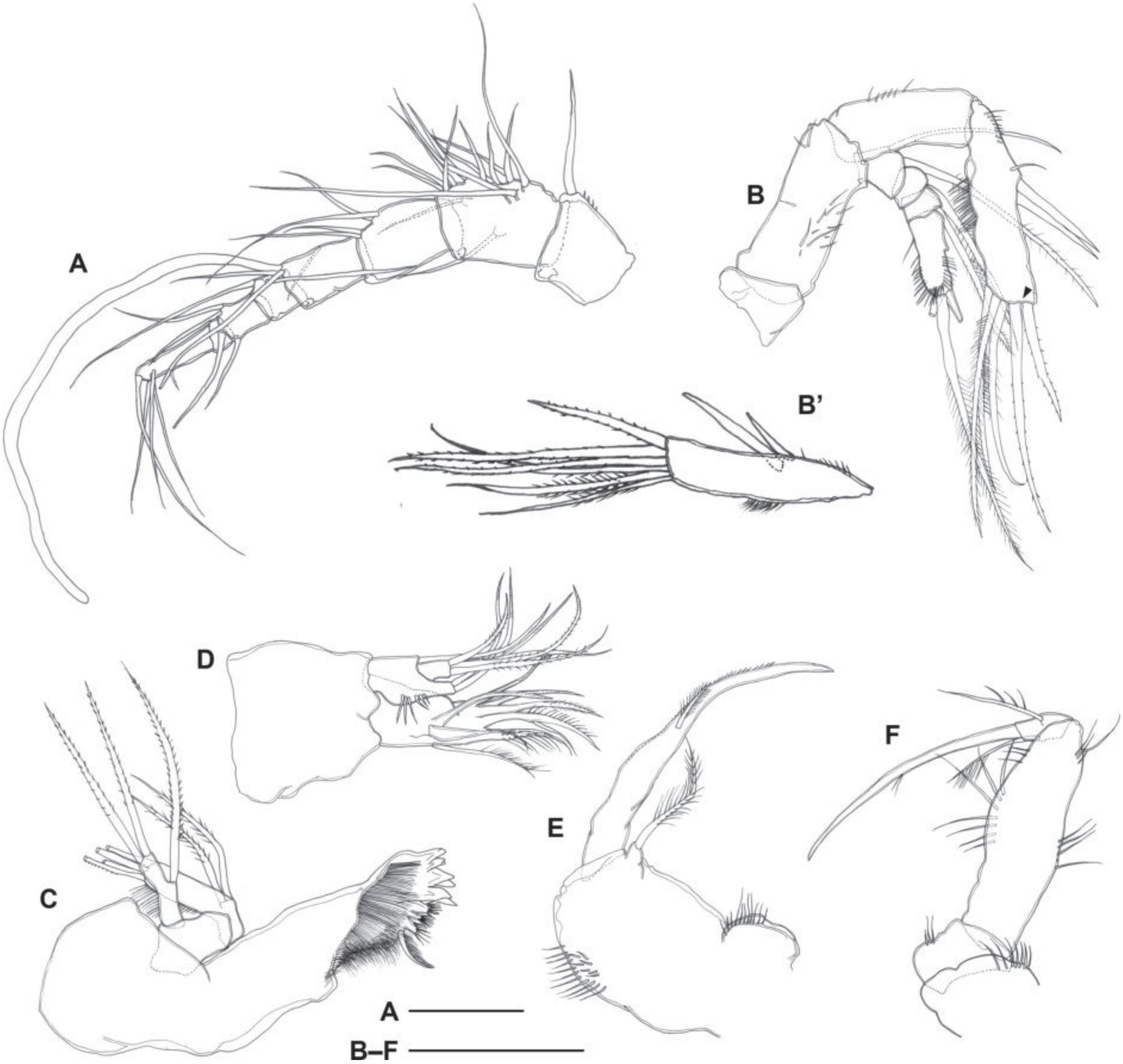

**Figure 4.** *Gyorome guttatum* gen. et sp. nov., adult female, paratype **A** right antennule, ventral view **B** right antenna **C** left mandible **D** right maxillule **E** right maxilla **F** left maxilliped, posterior view. Scale bars: 0.1 mm.

~ 3.5× as long as maximum width; unarmed; medial margin slightly expanded, with sparse long spinules in middle third and shorter spinules further distally; outer margin with two groups of long spinules as figured. Endopod small, subrectangular; outer margin with one unipinnate seta; distal margin with long, slender claw accompanied at base by plumose seta; claw with two closely set spinules halfway the inner margin.

***Legs 1–4*** (Fig. 5A–H) with large coxa, narrow basis and 3-segmented rami; without minute surface denticles. Coxa with several spinule rows along outer margin (particularly P2–P4) as figured. Basis with short spine (leg 1) or long naked seta (legs 2–4) on outer margin; inner lobate expansion with numerous long and/or short setules/spinules. Endopod longer (leg 1) or distinctly shorter (legs 2–4) than exopod.

***Leg 1*** (Fig. 5A, B). Basis with long inner spine, extending to middle of enp-2, bipinnate except for plumose proximal quarter; distal margin with anterior

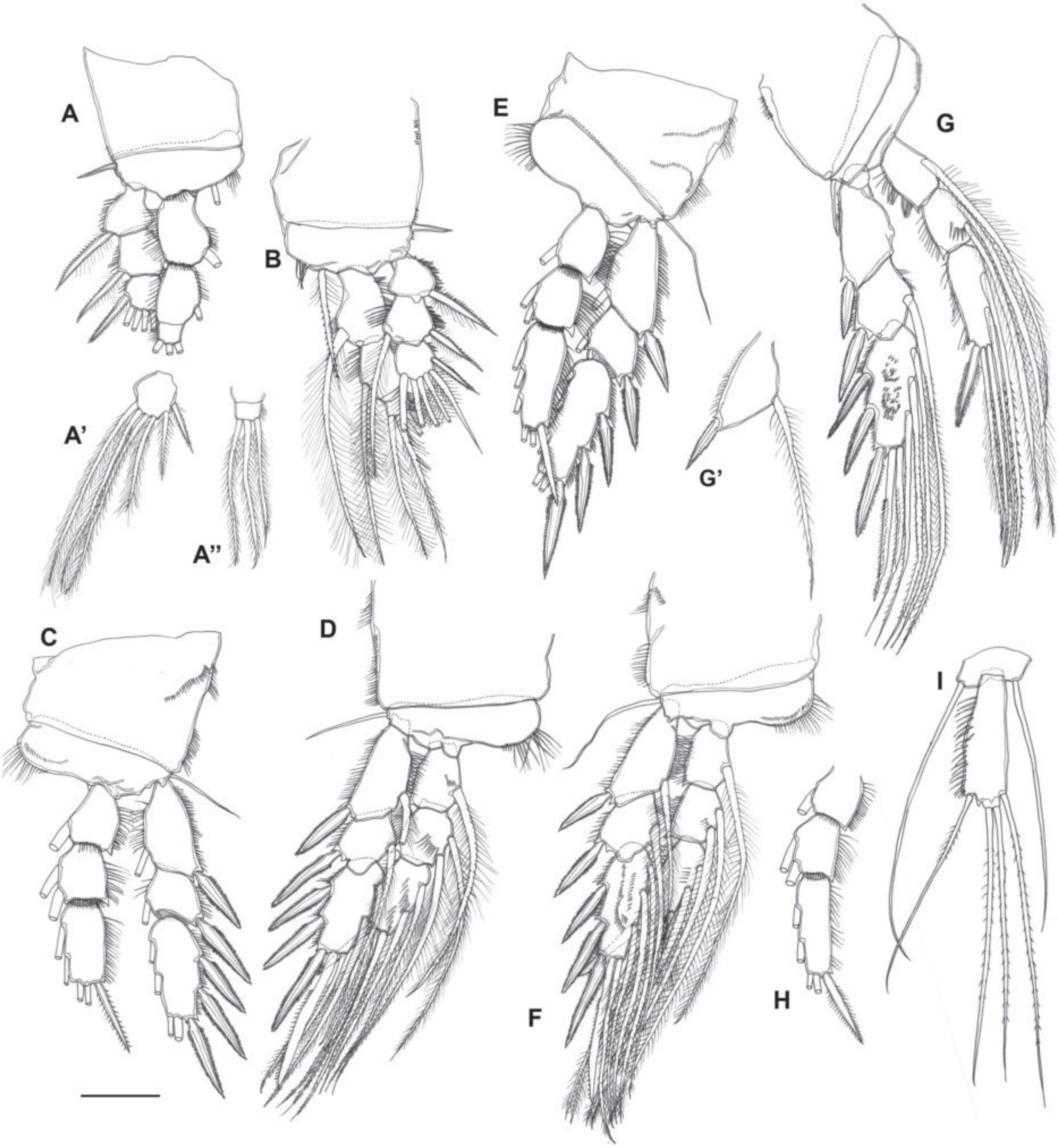

**Figure 5.** *Gyorome guttatum* gen. et sp. nov., adult female, paratype **A, B** right leg 1, anterior and posterior views, respectively **A', A''** distal exopodal (A') and endopodal (A'') segment of left leg 1, posterior view showing setae at full length **C, D** left leg 2 anterior and posterior views, respectively **E, F** left leg 3, anterior and posterior views, respectively **G** left leg 4, posterior view **H** endopod of left leg 4, anterior view **I** right leg 5, anterior view. Scale bar: 0.1 mm.

spinules near articulation with endopod. Exopodal segments with spinules along outer margins; exp-2 not markedly longer than other segments, with setules along inner margin; outer spines without spinular combs. Endopod indistinctly 3-segmented with transverse surface suture marking original segmentation between enp-2 and -3; outer margins of all segments with spinules, additional spinules along inner margins of enp-1 and -2; enp-1 expanded in distal half forming lobate extension along medial margin; enp-3 small.

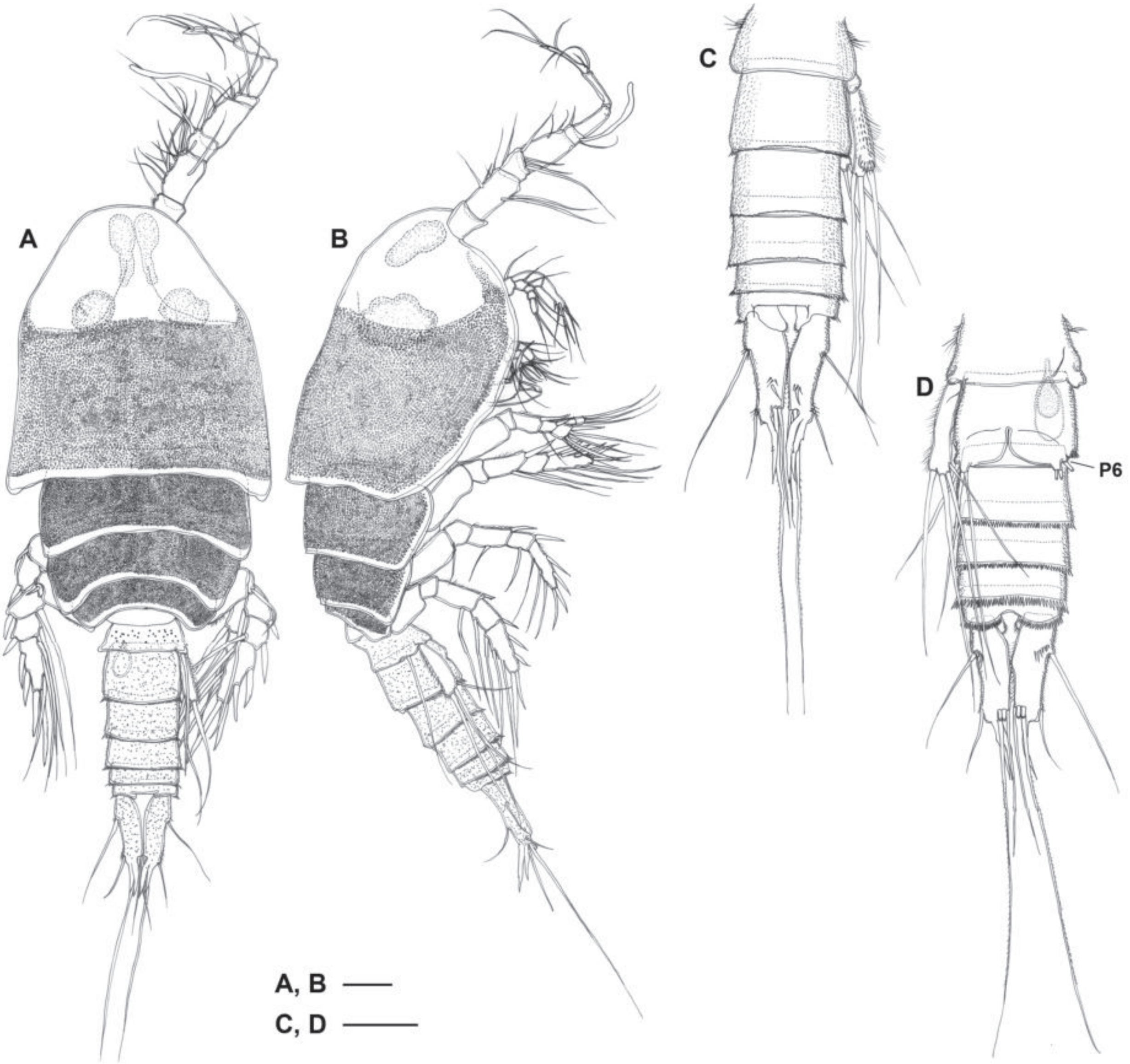

**Figure 6.** *Gyorome guttatum* gen. et sp. nov., adult male, paratype **A, B** habitus, internal structures omitted, dorsal and lateral views, respectively **C, D** urosome, dorsal and ventral views, respectively (surface denticles partly omitted to reveal other structures). Abbreviation: P6, leg 6. Scale bars: 0.1 mm.

***Legs 2–4*** (Fig. 5C–H). Exp-2 markedly shorter than proximal and distal segments. Exopodal spines more robust than in P1. Spinular ornamentation present along outer margins of all exopodal and endopodal segments, and along inner margin of exp-1; few spinules also discernible along inner margin of exp-2. Posterior surface of P3–P4 exp-3, P2 enp-1–3, P3 enp-2 and P4 enp-2–3 with additional spinules. Armature formula as for genus.

***Leg 5*** (Fig. 5I) 2-segmented, comprising baseoendopod and 1-segmented exopod. Baseoendopod apparently fused basally to somite; endopodal lobe obsolete, armature represented by one very long seta (twice length of exopod); outer basal seta very long and naked. Exopod elongate, gradually widening towards distal margin; ~ 2.8× as long as maximum width; with setules along outer margin; armature consisting of one inner, one outer and two terminal setae (all elements sparsely bipinnate); small apical tubercle discernible between outer and outer terminal setae.

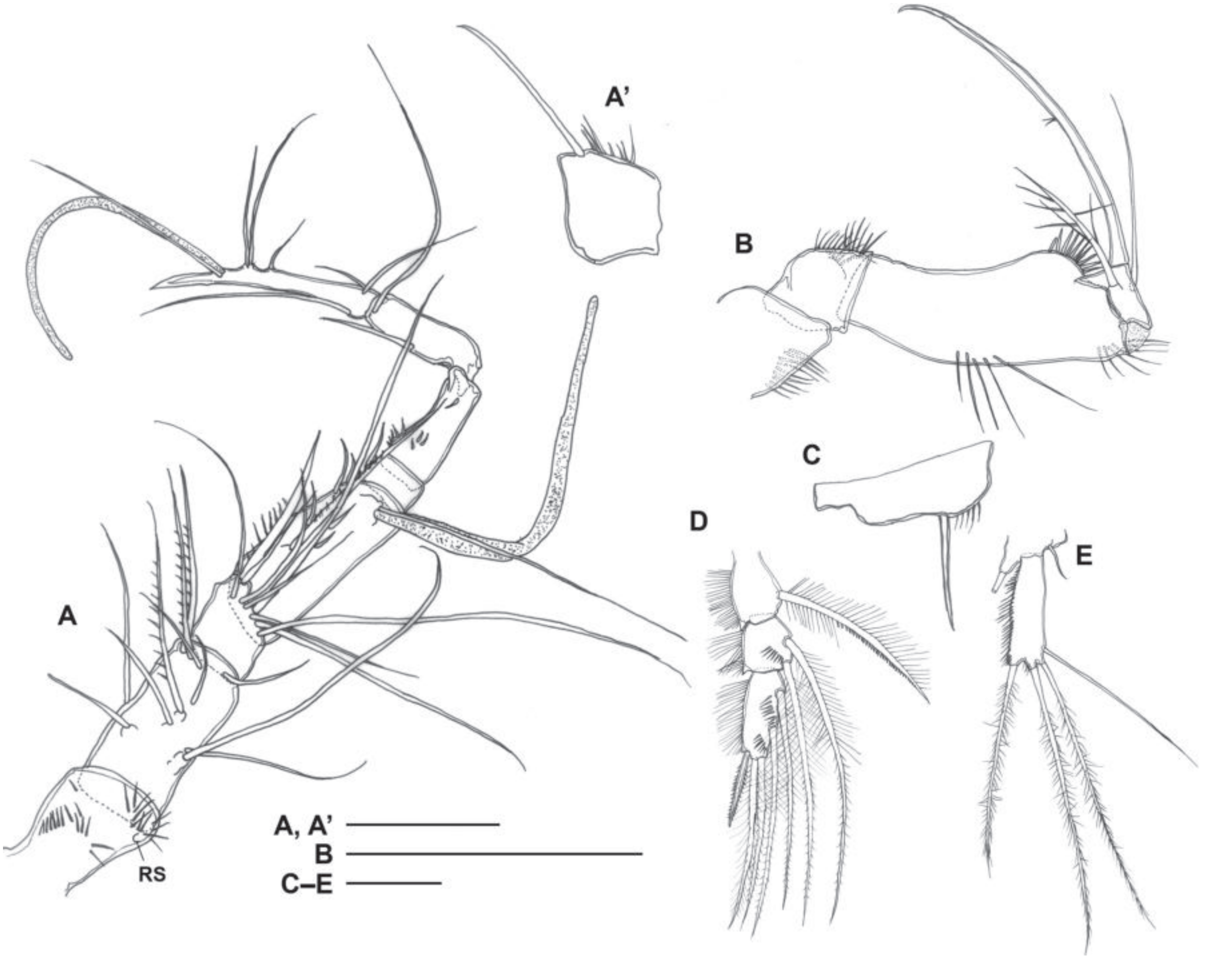

**Figure 7.** *Gyorome guttatum* gen. et sp. nov., adult male, paratype **A** left antennule, ventral view **A'** segment 1 of left antennule showing detached seta **B** right maxilliped, anterior view **C** left basis of leg 1, posterior view **D** endopod of left leg 2, posterior view **E** right leg 5, anterior view. Abbreviation: RS, root of detached seta. Scale bars: 0.1 mm.

***Sixth pair of legs*** (P6 in Fig. 3B) fused medially, forming common plate closing off genital slit; each leg represented by one long outer and one short inner setae. Egg-sac not observed.

**Description of adult male.** Total body length 1.47 mm (*n* = 1). Sexual dimorphism in prosomal ornamentation, antennule, maxilliped, P2 endopod, P5, P6 and urosomal segmentation.

Prosome resembling that of female except for denticles covering dorsal surface of cephalothorax and pedigerous somites much denser and middorsal protrusion around posterior margin of cephalothorax not expressed (Fig. 6A, B). Urosome (Fig. 6C, D) 6-segmented; denticles covering surface sparser than on prosome; spermatophore located in left half of genital somite; caudal ramus similar to that of female.

***Antennule*** (Fig. 7A, A') 8-segmented, ~ 0.4× as long as body length; armature as follows: 1-(1), 2-(11), 3-(9), 4-(6 + ae), 5-(1), 6-(0), 7-(2), 8-(7 + ae); segment 1 with spinular pattern on ventral surface; segment 6 with spinules; geniculation between segments 6 and 7; terminal portion of segment 8 digitiform and slowly curved.

***Maxilliped*** (Fig. 7B) 4-segmented; palmar margin of basis with lobate spinular expansion in distal third; medial margin of endopod produced into triangular unguiform projection.

***Legs 1–4*** similar to female condition except for inner basal spine of leg 1 without setulae or spinules (Fig. 7C) and inner seta of proximal endopodal segment of leg 2 (Fig. 7D) displaying pinnate ornamentation along distal half of outer margin (instead of plumose in female).

***Leg 5*** (Fig. 7E) 2-segmented as in female; endopodal seta much shorter, only ~ one-third the length of exopod; exopod ~ 3.1× as long as maximum width; outer margin with spinules.

***Sixth pair of legs*** (P6 in Fig. 6D) symmetrical, each represented by ovoid plate closing off genital aperture and bearing three naked, well developed setae.

**Etymology.** The specific name is derived from the Latin *guttatum* meaning spotted or speckled and alludes to the dense denticular ornamentation on the male prosome (Fig. 6A, B).

## Key to planktonic Tisbidae

With the addition of *Gyorome*, four genera in the Tisbidae are now known to inhabit the meso- and bathypelagic oceanic zones. Three of these genera are monotypic while two species were assigned to *Volkmannia* (Boxshall 1979). Bradford and Wells (1983) described both sexes of *Tisbe spinulosa* Bradford & Wells, 1983 from a bait trap collected at nearly 600 m below sea level beneath the Ross Ice Shelf in Antarctica. They stated that it belongs among those species of *Tisbe* that display a P1 setation different from the normal type as defined by Volkmann (1979b). Based on aspects of the female antennule, mandible, P1 armature, P5 and genital field the species was regarded as intermediate between *T. finmarchica* (Sars, 1905) and the *T. gracilis*-group. In addition, Bradford and Wells (1983) considered two male characters, the maxilliped and the inner seta of P2 enp-1, that suggested a possible link with the latter group, admitting however that the resemblance in these sexually dimorphic features is not exact. The maxilliped in males of the *T. gracilis*-group displays (a) a lobate spinular expansion along the distal palmar margin of the basis, (b) a terminal endopodal claw which is much shorter than in the female, often slightly sinusoid, and bears a characteristic protuberance ("knee" sensu Volkmann 1979b) along the inner margin, and (c) usually an unguiform projection on the inner margin of the free endopodal segment (this can be absent in some species, e.g., *T. dahmsi* Ivanenko, Ferrari, Defaye, Sarradin & Sarrazin, 2011). The lobate basal expansion and the unguiform endopodal projection are both expressed in the male maxilliped of *T. spinulosa*, however, the endopodal claw is not sexually dimorphic and lacks the proximal protuberance. In all male members of the *T. gracilis*-group the inner seta of the proximal endopodal segment of P2 is transformed into a robust spine, typically displaying a species-specific shape and ornamentation. In *T. spinulosa* this seta is not spiniform but differs from the female condition in its shorter length and more elaborate ornamentation along the proximal outer margin. Although Bradford and Wells (1983) considered including *T. spinulosa* in the *gracilis*-group, they refrained from this course of action due to two characters preventing such an assignment, i.e., the armature pattern on the distal exopodal segment of P1 (3 setae + 3 spines), and the pustulate ornamentation of the body surface. The latter character was viewed as potential supporting evidence for the exclusion of *T. spinulosa* from the genus. Both Gómez et al. (2004) and Ivanenko et al. (2011) cursorily mentioned the species but no new insights emerged from their discussions. Finally, based on the sexual dimorphism of the maxilliped, morphology of P1 and spinular ornamentation of the body, Huys (2021) concluded that *T. spinulosa* must be assigned to *Volkmannia* and formally transferred it to this genus as *V. spinulosa* (Bradford & Wells, 1983). Additional morphological characters in support of its removal from the genus *Tisbe* include the unarmed mandibular basis, the absence of spinular combs on the exopodal spines of P1, the lateral displacement of caudal ramus setae IV–V, and the length:width ratio (> 2.0) of the caudal rami. *Volkmannia spinulosa* is most closely related to *V. forficula* Boxshall, 1979 and can be differentiated by small differences in the caudal rami and P5 of both sexes. The six species of the *Bathyidia*-lineage can be differentiated by the key below:

1 P1 exp-2 elongate, markedly longer than exp-1 and exp-2; P1 endopod prehensile, enp-1 and -2 distinctly elongate (at least 2.5–3× as long as maximum width), enp-1 not expanded in distal half, enp-3 minute with outer spine and two terminal setae; P5 ♀ with three endopodal setae *Volkmannia* ....... **2**

– P1 exopodal segments subequal in size; P1 endopod non-prehensile, enp-1 and -2 less than twice as long as maximum width, enp-1 with medial lobate expansion in distal half, enp-3 moderately developed or fused to enp-2 forming 2-segmented ramus, with three terminal setae; P5 ♀ with one endopodal seta....................................................................................... **4**

2 P1 endopod ~ 1.7× as long as exopod; P5 ♀ exopod 3× as long as maximum width; caudal ramus ~ 1.8× as long as wide.................... ***V. attenuata***

– P1 endopod ~ 1.3–1.4× as long as exopod; P5 ♀ exopod 2.5× as long as maximum width; caudal ramus > 2× as long as wide ................................ **3**

3 Caudal ramus 2.2× as long as wide; P5 ♀ outer endopodal seta minute, ~ 1/5 length of exopod, inner seta shorter than exopod; P5 ♂ with two endopodal setae .................................................................................. ***V. spinulosa***

– Caudal ramus 2.65× as long as wide; P5 ♀ outer endopodal seta ~ 1/2 as long as exopod, inner seta longer than exopod; P5 ♂ with one endopodal seta.......................................................................................... ***V. forficula***

4 Antenna with one seta on exp-1; mandibular endopod with one lateral seta; P1 endopod distinctly 2-segmented ........................ ***Neotisbella gigas***

– Antenna with two setae on exp-1; mandibular endopod with two lateral setae; P1 inner basal spine not sexually dimorphic; P1 endopod distinctly or indistinctly 3-segmented ......................................................................... **5**

5 Cephalosome with paired, frontal, modified eyes; antennary basis unarmed; mandibular endopod with four terminal setae.................................
....................................................... ***Gyorome guttatum* gen. nov. et sp. nov.**

– Cephalosome without frontal modified eyes; antennary basis with abexopodal seta; mandibular endopod with five terminal setae ...... ***Bathyidia remota***

## Discussion

### Taxonomic position of *Gyorome* gen. nov. within the Tisbidae

Within the family Tisbidae, *Gyorome* gen. nov. belongs to a close-knit group of exclusively planktonic deepwater genera, including *Bathyidia*, *Neotisbella* and *Volkmannia* (Table 1). Members of this *Bathyidia*-lineage are generally large (in

**Table 1.** Morphological comparison of pelagic genera in the family Tisbidae.

| | ***Volkmannia*** | ***Bathyidia*** | ***Gyorome* gen. nov.** | ***Neotisbella*** |
|---|---|---|---|---|
| Enlarged modified eyes | absent | absent | present | absent |
| Antennary basis | with seta | with seta | unarmed | unarmed |
| Antennary exopod armature | 2-1-1-3 | 2-1-1-3 | 2-1-1-3 | 1-0-1-3 |
| Mandibular endopod armature | 3 lateral + 6 terminal setae | 2 lateral + 5 terminal setae | 2 lateral + 4 terminal setae | 1 lateral + 4 terminal setae |
| P1 inner basal spine ♂ | as in ♀ | as in ♀ | sexually dimorphic | sexually dimorphic |
| P1 exp-2 | elongate, longer than exp-1 | as long as exp-1 | as long as exp-1 | as long as exp-1 |
| P1 endopod segmentation | 3-segmented | 3-segmented | indistinctly 3-segmented | 2-segmented |
| P1 endopod | prehensile; enp-1 and -2 distinctly elongate (at least 2.5× as long as maximum width), enp-3 minute | non-prehensile; enp-1 and -2 less than twice as long as maximum width, enp-3 moderately developed | non-prehensile; enp-1 and -2 less than twice as long as maximum width, enp-3 moderately developed | non-prehensile; enp-1 and compound enp-2 subequal, ~ 2× as long as maximum width |
| P1 enp-1 shape | not expanded distally | expanded in distal half | expanded in distal half | expanded in distal half |
| P1 distal endopodal segment armature | outer spine + 2 terminal setae (on enp-3) | 3 terminal setae (on enp-3) | 3 terminal setae (on enp-3) | 1 lateral and 3 terminal setae (on enp-2) |
| P5 exopod ♀/♂ armature | 4 long + 1 short setae | 4 long + 1 vestigial setae | 4 long setae | 4 long + 1 short setae |
| P5 endopod ♀ armature | 3 setae | 1 seta | 1 seta | 1 seta |
| P5 endopod ♂ armature | 1–2 setae | 1 seta | 1 seta | 1 seta |
| P6 ♀ armature | 3 well developed setae | 2 minute setae | 1 minute and 1 well developed setae | 2 minute and 1 well developed setae |

excess of 1 mm) and characterized by the following suite of characters: (a) prosome (cephalothorax and pedigerous somites) with pustulate integument (ornamentation consisting of dense pattern of small tubercles and denticles); (b) female antennule short and compact compared to other free-living tisbid genera, 8-segmented; (c) antenna without seta on proximal endopodal segment; (d) mandibular basis without armature; (e) distal palmar margin of male maxilliped produced into lobate spinular expansion and endopod with unguiform projection; (f) P1–P4 with dense pattern of minute spinules on anterior surface of protopod and rami; (g) P1 spines on middle and distal exopodal segments without spinular combs; (h) inner seta of proximal endopodal segment of P2 modified in male, displaying pinnate ornamentation along distal half of outer margin (instead of plumose in female); and (i) caudal ramus with paired multibranched tube-pores along posterior margin, displacing setae IV–V towards inner distal corner. At least (a), (c)–(f), (h) and (i) can be considered as shared derived characteristics supporting the monophyly of the four deep water genera. Character states (b) and (g) will require further assessment across the entire family before their potential status as synapomorphies can be ascertained. Within this clade, *Volkmannia* displays the most primitive armature on the female leg 5 with three setae remaining on the endopod while in the other genera the endopodal armature is reduced to a single seta. Similarly, the male P5 in *V. spinulosa* (but not in *V. forficula*, unknown in *V. attenuata*) exhibits two endopodal setae vs only one seta in the remaining genera. Members of *Volkmannia* also (a) have the most primitive armature pattern on the mandibular endopod, displaying three lateral and six terminal setae (vs at most two lateral and five apical setae in the other genera), (b) display elongation of the middle segment of the P1 exopod (vs all exopodal segments subequal), (c) possess a prehensile P1 endopod with distinctly elongate enp-1 and -2, and a minute apical segment (enp-3) bearing one outer spine and two terminal setae (vs non-prehensile without distinct elongation of segments and three setae on terminal segment), and (d) show three well developed setae on the female sixth legs. *Bathyidia*, *Neotisbella*, and *Gyorome* collectively form the sister group of *Volkmannia* and, in addition to the setal reductions in the mandibular endopod and P5 baseoendopod mentioned above, share the characteristic shape of the proximal segment of P1 endopod. Unlike in other tisbid genera this segment has undergone allometric growth medially, forming a distinct lobate expansion in its distal half from where the inner seta originates.

*Gyorome* appears most closely related to *Neotisbella* based on the unarmed antennary basis (loss of abexopodal seta), further reduction in mandibular armature (endopod with only four terminal setae instead of 5–6), and the virtually identical morphology of the P1 endopod (indistinctly 3-segmented in *Gyorome*, with original segmentation marked by transverse surface suture between enp-2 and -3; genuinely 2-segmented in *Neotisbella*). Both genera also share, to a certain degree, a bilaterally and dorsoventrally expanded prosome, giving it a vaulted appearance. *Neotisbella* differs from *Gyorome* in the reduced armature of the antennary exopod (1-0-1-3 vs the ancestral pattern 2-1-1-3 retained *Gyorome*), the presence of only one lateral seta (vs two) on the mandibular endopod, the sexual dimorphism expressed in the inner basal spine of leg 1 (transformed into a seta in the male), and short caudal ramus setae IV and V. The new genus can readily be differentiated from *Neotisbella* by the presence of paired, frontal, modified eyes, and the reduction in the number of armature elements on the P5 exopod in both sexes.

## Caudal ramus morphology

Huys (1988) proposed a standard terminology for the seven caudal setae displayed by the generalized paramesochrid caudal ramus and stated that it is universally applicable to all harpacticoid families. The system was subsequently adopted by Huys and Boxshall (1991) who extended its application to all copepod orders and posited that the hypothetical copepod ancestor exhibited no more than seven setae on the caudal ramus. It had previously been pointed out that the report by Lang (1948) of eight setae in *Canuella* Scott & Scott, 1893 and *Sunaristes* Hesse, 1867 (Canuellidae now removed from the Harpacticoida) was based on observational errors (Huys 1988). Similarly, Boxshall (1979) reported up to nine elements on the caudal rami of three meso/bathypelagic genera (*Bathyidia*, *Neotisbella*, *Volkmannia*) in the family Tisbidae. The supernumerary elements in these genera originate from the posterior margin of the caudal ramus between setae III and IV and are typically thin-walled and flaccid. Huys and Boxshall (1991: fig. 3.12.1B, C) re-examined *Bathyidia remota* Farran, 1926 and revealed that the additional "setae" were extremely elongate and complex multi-branching tube-pores rather than articulating armature elements (Fig. 8: IT, OT). Examination of the types of *Neotisbella gigas* Boxshall, 1979 (NHMUK reg. nos 1977.266–232), *Volkmannia forficula* (NHMUK reg. nos 1977.233–241), and *V. attenuata* Boxshall, 1979 (NHMUK reg. no. 1977.324) confirmed the presence of similar caudal ramus tube-pores while inspection of material of other tisbid genera failed to reveal such structures. The discovery of these pores in *Gyorome* (Fig. 3A, C, D: IT, OT) points to a common ancestry of the deepwater planktonic genera in the Tisbidae. The function of these tube-

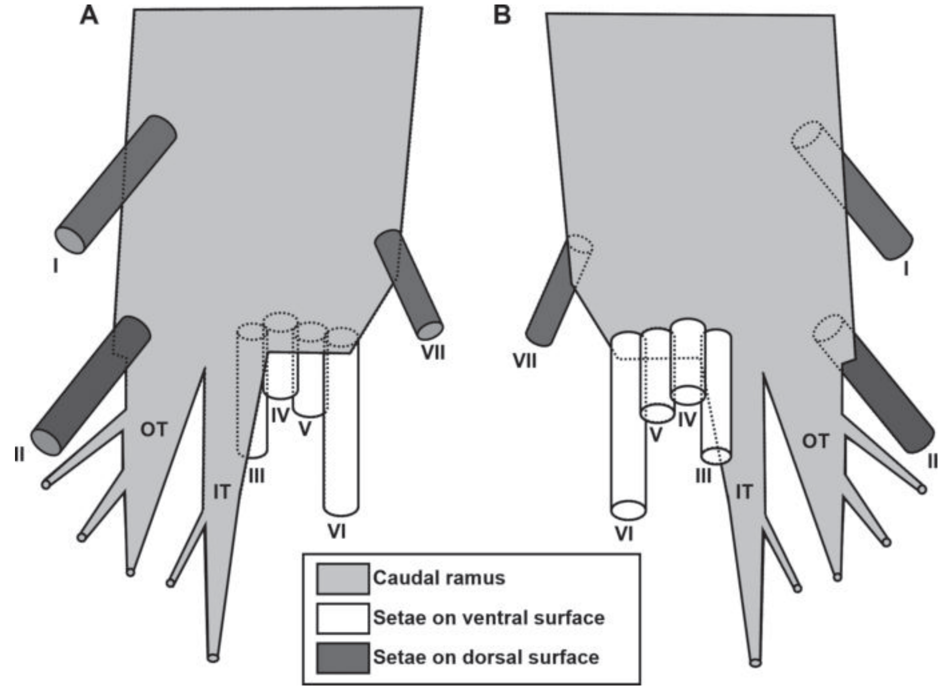

**Figure 8.** Schematic diagram of left caudal ramus of *Gyorome* gen. nov. **A** dorsal view **B** ventral view. I–VII, caudal ramus setae I–VII; IT, inner branching tube-pore; OT, outer branching tube-pore.

pores is as yet unknown but their complex morphology, in conjunction with the significant displacement of setae IV and V towards the inner distal corner of the ramus, is here regarded as a synapomorphy supporting the monophyly of the four pelagic genera in the family. The only exception in this lineage is *Volkmannia spinulosa* (Bradford & Wells, 1983) which apparently lacks such tube-pores, however, the distinct gap between seta III and the laterally displaced setae IV and V suggests that these transparent structures were overlooked in the original description (Bradford and Wells 1983: fig. 7d, h, i).

## Modified naupliar eyes in Harpacticoida

Adult copepods typically have tripartite naupliar eyes consisting of three fused ocellar units (paired dorsolateral ocelli and one unpaired ventral ocellus). Each unit is made up of a retinal photoreceptor sphere, a tapetal layer and a surrounding pigment cup. However, the evolution of different designs from this simple eye generated more novelty and diversity in form than that of the more complex compound eye types found across the rest of the Crustacea (Steck et al. 2023). In several lineages secondary modifications of the ocellar components of the typical naupliar eye have evolved, ranging from complete loss to extreme enlargement, separation of the cups into three independent eyes, and the addition of structures used to focus light onto the retina such as crystalline or cuticular lenses. Extreme eye modification has been histologically documented in at least four orders, including the Calanoida (e.g., Pontellidae, *Cephalophanes*), Cyclopoida (e.g., Corycaeidae, Sapphirinidae), Siphonostomatoida (Caligidae) and Harpacticoida (e.g., Elofsson 1966; Huys and Böttger-Schnack 1994; Land 1984, 1988; Nishida et al. 2002; Vaissière 1961). While most species in the latter order are thought to have typical naupliar eyes or have secondarily lost them, there are a few notable exceptions. Within the Harpacticoida elaborate eyes are only found in members of the planktonic subfamily Miraciinae (Miraciidae) with three of its four monotypic genera (*Miracia* Dana, 1846; *Oculosetella* Dahl, 1895; *Distioculus* Huys & Böttger-Schnack, 1994) displaying eyes of the telescopic type with double lenses oriented in the same light path with one distal to the other. The paired ocelli of the large anteriorly directed naupliar eyes each have an exterior lens of unknown origin, with both lenses being linearly arranged along the frontal margin of the cephalic shield, as well as a second lens directly in front of the retina (Claus 1891; Elofsson 1966; Huys and Böttger-Schnack 1994). Unlike the Corycaeidae and Sapphirinidae which also exhibit telescopic eyes, the dorsolateral ocelli have not undergone lateral displacement in the three miraciinid genera and the basic tripartite structure of the naupliar eye is retained. Phylogenetic analysis suggests that the frontal lenses were secondarily lost in the fourth genus, *Macrostella* A. Scott, 1909, possibly because of its intimate association with filamentous cyanobacteria (Huys and Böttger-Schnack 1994).

Some members of the genus *Paradactylopodia* Lang, 1944 (Dactylopusiidae) display lens-like structures on the frontal part of the cephalothorax. In *P. spinipes* (Brady, 1910) and *P. oculata* (Gurney, 1927) paired subintegumental lenses are positioned near the bases of the antennules (Brady 1910; Gurney 1927) and discernible in both dorsal and lateral aspects. In *P. trioculata* Hicks, 1988a the frontal portion of the cephalothorax displays lens-like structures set in a triangle with the anteriormost located at the base of the rostrum (note that it is conceivable that the latter was overlooked in *P. spinipes* and *P. oculata*). According to Hicks (1988a) the structures in *P. trioculata* are not merely sacs containing deposits of oil but genuine corneal lenses with high refractive properties. Two species in the speciose family Laophontidae, *Heterolaophonte oculata* (Gurney, 1927) and *Laophonte pseudoculata* Krishnaswamy, 1959, also display paired refringent lens-like structures, but nothing is known about their visual function. Interestingly, both *P. trioculata* and *L. pseudoculata* were collected from wood infested with shipworms, the former from a waterlogged teredinid bored log at 51 m depth, the latter from floating logs.

The photoreceptors displayed in *Gyorome guttatum* are of a level of complexity not previously observed in the Tisbidae. The majority of free-living tisbids display simple tripartite naupliar eyes such as in members of the genera *Drescheriella* (Dahms and Bergmans 1988), *Paraidya* (Humes and Ho 1969), *Sacodiscus* (Sars 1904, 1905), *Scutellidium* (Branch 1974; Itô 1976), *Tisbe* (Bergmans 1979; Bocquet 1951; Vaissière 1961; Volkmann 1979b; Chullasorn et al. 2009), *Tisbella* (Volkmann 1979a), and *Tisbintra* (Ummerkutty 1961). No photoreceptors have been reported in the deepwater genera *Bathyidia*, *Neotisbella*, and *Volkmannia* (Boxshall 1979), however, it remains unclear whether this absence is genuine, or the coloration had already disappeared in the preserved material. The paired enlarged modified eyes in *G. guttatum* essentially each consist of three major components, i.e., (a) a baculiform ocellus (Fig. 2A, B: BO), (b) a semi-parabolic plate (Fig. 2A, B: SP) and (c) a globular organ (Fig. 2A, B: GO). The position and close connection between the large rod-shaped ocelli (Fig. 2A, B: BO) suggest that they are homologous with the paired dorsolateral ocelli expressed in the basic tripartite naupliar eye of most copepods. The unpaired ventral ocellus was not observed in the present study and is probably very reduced or absent.

The semi-parabolic plates bear a superficial resemblance to the semi-parabolic reflective mirrors that replace the tapetal and pigment cells in the paired eyes in members of the calanoid genus *Cephalophanes* Sars, 1907 (Phaennidae) (Nishida et al. 2002) and ostracods belonging to the genus *Gigantocypris* Müller, 1895 (Cypridinidae) (Land 1978, 1984; Nilson 1997). However, the reflectors in these taxa are distinctly colored and have a multilayer structure made up of stacks of thin platelets of putative chitinous material while in *G. guttatum* the semi-parabolic plates are thin and colorless, casting doubt on their reflective potential. Based on muscle anatomy, Nishida et al. (2002) suggested that *Cephalophanes* species can control reflector direction, making their eyes one of the most effective broadband light detectors in the invertebrates; no such musculature was observed in association with the semi-parabolic plates of *G. guttatum*. It is postulated here that these plates merely serve as partitions, separating the spaces occupied by the ocelli and globular organs from the lipid droplets (LD in Fig. 2B), ovary (OV in Fig. 2B) and other organs. This space delimitation and compartmentalization, in conjunction with the apparent absence of dense surface ornamentation in the anterior portion of the cephalothorax, conceivably reduces or minimizes potential interference with the amount of incident light reaching the retinal cells in the ocellar region. With only two receptor cells in each reflector focal area, it is unlikely that the eyes of *Cephalophanes refulgens* Sars, 1907 have any image-resolving power; however, the presence of parabolic mirrors that direct light back to the retinal cells from all frontal angles optimizes their light-gathering efficiency in deep-sea habitats. It has been suggested that these large eyes are likely to aid in foraging in low light conditions and gut contents analysis of *Cephalophanes* spp. revealed that these detritivores feed primarily on the shower of carcasses (“Leichenregen”) falling from the upper layers of the water column (Nishida et al. 2002; Steuer 1928). The visual detection of these carcasses is potentially facilitated by luminous bacteria that are commonly found associated with them and as such act as biomarkers of detrital food (Ohtsuka et al. 2019). It is unlikely that the presence of enlarged ocelli in *G. guttatum*, which coincidentally occurs in the same habitat as *Cephalophanes* spp., is related to either mate recognition or predator avoidance. Although no information exists on its overall photosensitivity and light-mediated behaviors, we speculate that food detection in *G. guttatum* is also directly mediated by vision. The development of specialized eyes in this species can be interpreted as the product of convergent evolution that, as in *Cephalophanes*, may provide a means for detecting bioluminescent food particles in oligotrophic mesopelagic environments.

The paired globular organs in *G. guttatum* (Fig. 2A, B: GO) are reminiscent of the paired “accessory photoreceptors” observed in some species of *Calanus* Leach, 1816 (Frost 1974). These receptors, collectively called Gicklhorn’s organ, are supplied by a pair of nerves arising laterally from the central nervous system, independent of the optic nerves. Although their innervation was not investigated, the location of the globular organs in *G. guttatum* suggests that they are homologous with the paired Gicklhorn’s organ documented in various calanoids, cyclopoids and harpacticoids (Dudley 1972; Elofsson 1966, 1970, 1971; Frost 1974; Gicklhorn 1930). The organ has variously been interpreted as a non-visual light-sensing structure, an internal chemosensor or a structure involved in controlling the release of neurosecretory products (Elofsson 1966, 1970, 1971) while recent studies using antibody neural tracing suggested that the paired receptors of the Gicklhorn's organ may be homologous to the arthropod compound eye (Frase and Richter 2020). Pending the arrival of convincing behavioral or physiological evidence, the function and evolutionary origin of this organ remain enigmatic as ever (Steck et al. 2023).

## Colonization of the open pelagic

Within the Tisbidae only members of the four genera of the *Bathyidia*-lineage are strictly holoplanktonic and oceanic. They inhabit the mesopelagic and bathypelagic zones but are only rarely encountered in plankton samples. *Bathyidia remota* is typically bathypelagic and has only been found on three occasions in the North Atlantic Ocean since its original description nearly one century ago. Farran (1926) discovered the female holotype in the Bay of Biscay in a plankton haul taken between 1,370 and 1,830 m depth. Deevey and Brooks (1977) subsequently recorded the male at 1,000–1,500 m in the Sargasso Sea while Boxshall (1979) reported both sexes off the Cape Verde Islands at 1,000–1,250 m depth. The species is further only known from a single outlier in the Arabian Sea where Böttger-Schnack (1996) recorded it at 1,050–1,850 m together with a second, as yet undescribed, species of *Bathyidia*. *Neotisbella gigas* has not been recorded again since its original description from mesopelagic depths (300–900 m) in the northeastern Atlantic (Boxshall 1979). The exact depth at which *Gyorome guttatum* was collected is unknown (0–935 m) but it appears that it assumes a mesopelagic depth distribution. Members of the genus *Volkmannia* are found at both mesopelagic and bathypelagic depths. The type species, *V. forficula*, is known from a single plankton haul taken between 410 and 890 m depth off the Cape Verde Islands (Boxshall 1979). *Volkmannia attenuata* is a typical bathypelagic species with records from the northeastern Atlantic (3,760–3,920 m) (Boxshall 1979) and the Clarion-Clipperton Zone in the Eastern Pacific (4,123 m) (Khodami et al. 2017). Finally, *V. spinulosa* was obtained from a bait bottle containing seal and fish meat which had been deployed near the sea floor beneath the Ross Ice Shelf (Antarctica) where the sea floor is 597 m below sea level and the water column 237 m thick (Bradford and Wells 1983). Gut contents analysis revealed that *V. spinulosa* had been feeding on the bait but it remains unknown whether this necrophagous (scavenging) habit is the only feeding strategy of the species, or indeed can be extrapolated to other members of the *Bathyidia*-lineage. Some species of the family Tisbidae are known to be omnivores and opportunistic feeders (Hicks and Coull 1983) and scavenging behaviour has previously been observed in *Tisbe furcata* (Baird, 1837) (Garstang 1900) and other members of the genus (Lee 2004; Lee and Morton 2004). Although the feeding strategy of *Gyorome guttatum* is not revealed, its large, vaulted prosome suggests an opportunistic macrophage that has adopted gorging. The flexible integument and posterodorsal extension of the prosome (in females only) presumable allows for considerable lateral and dorsal distension of the midgut in the similar way to the misophrioid one reported by Boxshall and Roe (1980).

Occasionally, other tisbid species have been recorded from the plankton in the neritic zone, but in most cases, these are temporarily displaced littoral forms (Wells 1970). Similarly, some littoral Tisbidae are known to disperse by clinging to marine algae (e.g., *Sargassum*) drifting in the open ocean currents but such species are not permanent members of the plankton and should be regarded as expatriated forms (Yeatman 1962). In seagrass beds, some tisbids as well as many other phytal harpacticoids demonstrate active emergence, particularly during nighttime, and their entry into the column appears to be linked to precopulatory mate behavior, as evidenced by the predominance of adult males and copepodid V females (Bell et al. 1988; Hicks 1988b; Walters and Bell 1986).

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

S.K. performed the microscopic observations. S.O. provided copepod samples. R.H. and S.K. wrote the manuscript with additional input and review from S.O.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# Six new species of *Margattea* Shelford, 1911 (Blaberoidea, Pseudophyllodromiidae, Neoblattellini) from China

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## Abstract

Six *Margattea* species are established and described: three are cryptic species, namely, *M. parabisignata* Li & Che, **sp. nov.**, *M. semicircularis* Li & Che, **sp. nov.**, and *M. forcipata* Li & Che, **sp. nov.** They are distinguished from known species *M. bisignata*, *M. spinifera*, and *M. paratransversa* by their male genitalia with the aid of molecular species delimitation method (ABGD) using *COI* as the molecular marker. The other three new species are *M. pedata* Li & Che, **sp. nov.**, *M. undulata* Li & Che, **sp. nov.**, and *M. bisphaerica* Li & Che, **sp. nov.** Morphological and genitalia photographs of these new species of *Margattea*, as well as a key to the species of *Margattea* from China, are provided.

**Key words:** ABGD, DNA barcoding, *Margattea*, new species

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## Introduction

A total of 63 species of the genus *Margattea* in Neoblattellini have been recorded in Asia, Africa, and parts of Oceania (Beccaloni 2014), and 26 of them are known from China (He et al. 2021). There are twelve genera in Neoblattellini. *Margattea* is the only genus that is not distributed in the New World, while all the other eleven genera are only present in the New World. *Margattea* is morphologically similar to the genus *Balta* in the yellowish brown body, the subelliptical pronotum (sometimes with spots), and wings that usually exceed the end of the abdomen (He et al. 2021). Despite being a relatively well-diversified genus, only four molecular phylogenetic analyses sampled *Margattea* species (Evangelista et al. 2021, 2023; Liu et al. 2023; Wang et al. 2023). Due to the different molecular data and sampling taxa in molecular analyses listed above, the sister group of *Margattea* was inconsistently recovered, but *Balta* was always found phylogenetically distant from *Margattea*.

At present, members of *Margattea* are identified by the simple, cylindrical, and symmetrical styli, the usually specialized eighth abdominal tergum, the pronotal disc with symmetrical stripes and maculae, and the median phallomere usually with accessory structure (Roth 1989; Wang et al. 2009; Liu and Zhou 2011; He et al. 2021). However, these diagnostic characteristics can be found separately in other genera; moreover, the styli of *Margattea* are diverse:

asymmetrical in *Margattea pseudolimbata* Wang, Li, Wang & Che, 2014 (Wang et al. 2014), symmetrical and foot-shaped styli or asymmetrical and spherical styli in other samples we examined. Therefore, it is still necessary to further determine the diagnostic characteristics of *Margattea*.

DNA barcoding (Hebert et al. 2003) has been widely used in the identification of cockroach species (Knebelsberger and Miller 2007; Evangelista et al. 2013; Wang et al. 2021), the estimation of cockroach species richness (Evangelista et al. 2014), the matching of individuals with sexual dimorphism (Yang et al. 2019; Deng et al. 2020; Han et al. 2022; Luo et al. 2023) and the discovery of cryptic species (Bai et al. 2018; Zhu et al. 2022). In this study, we combine molecular species delimitation methods with morphological characteristics, including male genitalia, to determine species found in China. In addition, the generic diagnosis of *Margattea*, mainly concerning the styli, left and median phallomere, is redefined after the examination of most *Margattea* species on the basis of the specimen or the original description (but not for *M. beauvoisii* (Walker, 1868), *M. baluensis* (Hanitsch, 1933), *M. bipunctata* (Hanitsch, 1933), *M. buitenzorgensis* Caudell, 1927, *M. centralis* (Gerstaecker, 1883), *M. crucifera* (Hanitsch, 1925), *M. diacantha* (Hebard, 1929), *M. gulliveri* Hanitsch, 1928, *M. importata* Bey-Bienko, 1964, *M. microptera* (Hanitsch, 1925), *M. nana* (Saussure, 1869), *M. nebulosa* (Shelford, 1907), *M. obtusifroms* (Walker, 1868), *M. philippinensis* (Roth, 1990), *M. remota* (Hebard, 1933), *M. sinclairi* Hanitsch, 1928, and *M. variegata* (Brunner von Wattenwyl, 1898)).

## Materials and methods

### Morphological study

All type specimens are deposited in College of Plant Protection, Southwest University, Chongqing, China (**SWU**). Male genital segments were immersed in 10% NaOH solution and incubated with water at 90 °C for 15 minutes to dissolve the fat. All segments were dissected and stored in glycerol for observation, and preserved along with the remainder of the specimen which is stored in ethyl alcohol. All photos were taken by a Leica DFC digital microscope camera attached to a Leica M205A stereomicroscope, then modified with Adobe Photoshop CC 2019. Specimens examined were measured by Vernier Caliper. Morphological terminology mainly follows Roth (2003). The sclerites of male genitalia mainly follows McKittrick (1964). The terminology of veins follows Li et al. (2018). Abbreviations of veins are as follows:

| | |
|---|---|
| **ScP** | subcosta posterior; |
| **R** | radius; |
| **RA** | radius anterior; |
| **RP** | radius posterior; |
| **Pcu** | postcubitus; |
| **M** | media; |
| **CuA** | cubitus anterior; |
| **CuP** | cubitus posterior; |
| **V** | vannal. |

### DNA extraction, amplification, and sequencing

Total DNA was obtained from legs and thoracic muscle using the Hipure Tissue DNA Mini Kit, and the remainder of the specimen was stored in ethyl alcohol. The primers were used to amplify the 658 bp cytochrome c oxidase subunit I (*COI*) fragment (Table 1). The amplification conditions were: initial denaturation at 98 °C for 2 min, followed by 35 cycles for 10 sec at 98 °C, 10 s at 49–51 °C, and 3 min for 72 °C, with final extension of 3 min at 72 °C, then held at 4 °C. The amplified samples showing bands in agarose gels were sequenced by Beijing Tsingke Biotech Co., Ltd.

### Sequence processing and molecular analysis

A total of 105 *COI* sequences were analyzed, of which 53 sequences are obtained in this study and 52 sequences were downloaded from GenBank (*Balta vilis*, *Sorineuchora nigra*, and *Mantis religiosa* were selected as outgroups) (Table 2). All sequences were aligned by MEGA 7 (Kumar et al. 2016) and adjusted after translation into amino acid sequences. The genetic divergence value was quantified based on Kimura 2-parameter (K2P) (Kimura 1980) by MEGA 7. The Maximum Likelihood (ML) tree was constructed in PhyloSuite v. 1.2.2 (Zhang et al. 2020), using IQ-TREE v. 1.6.8 (Nguyen et al. 2015) with 1,000 ultrafast bootstrap replicates (Hoang et al. 2018). The GTR+G4+F model was selected by ModelFinder 2 (Kalyaanamoorthy et al. 2017) according to the corrected Akaike Information Criterion (AICc).

We used a molecular species delimitation method (ABGD: Puillandre et al. 2012) to delimit *Margattea* species based on *COI* sequences. ABGD, compared to GMYC and bPTP, provides more conservative estimates, which did not overestimate the number of entities (Puillandre et al. 2012; He et al. 2021). For ABGD, the analysis result was displayed on a web interface (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html). The default parameters were used except for the relative gap width set at 1.0 and using the Jukes-Cantor (JC69) distance.

## Results

### Morphological species delimitation based on external morphology

Combining the external morphological character, we identified 22 morphospecies of *Margattea* from a large number of samples collected, including three new species, *M. pedata* Li & Che, sp. nov., *M. undulata* Li & Che, sp. nov., and *M. bisphaerica* Li & Che, sp. nov. (Fig. 1A).

**Table 1.** Primers used in the molecular study.

| Primers | Base sequence | | Reference |
|---|---|---|---|
| | F | R | |
| *COI*-F6/R6 | 5’-CAACYAATCATAAAGANATTGGAAC-3’ | 5’-TAAACTTCAGGGTGACCAAARAATCA-3’ | Yang et al. 2019 |
| *COI*-F5/R5 | 5’-GGTCAACAAATCATAAGATATTGG-3’ | 5’-TAAACTTCAGGGTGACCAAAAAATCA-3’ | Folmer et al. 1994 |

**Table 2.** Samples used in the molecular study.

| Species | Voucher number | Accession number | Location |
|---|---|---|---|
| **Ingroups** | | | |
| *M. angusta* | | MW970280 | |
| | | KY349624 | |
| *M. bicruris* | EX_1 | PP135569 | Mengla, Xishuangbanna, Yunnan |
| | EX_2 | PP135570 | |
| | | MW970303 | |
| *M. bisignata* | SY_1 | PP135579 | Dabie Mountain, Huanggang, Hubei |
| | SY_3 | PP135580 | Tangkou, Huangshan, Anhui |
| | SY_4 | PP135581 | Jinyun Mountain, Beibei, Chongqing |
| | SY_5 | PP135582 | Huangtangxi, Quanzhou, Fujian |
| | SY_6 | PP135583 | Yinshan Park, Jinxiu, Guangxi |
| | SY_7 | PP135584 | Mangshan Forest Park, Hunan |
| | SY_8 | PP135585 | Liupan, Jinhua, Zhejiang |
| | SY_9 | PP135586 | Huanglong Mountain, Lushan, Jiangxi |
| | SY_10 | PP135587 | Fanjing Mountain, Tongren, Guizhou |
| | SY_11 (F) | PP135588 | E'mei Mountain, Leshan, Sichuan |
| | | MW970310 | |
| | | MW970317 | |
| | | MW970315 | |
| | | KY349596 | |
| | | KY349607 | |
| | | KY349603 | |
| | | KY349604 | |
| *M. bisphaerica* sp. nov. | SP1 | PP135563 | Shengtang Mountain, Jinxiu, Guangxi |
| | Q5_34 (F) | PP135562 | |
| *M. caudata* | WB_3 | PP135610 | Meizi Lake, Pu'er, Yunnan |
| | | MW970283 | |
| | | MW970284 | |
| *M. concava* | AY_1 | PP135572 | Diaoluo Mountain, Lingshui, Hainan |
| | AY_3 (F) | PP135574 | |
| | AY_4 | PP135575 | |
| | AY_2 | PP135573 | Menglun, Xishuangbanna, Yunnan |
| | AY_5 | PP135576 | Maogan, Baoting, Hainan |
| | | KY349650 | |
| | | MW970253 | |
| | | KY349647 | |
| | | MW970254 | |
| | | MW970252 | |
| *M. cuspidata* | | MW970300 | |
| | | MW970301 | |
| *M. deltodonta* | ZT_3 | PP135609 | Dawei Mountain, Pingbian, Yunnan |
| | | MW970294 | |
| *M. deltodonta* | ZT_3 | MW970295 | Dawei Mountain, Pingbian, Yunnan |
| *M. disparilis* | | MW970290 | |
| | | MW970291 | |
| | | MW970292 | |
| *M. forcipata* sp. nov. | HD_3 | PP135604 | Golden Gully, Zhaoqing, Guangdong |
| | SHD_1 | PP135605 | |
| | SP8 (F) | PP135606 | |
| *M. limbata* | | MW970281 | |
| | M2 (F) | PP135607 | Dushan, Qiannan, Guizhou |
| *M. mckittrickae* | MS_3 | PP135612 | Diaoluo Mountain, Lingshui, Hainan |

| Species | Voucher number | Accession number | Location |
|---|---|---|---|
| *M. multipunctata* | DB_1 (F) | PP135566 | Menglun, Xishuangbanna, Yunnan |
| | DB_2 (F) | PP135567 | |
| | DB_3 | PP135568 | |
| | | KY349646 | |
| | | MW970269 | |
| *M. nimbata* | | KY349658 | |
| | | MW970261 | |
| | | MW970259 | |
| | | KY349653 | |
| *M. parabisignata* sp. nov. | SY_2 | PP135600 | Limu Mountain, Qiongzhong, Hainan |
| | SP4 | PP135598 | |
| | SP5 (F) | PP135599 | |
| *M. paratransversa* | | MW970262 | |
| | | MW970263 | |
| *M. pedata* sp. nov. | NZ_3 (F) | PP135564 | Nabang, Yinjiang, Yunnan |
| | NZ_4 (F) | PP135565 | |
| *M. perspicillaris* | M7 | PP135578 | Yinggeling, Baisha, Hainan |
| | H_2 | PP135577 | |
| *M. semicircularis* sp. nov. | CY_7 | PP135595 | Baishaogou, Zunyi, Guizhou |
| | SP9 | PP135596 | |
| | SP10 (N) | PP135597 | |
| *M. speciosa* | HL_3 | PP135571 | Libo, Qiannan, Guizhou |
| | | KY349620 | |
| | | KY349618 | |
| | | MW970279 | |
| *M. spinifera* | CY_1 | PP135589 | Diaoluo Mountain, Lingshui, Hainan |
| | CY_2 | PP135590 | |
| | CY_3 | PP135591 | Wuyi Mountain, Wuyishan, Fujian |
| | CY_4 | PP135592 | Dayao Mountain, Jinxiu, Guangxi |
| | CY_6 | PP135593 | Menglun, Xishuangbanna, Yunnan |
| | M1 (F) | PP135594 | Maolan National Forest Park, Guizhou |
| | | KY349628 | |
| | | MW970274 | |
| | | KY349636 | |
| *M. spinifera* | M1 (F) | KY349639 | Maolan National Forest Park, Guizhou |
| | | MW970278 | |
| *M. spinosa* | DC_1 (F) | PP135611 | Wuzhi Mountain, Wuzhishan, Hainan |
| | | MW970299 | |
| | | KY349617 | |
| | | KY349613 | |
| | | KY349615 | |
| | | KY349610 | |
| *M. transversa* | | MW970264 | |
| | | MW970265 | |
| | | KY349659 | |
| *M. trispinosa* | SC_3 (F) | PP135614 | Butterfly Valley, Honghe, Yunnan |
| | M4 | PP135613 | |
| *M. undulata* sp. nov. | SP_2 | PP135602 | Jinyun Mountain, Beibei, Chongqing |
| | Q1_29 | PP135601 | |
| | SP6 (F) | PP135603 | |
| **Outgroups** | | | |
| *Balta vilis* | | KT279743 | |
| *Mantis religiosa* | | KM29415 | |
| *Sorineuchora nigra* | | MF612149 | |

Abbreviations: female (F); nymph (N).

## Molecular phylogeny and species delimitation based on COI

In this study, we acquired 105 *COI* sequences of *Margattea* representing 22 morphospecies of *Margattea*. The ML phylogenetic tree showed that samples (including males, females, and nymphs) of the same morphospecies form monophyletic groups, although most of the nodes did not have high bootstrap values (Fig. 1). 24 molecular operational taxonomic units (MOTUs) were delimited by ABGD (Fig. 1B).

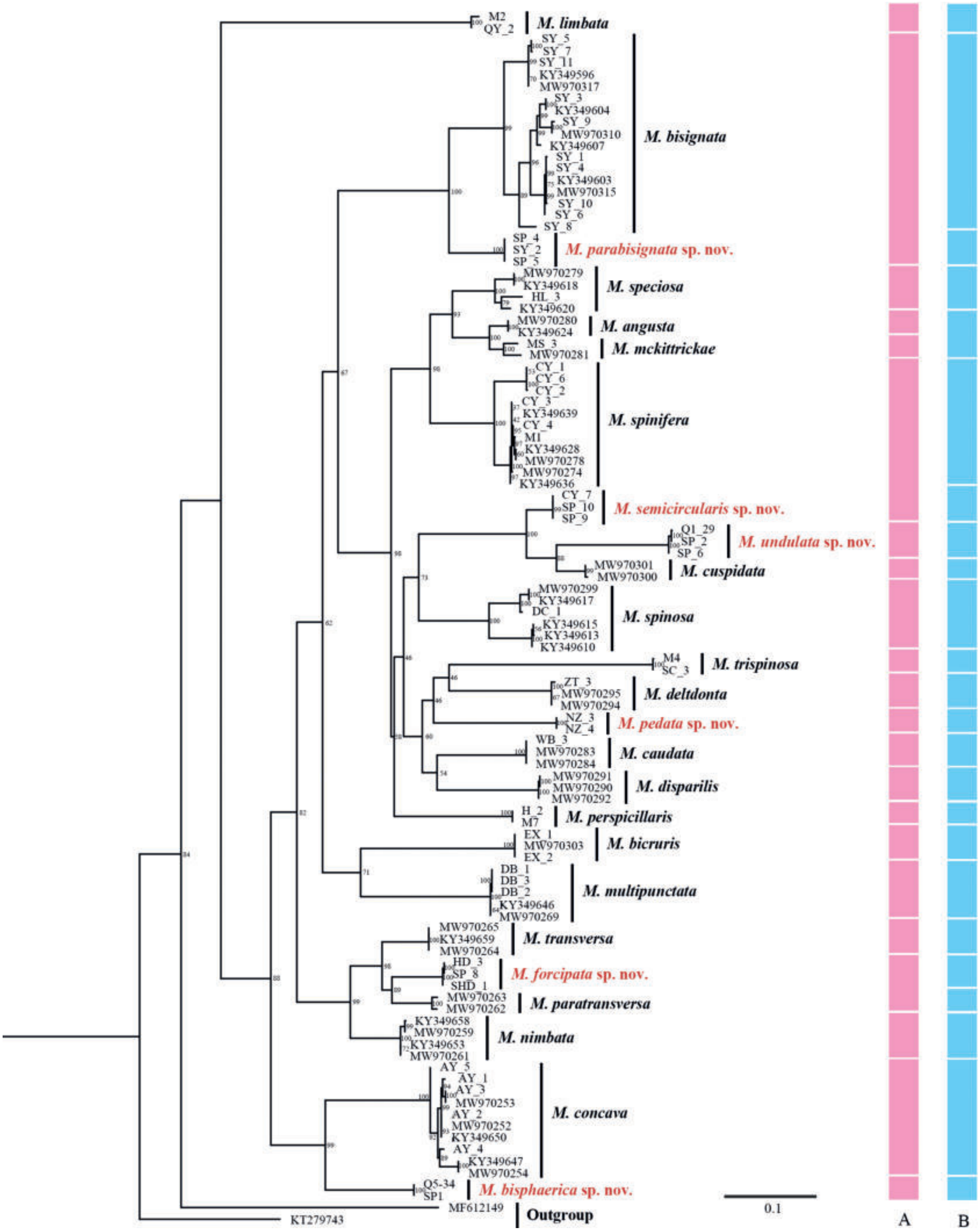

**Figure 1.** Maximum likelihood (ML) tree and species delimitation of *Margattea* based on *COI* sequence. Branches labels are bootstrap support percentage. Colored bars indicate different species delimitation by different methods **A** morphology (pink) **B** ABGD results (blue).

## Establishment of three new cryptic species based on molecular data and male genitalia

Eighteen of 22 morphological species were well supported by the ABGD result. *M. angusta* Wang, Li, Wang & Che, 2014 and *M. mckittrickae* Wang, Che & Wang, 2009 were considered as one MOTU. He et al. (2021) found some stable morphological differences between the two species, although the genetic distance between them was only ~ 5%. *M. spinifera* Bey-Bienko, 1958, *M. bisignata* Bey-Bienko, 1970, and *M. paratransversa* He & Wang, 2021 were all divided into two MOTUs. These results suggest that it was insufficient and challenging to distinguish the specimens of *Margattea* only based on the external morphological characters. Therefore, we examined the male genitalia of *M. spinifera*, *M. bisignata*, and *M. paratransversa* carefully. For *M. spinifera*, the left end of the accessory sclerite of samples CY_7 and SP9 is trigonate (Fig. 2B), while that of samples CY_1, CY_2, CY_3, CY_4, CY_6, KY349628, MW970274, KY349636, KY349639 and MW970278 is expanded with fuzz (Fig. 2A). For *M. bisignata*, the left phallomere of samples SY_2 and SP4 has a short spiny process (Fig. 2D), while that of samples SY_1, SY_3, SY_4, SY_5, SY_6, SY_7, SY_8, SY_9, SY_10, MW970310, MW970317, MW970315, KY349596, KY349607, KY349603 and KY349604 had a long spine process (Fig. 2C). For *M. paratransversa*, the apex of median phallomere of samples HD_3 and SHD_1 is enlarged and forceps-shaped (Fig. 2F), while that of samples MW970262 and MW970263 has a slightly curved spine (Fig. 2E). In conclusion, three cryptic new species, *M. parabisignata* Li & Che, sp. nov., *M. semicircularis* Li & Che, sp. nov., and *M. forcipata* Li & Che, sp. nov., are discovered mainly based on the male genitalia with the help of the molecular data.

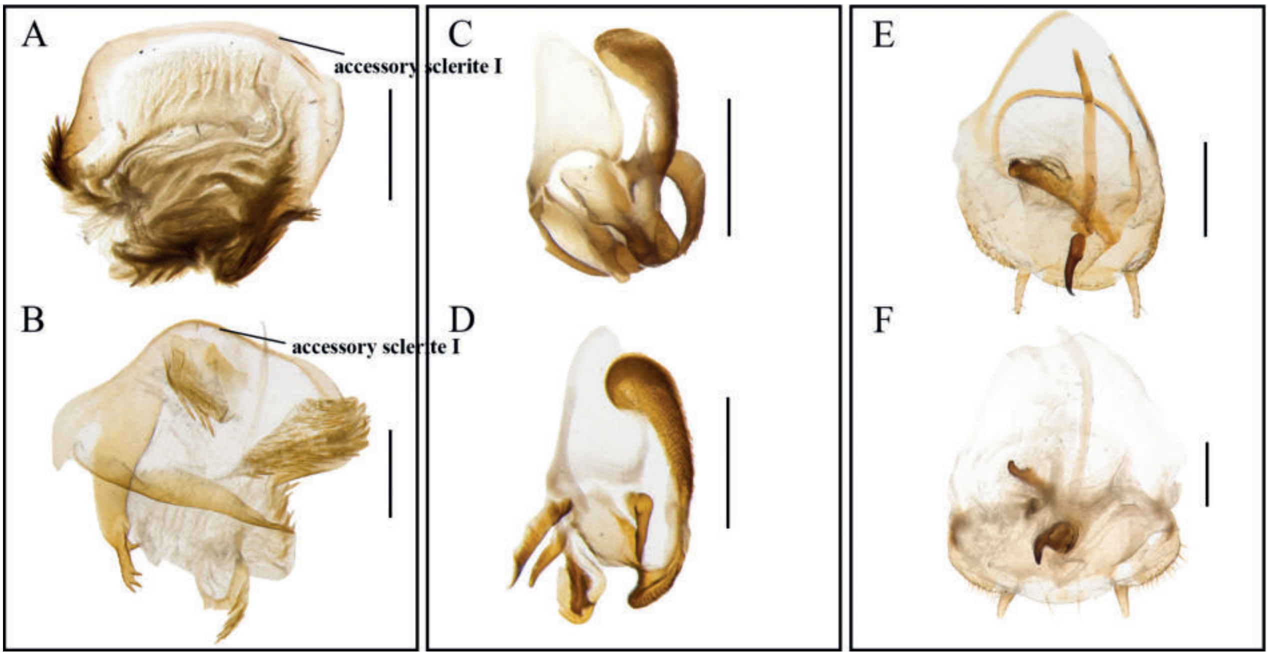

**Figure 2. A** *M. spinifera* Bey-Bienko, 1958, median phallomere, dorsal view (CY_2) **B** *M. semicircularis* Li & Che, sp. nov., median phallomere, dorsal view (CY_7) **C** *M. bisignata* Bey-Bienko, 1970, left phallomere, dorsal view (SY_3) **D** *M. parabisignata* Li & Che, sp. nov., left phallomere, dorsal view (SY_2) **E** *M. paratransversa* He & Wang, 2021, subgenital plate and median phallomere, dorsal view (MW970262) **F** *M. forcipata* Li & Che, sp. nov., subgenital plate and median phallomere, dorsal view (SHD_1). Scale bars: 0.5 mm.

## Taxonomy

### ***Margattea*** **Shelford, 1911**

*Margattea* Shelford, 1911: 155. Type species: *Blatta ceylanica* Saussure, 1868; by monotypy. Rehn 1931: 302; Bey-Bienko 1938: 121; Bey-Bienko 1950: 145; Princis 1969: 862; Roth 1989: 207; Roth 1991: 980; Wang et al. 2009: 51; Liu and Zhou 2011: 936; Wang et al. 2014: 31; He et al. 2021: 121.

*Kuchinga* Hebard, 1929: 41. Type species: *Phyllodromia longealata* Brunner von Wattenwyl, 1898; by selection. Hanitsch 1931: 392. Synonymized by Bey-Bienko 1938: 121. Princis 1969: 862.

*Theganosilpha* Kumar & Princis, 1978: 33. Type species: *Theganopteryx perspicillaris* Karny, 1915; by monotypy. Asahina 1979: 119. Synonymized by Roth 1989: 207.

*Molestella* Bruijning, 1948: 74. Type species: *Phyllodromia molesta* Brunner von Wattenwyl & Bruijning, 1948; by monotypy. Princis 1969: 803. Synonymized by Roth 1991: 980.

*Margattina* Bey-Bienko, 1958: 675. Type species: *Margattina trispina* Bey-Bienko, 1958. Synonymized by Liu et Zhou 2011: 936.

**Diagnosis.** Body small, usually yellowish brown. Interocellar distance slightly wider than the distance between eyes, narrower than the distance between antennal sockets. The fifth maxillary palp expanded, the third and fourth palpi both longer than the fifth palp. Pronotum subelliptical, broader than long, the disc usually with symmetrical maculae and stripes. Tegmina and hind wings fully developed, mostly both extending beyond the end of abdomen. Tegmina with M and CuA radial, M straight with 4–7 branches. Hind wings with ScP and RA expanded at apex, CuA with 4–6 complete branches. Anteroventral margin of front femur Type $B_2$ or $B_3$. Four proximal tarsomeres with pulvilli. The pretarsi with arolium, tarsal claws symmetrical and specialized, with minute denticles on ventral margins. Eighth abdominal tergum usually specialized, with a tuft of setae in the middle near posterior margin. Supra-anal plate usually short and transverse, paraprocts similar and flaky. Cerci long, with setae on the ventral surface. Male subgenital plate symmetrical or slightly asymmetrical. Styli symmetrical and cylindrical, rarely asymmetrical or non-cylindrical. ***Male genitalia*****.** Left phallomere small, irregularly bone-shaped, mostly with spine-like process. Median phallomere slender, rod-shaped, the apex irregular and variable; accessory sclerite complicated, generally arched. Hook phallomere on right side, apex usually curved inwards.

**Differential diagnosis.** The genus *Margattea* is supposedly closely related to *Chorisoserrata* (Wang et al. 2023) and morphologically similar to *Balta*, but *Margattea* could be distinguished from *Chorisoserrata* and *Balta* by the following characteristics. The genus *Margattea* can be distinguished from *Balta* (Asia, Africa, and parts of Oceania) by the following characteristics: 1) anteroventral margin of front femur Type $B_2$ or $B_3$, in contrast to $C_2$ (but rarely $B_3$) in *Balta*; 2) the tarsal claws symmetrical and specialized, but in the latter, the tarsal claws asymmetrical and unspecialized.

The genus *Margattea* can be distinguished from *Chorisoserrata* (parts of Asia and Indonesia) by the following characteristics: 1) anteroventral margin of front femur Type $B_2$ or $B_3$, in contrast to $C_2$ (but rarely $B_3$) in *Chorisoserrata*; 2) eighth abdominal tergum usually specialized, with a tuft of setae in the middle near posterior margin; while in the latter, abdominal terga unspecialized.

## Key to species of *Margattea* from China

1 Tegmina not extending beyond the end of abdomen .................................. **2**

– Tegmina extending beyond the end of abdomen .................................. **3**

2 Tegmina reaching the middle of abdomen..... ***M. hemiptera*** **Bey-Bienko, 1958**

– Tegmina extending beyond the middle of the abdomen but not reaching the end of abdomen ..................................... ***M. perspicillaris*** **(Karny, 1915)**

3 Pronotum without maculae ...................... ***M. immaculata*** **Liu & Zhou, 2011**

– Pronotum with maculae .................................. **4**

4 The distance between eyes narrow, nearly half of interocellar distance ...... ........................................................***M. angusta*** **Wang, Li, Wang & Che, 2014**

– The distance between eyes wide, wider than half of interocellar distance...... **5**

5 Anteroventral margin of front femur Type $B_3$ .................................. **6**

– Anteroventral margin of front femur Type $B_2$ .................................. **15**

6 Interstylar region nearly truncate, not produced .................................. **7**

– Interstylar region obviously produced .................................. **9**

7 Styli conical .................................. **8**

– Styli foot-shaped............................................... ***M. pedata*** **Li & Che, sp. nov.**

8 Median phallomere with three spinelike sclerites .......................................... ................................................................... ***M. trispinosa*** **(Bey-Bienko, 1958)**

– Median phallomere with small spines ........................................................... .................................................... ***M. mckittrickae*** **Wang, Che & Wang, 2009**

9 The trailing edge of interstylar region curls upward...................................... ............................................................................ ***M. furcata*** **Liu & Zhou, 2011**

– The trailing edge of interstylar region no curls upward ............................. **10**

10 Interstylar margin semicircular produced .................................. **11**

– Interstylar margin not semicircular produced .................................. **12**

11 Left phallomere with two small spines ................ ***M. semicircularis*** **sp. nov.**

– Left phallomere with three spine-like processes........................................... ........................................................................... ***M. spinifera*** **Bey-Bienko, 1958**

12 Two sides of interstylar protrusion curled .................................. **13**

– Two sides of interstylar protrusion not curled .................................. **14**

13 Interstylar region convex fishtail-shaped....... ***M. caudata*** **He & Wang, 2021**

– Interstylar region convex irregular................ ***M. disparilis*** **He & Wang, 2021**

14 Accessory sclerite with a bristle brush at right apex .................................... ....................................................................... ***M. cuspidata*** **He & Wang, 2021**

– Accessory sclerite without a bristle brush at right apex............................... ........................................................... ***M. flexa*** **Wang, Li, Wang & Che, 2014**

15 Head dark brown or reddish brown .................................. **16**

– Head yellowish brown .................................. **17**

16 Styli dissimilar .................. ***M. pseudolimbata*** **Wang, Li, Wang & Che, 2014**

– Styli similar....................................................... ***M. limbata*** **Bey-Bienko, 1954**

17 Pronotal disc with white maculae ................................................................... .................................................. ***M. multipunctata*** **Wang, Che & Wang, 2009**

– Pronotal disc with brown maculae .................................. **18**

18 Interstylar region concave ........................................ **19**
– Interstylar region not concave ........................................ **20**
19 Styli symmetrical, conical ................ ***M. concava*** **Wang, Che & Wang, 2009**
– Styli asymmetrical, the left shorter than the right ........................................ ***M. bisphaerica*** **Li & Che, sp. nov.**
20 Eighth abdominal tergum unspecialized........................................ **21**
– Eighth abdominal tergum specialized........................................ **22**
21 Posterior margin of supra-anal plate with sharp protrusions ........................................ ***M. producta*** **Wang, Che & Wang, 2009**
– Posterior margin of supra-anal plate without sharp protrusions ........................................ ***M. punctulata*** **(Brunner von Wattenwyl, 1893)**
22 Interstylar region with triangular protrusion ... ***M. deltodonta*** **He & Wang, 2021**
– Interstylar region without triangular protrusion........................................ **23**
23 Left phallomere without rodlike structure........................................ **24**
– Left phallomere with rodlike structure ........................................ **25**
24 Apex of median phallomere with sparse brush-like structure composed of similar spines........................................ ***M. bisignata*** **Bey-Bienko, 1970**
– Apex of median phallomere with sparse brush-like structure composed of uneven spines........................................ ***M. parabisignata*** **Li & Che, sp. nov.**
25 Body overall length not greater than 9.0 mm ........................................ **26**
– Body overall length greater than 12.0 mm........................................ **27**
26 Median phallomere with spinelike sclerite ..... ***M. nimbata*** **(Shelford, 1907)**
– Median phallomere without spinelike sclerite ........................................ ***M. spinosa*** **Wang, Li, Wang & Che, 2014**
27 Median phallomere with brush structure at apex........................................ **28**
– Median phallomere without brush structure at apex ........................................ 29
28 Interstylar margin sinuate ............................ ***M. undulata*** **Li & Che, sp. nov.**
– Interstylar margin not sinuate....................... ***M. speciosa*** **Liu & Zhou, 2011**
29 Accessory sclerite of median phallomere with a transverse rod ............. **30**
– Accessory sclerite of median phallomere without a transverse rod........................................ ***M. bicruris*** **He & Wang, 2021**
30 Apex of median phallomere enlarged, forceps........................................ ***M. forcipata*** **Li & Che, sp. nov.**
– Apex of median phallomere with a curved long spine ........................................ **31**
31 Left phallomere with three spines...... ***M. paratransversa*** **He & Wang, 2021**
– Left phallomere with four spines................ ***M. transversa*** **He & Wang, 2021**

### ***Margattea pedata*** Li & Che, sp. nov.

https://zoobank.org/072AC964-F06D-49DC-96F8-35A61A85C467
Fig. 3A–O

**Type material.** ***Holotype*:** China • ♂; Yunnan Province, Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Nabang Town; 282 m; 17 Aug. 2015; Xin-Ran Li, Zhi-Wei Qiu leg; SWU-B-PS000001. ***Paratypes*:** China • 1 ♂ & 1 ♀; same data as holotype; SWU-B-PS000002–000003 • 5 ♂ & 2 ♀; Yunnan Province, Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Nabang Town; 282 m; 11 Jul. 2012; Dong Wang leg; SWU-B-PS000004–000010.

**Measurements (mm).** Male ($n$ = 6), pronotum length × width: 2.4–2.7 × 3.4–3.7, tegmina length: 11.8–12.3, body length: 8.8–10.3, overall length: 13.2–13.7. Female ($n$ = 4), pronotum length × width: 2.4–2.9 × 3.2–3.9, tegmina length: 11.2–11.6, body length: 10.9–12.8, overall length: 13.2–14.0.

**Description. Male. *Coloration*.** Body pale yellow (Fig. 3A, B). Head yellowish brown. Face pale yellow. Interocular space with a wide brown transverse band. Ocellar spots white, interocellar space with a brown band. Antennal base pale yellowish brown, other segments dark brown (Fig. 3E). Maxillary palpi pale brown (Fig. 3J). Pronotal disc pale yellowish brown with reddish tan stripes, and two lateral borders pale linen-colored and transparent (Fig. 3F). Tegmina pale yellowish brown, hind wings brownish grey (Fig. 3G, H). Legs faint yellow. Abdomen yellowish brown, with black stripes along lateral margins of sterna and reaching the end of abdomen; both sides of each abdominal sternum with one small black spot on the inside of the longitudinal lines (Fig. 3B). Cerci yellowish brown to pale brown (Fig. 3L). Styli yellowish white (Fig. 3N).

***Head*.** Vertex slightly exposed, interocellar distance slightly wider than the distance between eyes, narrower than the distance between antennal sockets (Fig. 3F). Fifth maxillary palpus expanded, third and fourth maxillary palpi nearly equal in length, both longer than fifth maxillary palpus (Fig. 3J). Pronotum subelliptical, broader than long, anterior and posterior margins nearly straight, and postero-lateral angle blunt and round; disc with symmetrical spots and stripes (Fig. 3E). ***Tegmina and hind wings*.** Tegmina and hind wings fully developed, both extending beyond the end of abdomen (Fig. 3A, B). Tegmina with M and CuA radial, M straight with three complete branches and one incomplete branch. Hind wings with ScP and RA expanded at apex, M simple, without branches; CuA with four complete branches (Fig. 3G, H). ***Legs*.** Anteroventral margin of front femur Type $B_3$ (Fig. 3K). Four proximal tarsomeres with pulvilli. The pretarsi with arolium, tarsal claws symmetrical and specialized, with minute denticles on ventral margins.

***Abdomen and genitalia*.** Eighth abdominal tergum specialized, with a heart-shaped transparent area and a tuft of bristles in the middle (Fig. 3I). Supra-anal plate symmetrical, middle posterior margin slightly concave. Paraprocts simple, similar, and flaky (Fig. 3L). Cerci long, with setae on the ventral surface (Fig. 3L). Styli similar, foot-shaped (Fig. 3N). Subgenital plate nearly symmetrical, posterior margin truncate (Fig. 3N). Left phallomere small, irregular bone-shaped, with a long spine (Fig. 3M). Median phallomere slender rod-shaped, with base curved, apex with a row of spines; accessory sclerite I arched, accessory sclerite II complicated with an inverted bell-shaped structure covered with fuzz (Fig. 3N). Hook phallomere on the right side, apex curved inwards with a short spine (Fig. 3O).

**Female.** Similar to the male (Fig. 3C, D).

**Diagnosis.** This species is similar to *M. speciosa* Liu & Zhou, 2011 in general appearance, but can be differentiated from the latter by the following characters: 1) styli foot-shaped, while in the latter conical; 2) left phallomere with a long, curved spine, absent in the latter; and 3) accessory sclerite I without a brush-like structure at apex, while in the latter, accessory sclerite I with a brush-like structure at apex.

**Etymology.** The specific epithet is derived from the Latin word *pedatus*, referring to the foot-shaped styli.

**Distribution.** China (Yunnan).

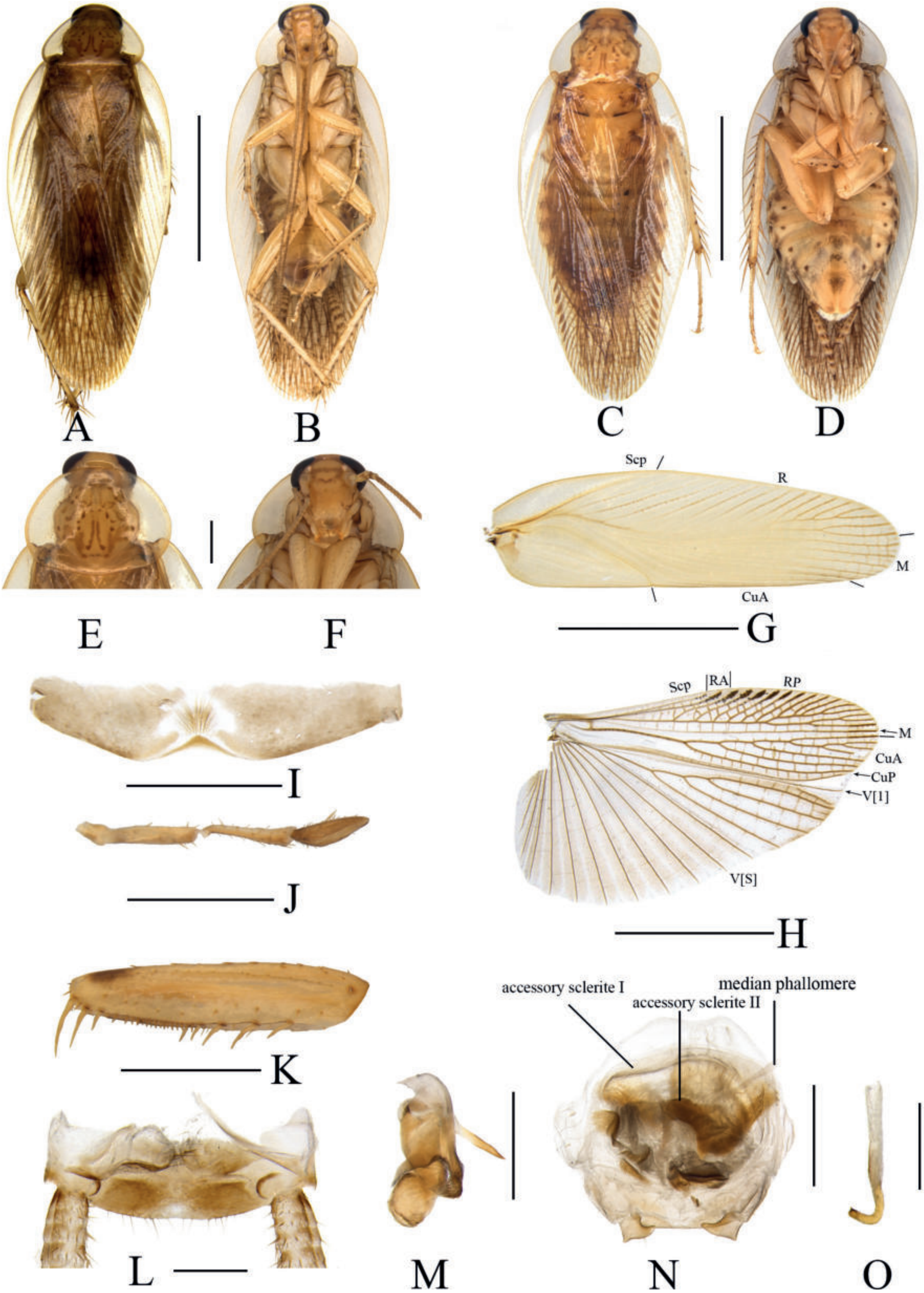

**Figure 3.** *Margattea pedata* Li & Che, sp. nov. **A, B, E–O** male **C, D** female **A** holotype, dorsal view **B** holotype, ventral view **C** paratype, dorsal view **D** paratype, ventral view **E** pronotum, dorsal view **F** head, ventral view **G** tegmen, ventral view **H** hind wing, ventral view **I** eighth abdominal tergum, ventral view **J** maxillary palpi segments 3–5 **K** front femur, ventral view **L** supra-anal plate, ventral view **M** left phallomere, ventral view **N** subgenital plate and median phallomere, ventral view **O** hook phallomere, ventral view. Scale bars: 5 mm (**A–D, G, H**); 1 mm (**E, F, I–L, N**); 0.5 mm (**M, O**).

### ***Margattea bisphaerica*** **Li & Che, sp. nov.**

https://zoobank.org/753866C7-1196-46B8-BBD0-0C935287AAF2

Fig. 4A–O

**Type material.** ***Holotype*****:** China • ♂; Guangxi Zhuang Autonomous Region, Laibin City, Jinxiu Yao Autonomous County, Mountain Shengtang; 1182 m; 5 Jun. 2014; Shun-Hua Gui, Xin-Ran Li leg; SWU-B-PS000011. ***Paratypes*****:** China • 3 ♂ & 1 ♀; same data as holotype; SWU-B-PS000012–000015 • 1 ♂; Guangxi Zhuang Autonomous Region, Laibin City, Jinxiu Yao Autonomous County, Mountain Shengtang; 400 m; 13 Jul. 2015; Lu Qiu, Qi-Kun Bai leg; SWU-B-PS000016.

**Measurements (mm).** Male (*n* = 6), pronotum length × width: 2.3–2.5 × 3.0–3.4, tegmina length: 11.8–12.5, body length: 9.8–11.6, overall length: 13.8–14.9. Female (*n* = 2), pronotum length × width: 2.3–2.5 × 3.3, tegmina length: 10.7–11.4, body length: 10.3–11.0, overall length: 13.8–13.9.

**Description. Male. *Coloration*.** Body brown (Fig. 4A, B). Head and face yellowish brown. Interocular space with a wide brown transverse band. Ocellar spots yellowish white, interocellar space with a brown band. Antennae blackish brown, antennal space with a brown band (Fig. 4F). Maxillary palpi dark brown (Fig. 4J). Pronotal disc pale brown with dark brown spots and maculae but without stripes, and two lateral borders pale linen-colored and transparent (Fig. 4E). Legs yellowish brown. Tegmina pale yellowish brown, hind wings brownish grey (Fig. 4G, H). Abdomen pale brown. Cerci brown (Fig. 4L). Styli yellowish brown (Fig. 4N).

***Head*.** Vertex slightly exposed, interocellar distance slightly much wider than the distance between eyes, narrower than the distance between antennal sockets (Fig. 4E). Pronotum subelliptical, broader than long, anterior and posterior margins nearly straight, and postero-lateral angle blunt and round; disc with symmetrical but irregular spots and maculae (Fig. 4F). Fifth maxillary palpus expanded, third and fourth maxillary palpi both longer than fifth maxillary palpus (Fig. 4J). ***Tegmina and hind wings*.** Tegmina and hind wings fully developed, both extending beyond the end of abdomen (Fig. 4A, B). Tegmina M and CuA radial, M straight with six complete branches. Hind wings with ScP and RA expanded at apex, M simple, without branches; CuA with four complete branches (Fig. 4 G, H). ***Legs*.** Anteroventral margin of front femur Type $B_2$ (Fig. 4K). Four proximal tarsomeres with pulvilli. The pretarsi with arolium, tarsal claws symmetrical and specialized, with minute denticles on ventral margins.

***Abdomen and genitalia*.** Eighth abdominal tergum specialized, with a tuft of bristles in the middle (Fig. 4I). Supra-anal plate symmetrical, anterior margin straight and truncate, the middle of posterior margin slightly concave. Paraprocts simple, similar, and flaky. Cerci long, with setae on the ventral surface (Fig. 4L). Subgenital plate asymmetrical. Styli dissimilar and spherical, the left stylus significantly smaller than the right stylus (Fig. 4N). Left phallomere small, irregular bone-shaped, with a slender curved spine (Fig. 4M). Median phallomere slender rod-shaped, with a curved spine at apex; accessory sclerite I arched, left end expanded, right end with a cluster of thorns; accessory sclerite II brush-shaped; accessory sclerite III slender rod-shaped (Fig. 4N). Hook phallomere on the right side, apex curved hook-shaped (Fig. 4O).

**Female.** Similar to the male. Subgenital plate symmetrical, middle posterior margin concave inward (Fig. 4C, D).

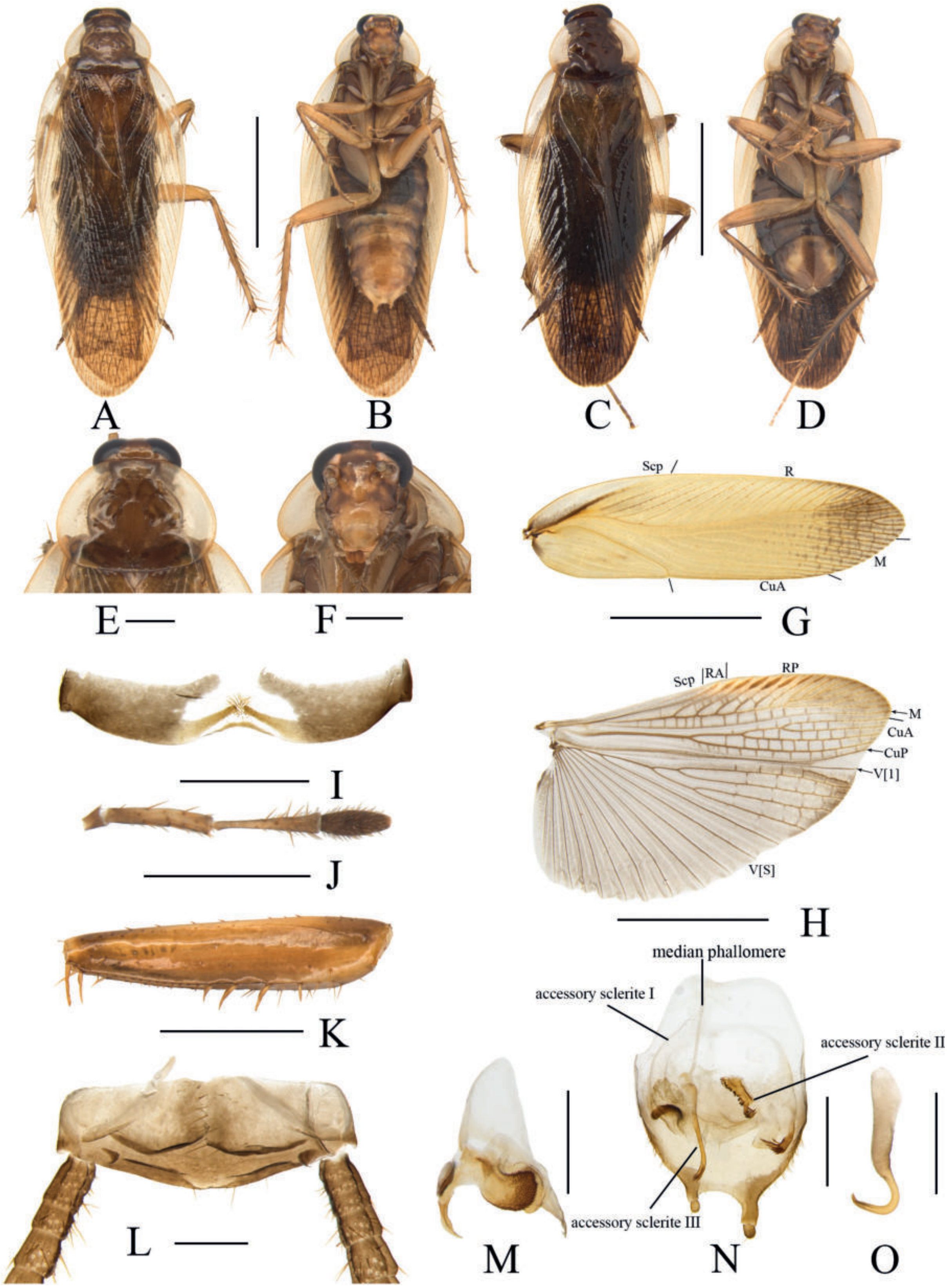

**Figure 4.** *Margattea bisphaerica* Li & Che, sp. nov. **A, B, E–O** male **C, D** female **A** holotype, dorsal view **B** holotype, ventral view **C** paratype, dorsal view **D** paratype, ventral view **E** pronotum, dorsal view **F** head, ventral view **G** tegmen, ventral view **H** hind wing, ventral view **I** eighth abdominal tergum, ventral view **J** maxillary palpi segments 3–5 **K** front femur, ventral view **L** supra-anal plate, ventral view **M** left phallomere, ventral view **N** subgenital plate and median phallomere, ventral view **O** hook phallomere, ventral view. Scale bars: 5 mm (**A–D, G, H**); 1 mm (**E, F, I–K, N**); 0.5 mm (**L, M, O**).

**Diagnosis.** This species is similar to *M. concava* Wang, Che & Wang, 2009 in general appearance, but can be differentiated from the latter by the following characters: 1) styli dissimilar and spherical, the left stylus significantly smaller than the right stylus; while in the latter, styli similar and conical; 2) left phallomere with a slender curved spine, absent in the latter.

**Etymology.** The specific name is derived from the Latin words, *bi* and *sphaericus*, referring to the dissimilar and spherical styli.

**Distribution.** China (Guangxi).

### ***Margattea undulata*** **Li & Che, sp. nov.**

https://zoobank.org/BB55B598-4B51-4F06-ABE0-01005C5A249F

Fig. 5A–O

**Type material.** ***Holotype*****:** China • ♂; Chongqing City, Beibei District, Mountain Jinyun; 550 m; 12 Jul. 2016; Lu Qiu, Zhi-Wei Qiu leg; SWU-B-PS000017. ***Paratypes*****:** China • 10 ♂ & 1 ♀; same data as holotype; SWU-B-PS000018–000028 • 2 ♂ & 1 ♀; Chongqing City, Jiangjin District, Mountain Simian; 425 m; 21 Sep. 2007; Wei-Wei Zhang leg; SWU-B-PS000029–000031 • 1 ♂ & 1 ♀; Chongqing City, Liangping District, Dongshan Forest Park; 2 Oct. 2007; Wei-Wei Zhang leg; SWU-B-PS000032–000033.

**Measurements (mm).** Male (*n* = 4), pronotum length × width: 2.4–2.9 × 3.6–3.8, tegmina length: 12.8–13.6, body length: 10.4–12.1, overall length: 14.9–16. Female (*n* = 4), pronotum length × width: 2.3–2.5 × 3.3, tegmina length: 10.7–11.4, body length: 10.3–11.0, overall length: 13.8–13.9.

**Description. Male.** ***Coloration*****.** Body, head and face yellowish brown (Fig. 5A, B). Interocular space with a brown transverse band. Ocellar spots small, yellowish white. Antennal base yellowish brown, other segments black-brown. The third and fourth maxillary palpi yellowish brown, the fifth palpus maxillary blackish brown (Fig. 5J). Pronotal disc yellowish brown with reddish tan spots and stripes, and two lateral borders pale linen-colored and transparent (Fig. 5E). Legs yellowish brown, with black spots at the base of the tibial spines. Tegmina yellowish brown, hind wings brownish grey (Fig. 5G, H). Abdomen yellowish brown, both sides of each abdominal sternum with one small round black spot on the inside of the longitudinal lines. Cerci yellowish brown (Fig. 5L). Styli pale yellow (Fig. 5N).

***Head*****.** Vertex slightly exposed, interocellar distance slightly wider than the distance between eyes, narrower than the distance between antennal sockets (Fig. 5F). Pronotum subelliptical, broader than long, anterior and posterior margins nearly straight, and postero-lateral margin blunt and round; disc with symmetrical spots and stripes (Fig. 5E). Fifth maxillary palpus expanded, third and fourth maxillary palpi nearly equal in length, both twice as long as fifth maxillary palpus (Fig. 5J). ***Tegmina and hind wings*****.** Tegmina and hind wings fully developed, both extending beyond the end of abdomen (Fig. 5A, B). Tegmina with M and CuA radial, M straight with seven complete branches. Hind wings with ScP and RA expanded at apex, M simple, without branches; CuA with four complete branches (Fig. 5G, H). ***Legs*****.** Anteroventral margin of front femur Type $B_3$ (Fig. 5K). Four proximal tarsomeres with pulvilli. The pretarsi with arolium, tarsal claws symmetrical and specialized, with minute denticles on ventral margins. ***Abdomen and genitalia*****.** Eighth abdominal tergum specialized, with a tuft of setae near the dis-

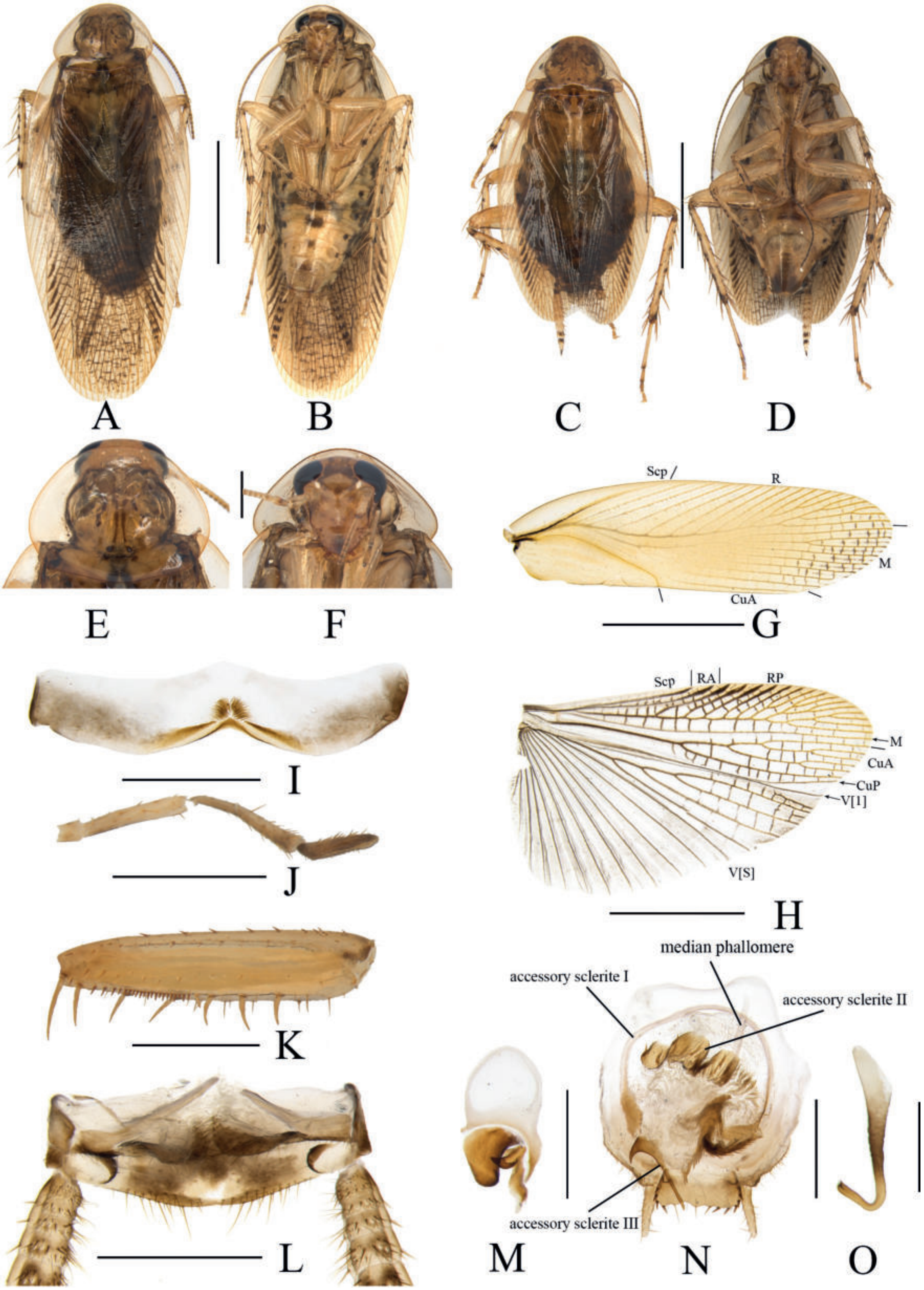

**Figure 5.** *Margattea undulata* Li & Che, sp. nov. **A, B, E–O** male **C, D** female **A** holotype, dorsal view **B** holotype, ventral view **C** paratype, dorsal view **D** paratype, ventral view **E** pronotum, dorsal view **F** head, ventral view **G** tegmen **H** hind wing **I** eighth abdominal tergum, ventral view **J** maxillary palpi segments 3–5 **K** front femur, ventral view **L** supra-anal plate, ventral view **M** left phallomere, ventral view **N** subgenital plate and median phallomere, ventral view **O** hook phallomere, ventral view. Scale bars: 5 mm (**A–D, G, H**); 1 mm (**E, F, I–L, N**); 0.5 mm (**M, O**).

tinctly concave middle posterior margin (Fig. 5I). Supra-anal plate symmetrical, anterior margin straight and truncate, posterior margin obtusely round. Paraprocts simple, similar and flaky. Cerci long, with setae on the ventral surface (Fig. 5L) Subgenital plate nearly symmetrical, anterior margin distinctly concave in the middle. Styli similar, slender; interstylar margin sinuate, left side with five or six small spines, right side with 5–7 small spines (Fig. 5N). Left phallomere small, irregular bone-shaped, with a small spine (Fig. 5M). Median phallomere slender rod-shaped, with a bristle brush at apex; accessory sclerite I arched, two ends enlarged, right end with a row of spines; accessory sclerite II with three lamellar structures with small spines; accessory sclerite III sickle-shaped (Fig. 5N). Hook phallomere on the right side, apex curved inwards with a short spine (Fig. 5O).

**Female.** Similar to the male but body and wings somewhat shorter (Fig. 5C, D).

**Diagnosis.** This species is similar to *M. flexa* Wang et al., 2014 in general appearance, but can be differentiated from the latter by the following characters: 1) interstylar margin sinuate, left side with 4–6 small spines, right side with 4–7 small spines; while in the latter, interstylar margin strongly produced, whose lateral sides upturned and scattered with spines; 2) left phallomere irregular bone-shaped, without a small spine; while in the latter, left phallomere irregular bone-shaped, with two spines; 3) accessory sclerite II with three lamellar structures with small spines; while in the latter, accessory sclerite II with lamellar structure without small spines.

**Etymology.** The specific name is derived from the Latin word *undulatus*, which refers to the sinuate interstylar margin.

**Distribution.** China (Chongqing).

### *Margattea semicircularis* Li & Che, sp. nov.

https://zoobank.org/94D4FBB8-6FD2-43CD-8F41-343E38F269DC
Fig. 6A–N

**Type material.** ***Holotype*:** China • ♂; Guizhou Province, Zunyi City, Suiyang County, Qingbantang Town, Baishao Ditch; 30 Jul. 2013; Xiu-Dan Wang leg; SWU-B-PS000034. ***Paratype*:** China • 1 ♂; same data as holotype; SWU-B-PS000035.

**Measurements (mm).** Male (*n* = 2), pronotum: length × width 2.3–2.5 × 3.0–3.4, tegmina length: 10.7–11.2, body length: 10.5–11.0, overall length: 12.9–13.2.

**Description. Male.** ***Coloration*.** Body, head and face yellowish brown (Fig. 6A, B). Interocular space with a wide brown transverse band. Ocellar spots small, white, with brown spots beside them. Antennal base pale yellowish brown, other segments brown (Fig. 6D). Maxillary palpi dark brown (Fig. 6H). Pronotal disc yellowish brown with reddish tan spots and stripes, and two lateral borders pale linen-colored and transparent (Fig. 6C). Legs yellowish brown, with black spots at the base of the tibial spines. Tegmina pale yellowish brown, hind wings brownish grey (Fig. 6F, G). Abdomen yellowish brown, with black stripes along lateral margins of sterna and reaching the end of abdomen; both sides of each abdominal sternum with one small black spot on the inside of the longitudinal lines (Fig. 6B). Cerci yellowish brown (Fig. 6K). Styli pale yellow (Fig. 6M).

***Head*.** Vertex slightly exposed, interocellar distance wider than the distance between eyes, narrower than the distance between antennal sockets (Fig. 6C, D). Pronotum subelliptical, broader than long, anterior and posterior

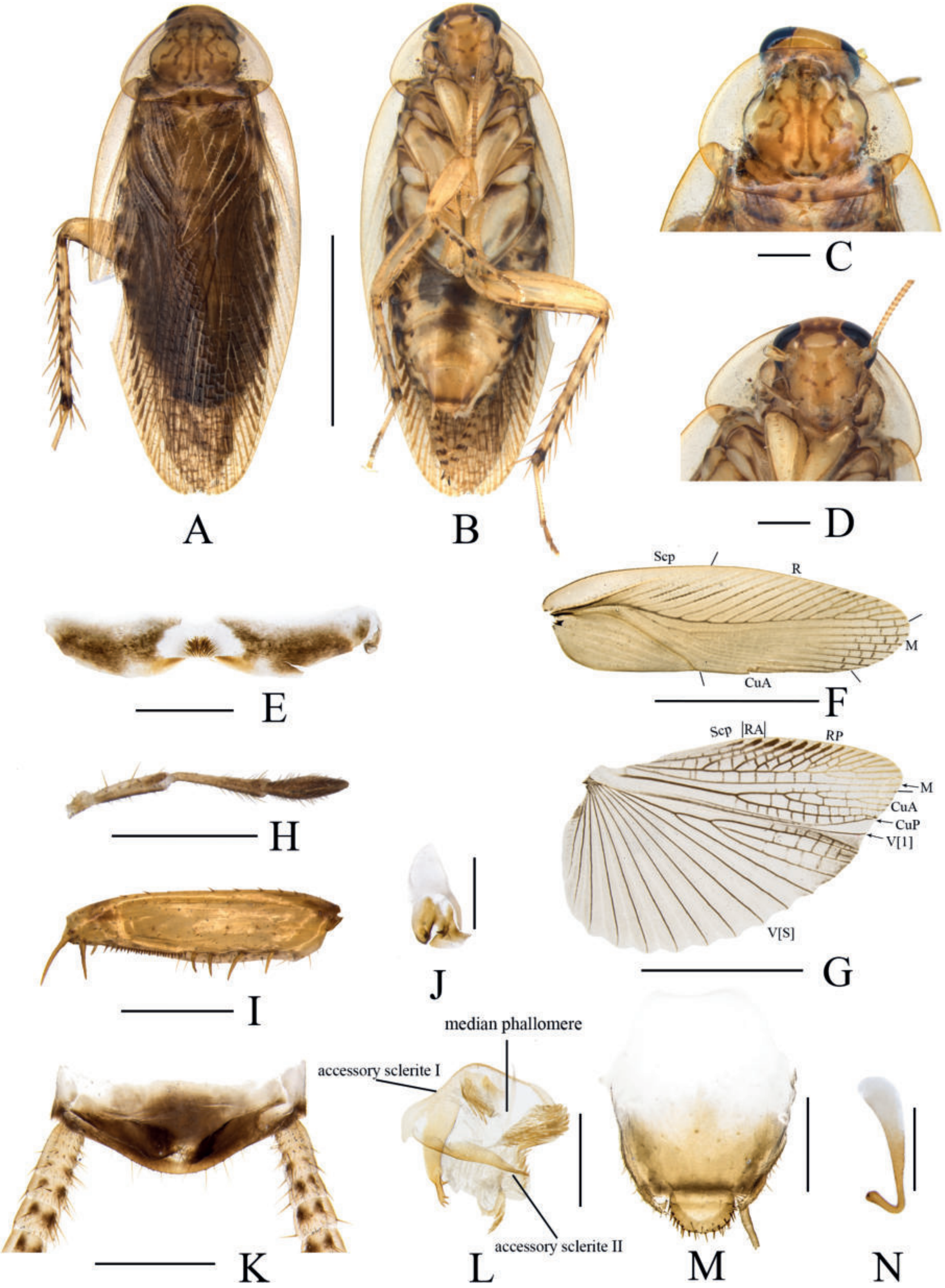

**Figure 6.** *Margattea semicircularis* Li & Che, sp. nov. **A–N** male **A** holotype, dorsal view **B** holotype, ventral view **C** pronotum, dorsal view **D** head, ventral view **E** eighth abdominal tergum, ventral view **F** tegmen, ventral view **G** hind wing, ventral view **H** maxillary palpi segments 3–5 **I** front femur, ventral view **J** Left phallomere, dorsal view **K** supra-anal plate, ventral view **L** median phallomere, ventral view **M** subgenital plate, ventral view **N** hook phallomere, ventral view. Scale bars: 5 mm (**A, B, F, G**); 1 mm (**C–E, H, I, K–M**); 0.5 mm (**J, N**).

margins nearly straight, and postero-lateral angle blunt and round; disc with symmetrical spots and stripes (Fig. 6C). Maxillary palpi slender, fifth maxillary palpus expanded, third and fourth maxillary palpi nearly equal in length, both longer than fifth maxillary palpus (Fig. 6H). ***Tegmina and hind wings*****.** Tegmina and hind wings fully developed, both extending beyond the end of abdomen (Fig. 6A, B). Tegmina with M and CuA radial, M straight with seven complete branches. Hind wings with ScP and RA expanded at apex; M simple, without branches; CuA with five complete branches (Fig. 6F, G). ***Legs*****.** Anteroventral margin of front femur Type $B_3$ (Fig. 6I). Four proximal tarsomeres with pulvilli. The pretarsi with arolium, trsal claws symmetrical and specialized, with minute denticles on ventral margins.

***Abdomen and genitalia*****.** Eighth abdominal tergum specialized, with a heart-shaped transparent area and a tuft of bristles in the middle (Fig. 6E). Supra-anal plate symmetrical, anterior margin straight and truncate, the middle of posterior margin slightly produced. Paraprocts simple, similar, and flaky. Cerci long, setae on the ventral surface (Fig. 6K). Subgenital plate nearly symmetrical, anterior margin slightly concave in the middle. Styli similar, conical; interstylar margin strongly semicircular produced, both sides with spines (Fig. 6K). Left phallomere small, irregular, bone-shaped, with two small spines (Fig. 6J). Median phallomere curved hook rod-shaped, with a row of spines at apex. Accessory sclerite I arched, two ends enlarged, left end trigonate, right end with a row of spines; accessory sclerite II long transverse (Fig. 6L, M). Hook phallomere on the right side, apex curved inwards with a short spine (Fig. 6N).

**Diagnosis.** This species is similar to *M. spinifera* Bey-Bienko, 1958a in general appearance, but can be differentiated from the latter by the following characters: 1) left phallomere with two small spines; while the latter, left phallomere with three spine-like processes; 2) accessory sclerite I arched, left end trigonate; while in the latter, accessory sclerite I arched, left end expanded with fuzz; 3) accessory sclerite II long transverse, and with two lamellar structures with a row of spines, while in the latter, without other accessory sclerites.

**Etymology.** The scientific name is derived from the Latin word *semicircularis*, which indicates the interstylar margin has a semicircular protrusion.

**Distribution.** China (Guizhou).

### ***Margattea parabisignata*** **Li & Che, sp. nov.**

https://zoobank.org/7B4FC2A3-9EA9-46F2-AEE8-55B12639511A
Fig. 7A–O

**Type material.** ***Holotype*****:** China • ♂; Hainan Province, Qiongzhong Li and Miao Autonomous County, Mountain Limu; 600 m; 16 May. 2015; Xin-Ran Li, Zhi-Wei Qiu leg; SWU-B-PS000036. ***Paratypes*****:** China • 2 ♂ & 1 ♀; same data as holotype; SWU-B-PS000037–000039 • 7 ♂ & 3 ♀; Hainan Province, Qiongzhong Li and Miao Autonomous County, Mountain Limu; 600 m; 16 May. 2015; Xin-Ran Li, Zhi-Wei Qiu leg; SWU-B-PS000040–000049.

**Measurements (mm).** Male (*n* = 7), pronotum length × width: 2.2–2.8 × 3.0–3.6, tegmina length: 11.3–12.2, body length: 10.1–11.1, overall length: 13.0–14.0. Female (*n* = 5), pronotum length × width: 2.2–2.8 × 3.0–3.6, tegmina length: 10.7–11.4, body length: 9.6–11.7, overall length: 12.9–13.7.

**Description. Male. *Coloration*.** Body pale yellowish brown (Fig. 7A, B). Head yellowish brown. Face pale yellow. Interocular space with a brown transverse band. Ocellar spots yellowish white (Fig. 7F). Antennal base pale yellow, other segments yellowish brown. The third and fourth maxillary palpi yellowish brown, the fifth maxillary palpus brown (Fig. 7J). Pronotal disc pale yellowish brown with reddish tan spots but without stripes, and two lateral borders pale linen-colored and transparent (Fig. 7E). Legs faint yellow, with black spots at the base of the tibial spines. Tegmina yellowish brown, hind wings brownish grey (Fig. 7G, H). Abdomen pale yellow, with black stripes along lateral margins of sterna and reaching the end of abdomen. Cerci pale yellow to yellowish brown (Fig. 7L). Styli yellowish brown (Fig. 7N).

***Head*.** Vertex slightly exposed, interocellar distance wider than the distance between eyes, narrower than the distance between antennal sockets (Fig. 7F). Pronotum subelliptical, broader than long, anterior and posterior margins nearly straight, and postero-lateral angle blunt and round; disc with symmetrical spots but without stripes (Fig. 7E). Fifth maxillary palpus expanded, third and fourth maxillary palpi nearly equal in length, both longer than fifth maxillary palpus (Fig. 7J). ***Tegmina and hind wings*.** Tegmina and hind wings fully developed, both extending beyond the end of abdomen (Fig. 7A, B). Tegmina with M and CuA radial, M straight with seven complete branches. Hind wings with ScP and RA expanded at apex, M simple, without branches; CuA with four complete branches (Fig. 7G, H). ***Legs*.** Anteroventral margin of front femur Type $B_2$ (Fig. 7K). Four proximal tarsomeres with pulvilli. The pretarsi with arolium, tarsal claws symmetrical and slightly specialized, with minute denticles on ventral margins.

***Abdomen and genitalia*.** Eighth abdominal tergum specialized, with a sparse tuft of bristles in the middle (Fig. 7I). Supra-anal plate symmetrical, the middle of anterior margin slightly concave, posterior margin arcuate produced with setae. Paraprocts simple, similar and flaky, obtuse at apex and each with a spiniform process at the base (Fig. 7L). Subgenital plate nearly symmetrical, anterior margin distinctly concave in the middle, left and right margins both produced in the middle, posterior margin truncate. Styli similar, conical. Cerci long, with setae on the ventral surface (Fig. 7N). Left phallomere large, irregular, bone-shaped, and with spines processes, apex curved upwards with rod-like structure (Fig. 7M). Median phallomere slender rod-shaped, apex with sparse brush-like structure composed of spines of various sizes; accessory sclerite I arched; accessory sclerite II with a lamellar structure with small spines (Fig. 7N). Hook phallomere on the right side, apex curved inwards with a short spine (Fig. 7O).

**Female.** Similar to the male (Fig. 7C, D).

**Diagnosis.** This species is similar to *M. bisignata* Bey-Bienko, 1970 in general appearance, but can be differentiated from the latter by the following characters: 1) left phallomere with a short spiny process; the latter with a long spine process; 2) median phallomere apex with sparse brush-like structure composed of spines of varying sizes; while in the latter, median phallomere curved at apex, sheet-like, and with brush-shaped structure.

**Etymology.** The species name *parabisignata* reflects its similarity to *M. bisignata* Bey-Bienko, 1970.

**Distribution.** China (Hainan).

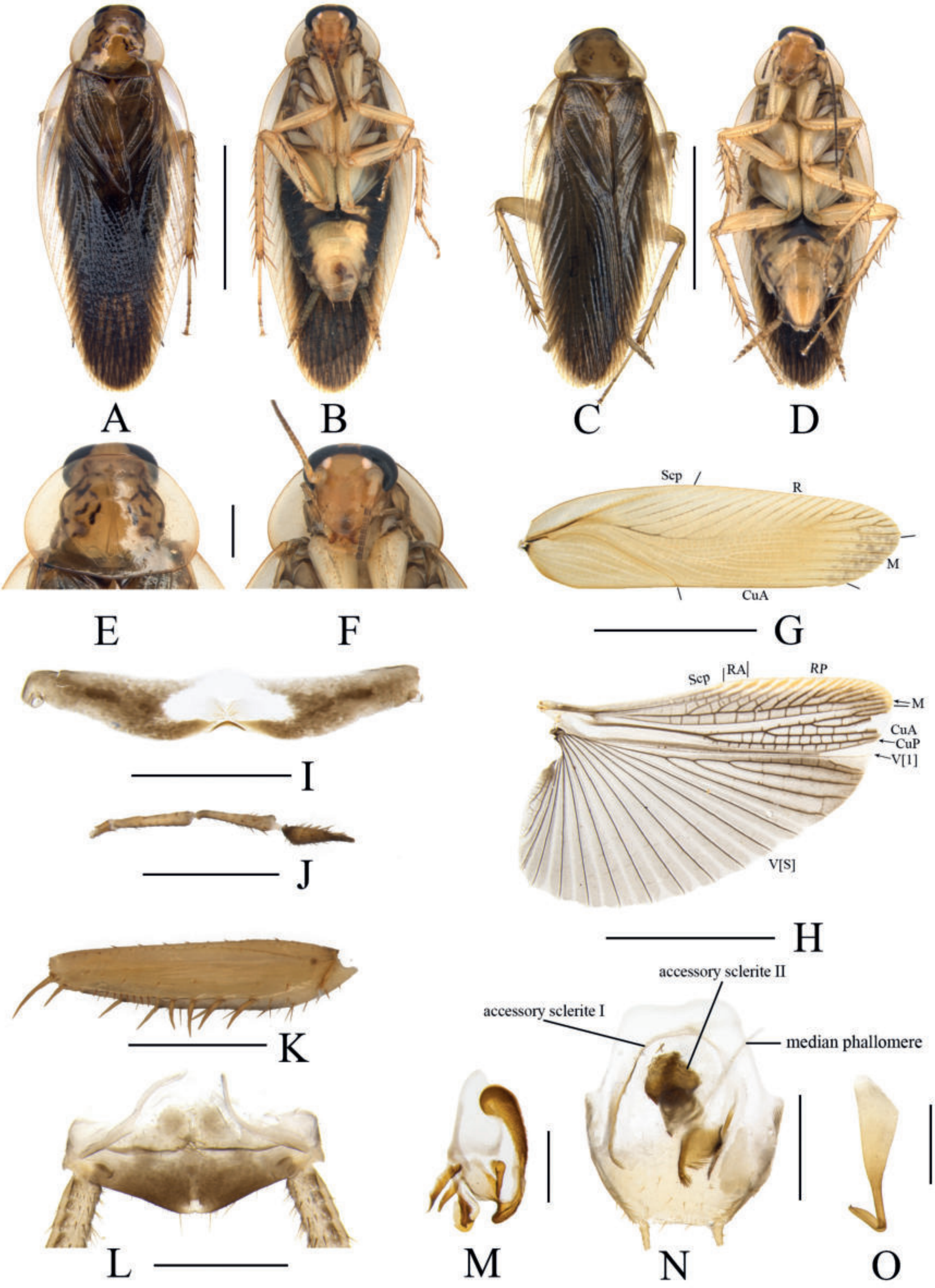

**Figure 7.** *Margattea parabisignata* Li & Che, sp. nov. **A, B, E–O** male **C, D** female **A** holotype, dorsal view **B** holotype, ventral view **C** paratype, dorsal view **D** paratype, ventral view **E** pronotum, dorsal view **F** head, ventral view **G** tegmen, ventral view **H** hind wing, ventral view **I** eighth abdominal tergum, ventral view **J** maxillary palpi segments 3–5 **K** front femur, ventral view **L** supra-anal plate, ventral view **M** left phallomere, ventral view **N** subgenital plate and median phallomere, ventral view **O** hook phallomere, ventral view. Scale bars: 5 mm (**A–D, G, H**); 1 mm (**E, F, I–L, N**); 0.5 mm (**M, O**).

### ***Margattea forcipata*** **Li & Che, sp. nov.**

https://zoobank.org/D3F9C77B-A78F-4D6E-A9B1-938A1b5E67EE
Fig. 8A–O

**Type material.** ***Holotype*****:** China • ♂; Guangdong Province, Zhaoqing City, Fenghuang Town, Jiukeng River, Gold Ditch; 3 Jul. 2015; Zhi-Wei Qiu, Yong-Quan Zhao leg; SWU-B-PS000050. ***Paratypes*****:** China • 6 ♂ & 1 ♀; same data as holotype; SWU-B-PS000051–000057 • 1 ♂; Guangdong Province, Zhaoqing City, Fenghuang Town, Jiukeng River, Lakeside Villa; 4 Jul. 2015; Zhi-Wei Qiu, Yong-Quan Zhao leg; SWU-B-PS000058.

**Measurements (mm).** Male (*n* = 4), pronotum length × width: 2.4–2.6 × 3.2–3.4, tegmina length: 10.5–11.5, body length: 10.4–10.8, overall length: 13.1–13.4. Female (*n* = 2), pronotum length × width: 2.5–2.7 × 3.4–3.6, tegmina length: 11.1–11.5, body length: 10.6–10.7, overall length: 13.4–13.7.

**Description. Male.** ***Coloration*****.** Body, head and face yellowish brown (Fig. 8A, B). Interocular space with a wider brown transverse band. Ocellar spots big and white (Fig. 8F). Antennal base pale yellow, other segments yellowish brown to brown. Maxillary palpi yellowish brown (Fig. 8J). Pronotal disc yellowish brown with dark brown spots and maculae, and two lateral borders pale linen-colored and transparent (Fig. 8E). Legs yellowish brown, with black spots at the base of the tibial spines. Tegmina pale yellowish brown, hind wings transparent, brownish grey (Fig. 8G, H). Abdomen yellowish brown, with black stripes along lateral margins of sterna and reaching the end of abdomen; both sides of each abdominal sternum with one small round black spot on the inside of the longitudinal lines. Cerci yellowish brown (Fig. 8L). Styli yellowish white (Fig. 8N).

***Head*****.** Vertex slightly exposed, interocellar distance wider than the distance between eyes, narrower than the distance between antennal sockets (Fig. 8F). Pronotum subelliptical, broader than long, anterior and posterior margins nearly straight, and postero-lateral angle blunt and round; disc with symmetrical irregular spots and maculae (Fig. 8E). Fifth maxillary palpus expanded, third and fourth maxillary palpi both longer than fifth maxillary palpus (Fig. 8J). ***Tegmina and hind wings*****.** Tegmina and hind wings fully developed, both extending beyond the end of abdomen (Fig. 8A, B). Tegmina with M and CuA radial, M straight with six complete branches. Hind wings with ScP and RA expanded at apex, M simple, without branches; CuA with four complete branches (Fig. 8G, H). ***Legs*****.** Anteroventral margin of front femur Type $B_2$ (Fig. 8K). Four proximal tarsomeres with pulvilli. The pretarsi with arolium, tarsal claws symmetrical and specialized, with minute denticles on ventral margins.

***Abdomen and genitalia*****.** Eighth abdominal tergum specialized, with a tuft of bristles in the middle (Fig. 8I). Supra-anal plate symmetrical, anterior margin straight and truncate, posterior margin produced, slightly concave in the middle. Paraprocts simple, similar, and flaky. Cerci long, setae on the ventral surface (Fig. 8L). Subgenital plate nearly symmetrical, anterior margin slightly concave in the middle. Styli similar, slender, conical; interstylar margin irregular produced (Fig. 8N). Left phallomere complex, irregular bone-shaped, with a long spine and three small spines (Fig. 8M). Median phallomere slender rod-shaped, with a forceps-shaped apex. Accessory sclerite I arched; accessory sclerite II with a transverse rod with denticulate (Fig. 8N). Hook phallomere on the right side, apex slightly curved inwards with a short spine (Fig. 8O).

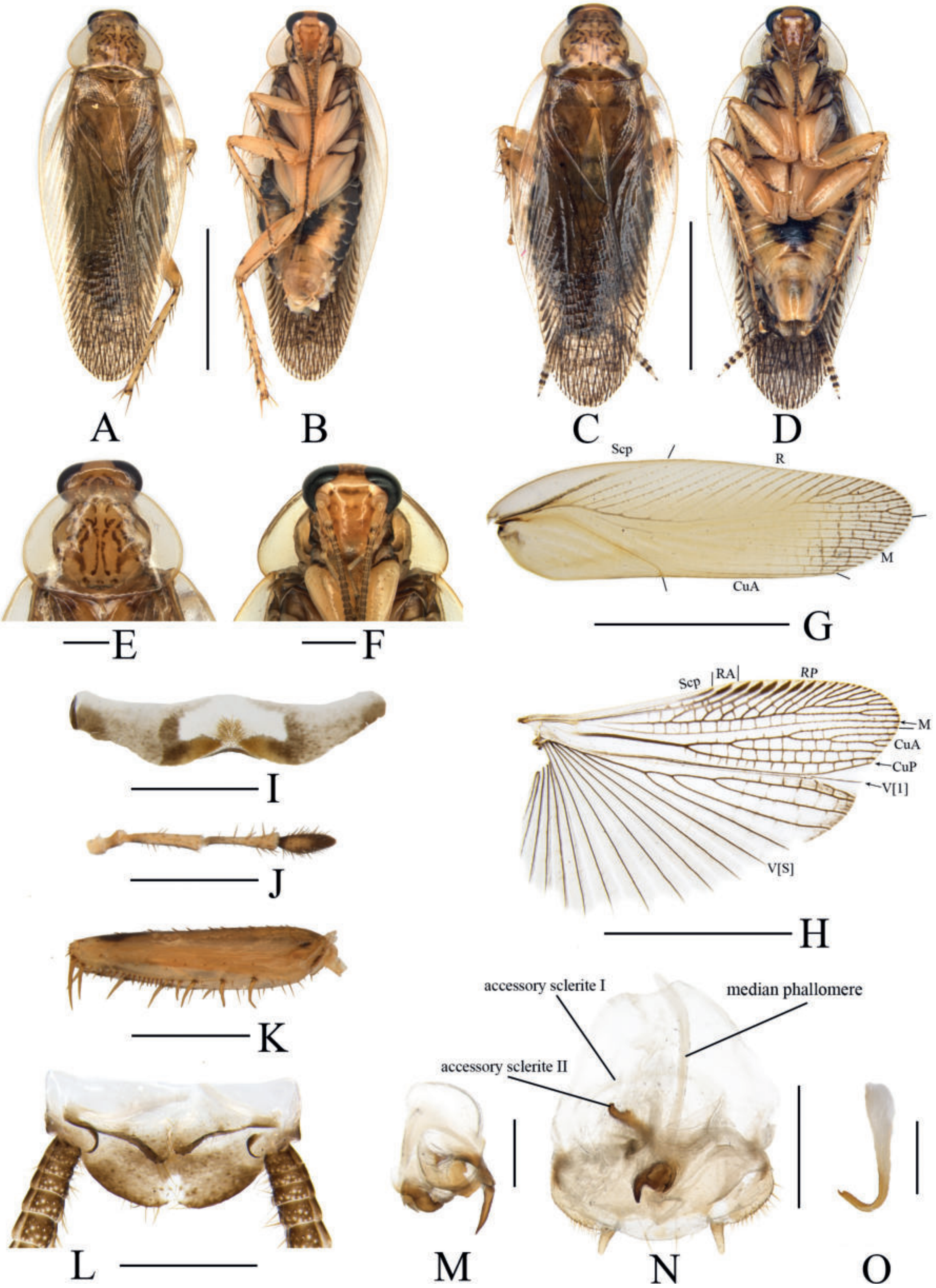

**Figure 8.** *Margattea forcipata* Li & Che, sp. nov. **A, B, E–O** male **C, D** female **A** holotype, dorsal view **B** holotype, ventral view **C** paratype, dorsal view **D** paratype, ventral view **E** pronotum, dorsal view **F** head, ventral view **G** tegmen, ventral view **H** hind wing, ventral view **I** eighth abdominal tergum, ventral view **J** maxillary palpi segments 3–5 **K** front femur, ventral view **L** supra-anal plate, ventral view **M** left phallomere, ventral view **N** subgenital plate and median phallomere, ventral view **O** hook phallomere, ventral view. Scale bars: 5 mm (**A–D, G, H**); 1 mm (**E, F, I–L, N**); 0.5 mm (**M, O**).

**Female.** Similar to the male.

**Diagnosis.** This species is similar to *M. transversa* He & Wang, 2021 in general appearance, but can be differentiated from the latter by the following characters: 1) left phallomere with a long spine; the latter with three long spine-like processes; 2) median phallomere with a forceps-shaped apex; while in the latter, median phallomere apex with a curved spine.

**Etymology.** The specific name *forcipatus*, derived from Latin, refers to the median phallomere with a forceps-shaped apex.

**Distribution.** China (Guangdong).

## Discussion

The intraspecific and interspecific genetic distances are considerably high in *Margattea* (Suppl. material 1). The maximum intraspecific genetic distance in this genus (6.6%) existed in two samples of *M. bisignata*, namely SY_1 and SY_7, which showed high similarity in external and genital morphology and were considered conspecific. The interspecific genetic distance (4.8%–33.1%) is much larger than that of other cockroach groups (Blattellidae: *Episymploce*: 6.9%–9.2%; Blattellidae: *Blattella*: 6.7% (Che et al. 2017); Blaberidae: *Cyrtonotula*: 10.6%–13.7% (Wang et al. 2021); Blattidae: *Periplaneta*: 9.9%–13.1% (Luo et al. 2023)). According to recent dating estimates, *Episymploce* and *Periplaneta* diverged from their sister-groups approximately 50 and 40 Ma, respectively, whereas *Margattea* approximately diverged from its sister clade 100 Ma (Liu et al. 2023). We speculate that the large intrageneric genetic distances of *COI* in *Margattea* may be associated with the deep divergence of this genus.

In this study, we initially determined three morphospecies, namely "*M. spinifera*", "*M. bisignata*", and "*M. paratransversa*", whose individuals are almost indistinguishable. In contrast, these morphospecies are each divided into two MOTUs in molecular species delimitation. We hence examined the male genitalia of different samples from each of these morphospecies and found differences in the accessory sclerite I of "*M. spinifera*" (Fig. 2A, B), the left phallomere of "*M. bisignata*" (Fig. 2C, D), and the median phallomere of "*M. paratransversa*" (Fig. 2E, F). With the assistance of male genitalia examination, these MOTUs were determined as different species. This also occurs in other genera in Blattodea, where large genetic distances among closely related species might occur despite small differences in external morphology (Bai et al. 2018; Han et al. 2022; Zhu et al. 2022). Nine *Cryptocercus* species were extremely similar in external morphology, five of which could be distinguished according to chromosome number and female genital characteristics. The other four species could not be distinguished solely based on chromosome number and female genital characteristics, but they could be distinguished by combining these with molecular species definition (Bai et al. 2018). *Anaplecta omei* Bey-Bienko, 1958b could be distinguished from the other three species with very similar external morphology by molecular species definition and female genitalia characteristics (Zhu et al. 2022). *Pseudoeupolyphaga simila* (Qui, 2022) was extremely similar to *Pseudoeupolyphaga yunnanensis* (Chopard, 1922) in external morphology, but they could be distinguished by combining female genitalia characteristics, oothecae characteristics, and molecular species definition (Han et al. 2022). In Blattodea and even the insect community, there is an increasing occurrence of closely resembling morphologies that do not necessarily belong to the same species. It is no longer possible to determine species only by morphological characteristics; it is also necessary to recognize species from various aspects, e.g., endosymbionts, cytological characteristics, and ecological characteristics.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Qianqian Li: Data curation (equal); methodology (lead); visualization (equal); writing – original draft (lead); writing – review and editing (equal). Wenwen Yao: Data curation (equal); visualization (supporting); writing – review and editing (supporting); Ke Zhang: Data curation (equal); visualization (supporting);Zongqing Wang: Funding acquisition (equal); methodology (supporting); project administration (equal); supervision (equal); writing – review and editing (equal); Yanli Che: Funding acquisition (equal); project administration (equal); supervision (equal); writing – review and editing (equal).

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### Interspecific and intraspecific genetic distances

Author: Qian-Qian Li

Data type: xls

Link: https://doi.org/10.3897/zookeys.1191.113147.suppl1

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DOI: 10.3897/zookeys.1191.118653

Research Article

# *Oblatopyrochroa bellula*, an enigmatic new genus and species of Pyrochroinae (Coleoptera, Pyrochroidae) from Xizang, China

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## Abstract

*Oblatopyrochroa bellula*, a new genus and species of Pyrochroinae Latreille, 1807 from Xizang, China, is described and illustrated. The antennae, cranial apparatus, and genitalia of the new genus form a truly unique set of characters not observed in any other pyrochroid genus. The taxonomic position and phylogenetic relationships of *Oblatopyrochroa* **gen. nov.** are also discussed but appear difficult to resolve.

**Key words:** Fire-colored beetle, taxonomy, Tibet

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## Introduction

Pyrochroinae Latreille, 1807 is the most speciose subfamily of Pyrochroidae Latreille, 1807 and is widely distributed in the Holarctic Region, especially in temperate areas of Asia. This subfamily includes more than 120 recent species in 14 genera (Young 1975, 2002; Young et al. 2020; Pan et al. 2021; Molfini et al. 2022): *Dendroides* Latreille, 1810 (8 species), *Dendroidopsis* Young, 2004b (4 species), *Eupyrochroa* Blair, 1914 (1 species), *Frontodendroidopsis* Young, 2004b (3 species), *Hemidendroides* Ferrari, 1869 (4 species), *Himalapyrochroa* Young, 2004a (2 species), *Neopyrochroa* Blair, 1914 (4 species), *Phyllocladus* Blair, 1914 (5 species), *Pseudodendroides* Blair, 1914 (7 species), *Pseudopyrochroa* Pic, 1906 (ca 70 species), *Pyrochroa* Geoffroy, 1762 (5 species), *Pyroghatsiana* Young, 2016 (1 species), *Schizotus* Newman, 1838 (5 species), and *Sinodendroides* Young, 2005 (2 species). However, most of the abovementioned genera include only few species, the only world revision was admittedly preliminary (Blair 1914), and no comprehensive taxonomic revision including phylogenetic hypotheses has been published for this subfamily. The taxonomic validity of some genera has been debated (e.g. *Eupyrochroa*, *Pseudopyrochroa*, etc.; Gao et al. 2024).

In May 2023, a unique species of fire-colored beetle was discovered in Xizang, China. The antennae, cranial apparatus, and male genitalia form a truly unique set of characters not observed in any other described pyrochroid genus. Therefore, we propose it as a new pyrochroine genus, which is described and illustrated below.

## Material and methods

The male holotype is deposited at the Museum of Hebei University, Baoding, China (**MHBU**). The specimen was studied using a Nikon SMZ1500, and the images were taken using a Canon EOS 5D Mark III (Canon Inc., Tokyo, Japan) with a Laowa FF 100 mm F2.8 CA-Dreamer Macro 2× or Laowa FF 25 mm F2.8 Ultra Macro 2.5–5× (Anhui Changgeng Optics Technology Co., Ltd, Hefei, China). The figure of the antenna was drawn by hand using a Nikon SMZ1500 with a camera lucida. Label data are presented verbatim. Line breaks on labels are denoted by a double slash (//); metadata and notes (not written on the labels, themselves) are presented in square brackets ([ ]). Scientific names are uniformly presented in italics.

Most of the terms in the description are from previous literature (e.g. Young 1975). The ocular index (OI) was first used to quantify the relative distance between the compound eyes of Alleculinae Laporte, 1840 (Campbell and Marshall 1964).

$$\mathrm{OI} = \frac{\text{Minimum dorsal distance between compound eyes}}{\text{Maximal dorsal width across compound eyes}} \times 100.$$

## Results

**_Oblatopyrochroa_ Gao, Young & Pan, gen. nov.**
https://zoobank.org/87AF31B8-8653-45FB-801C-3F9A4E1154B3
Fig. 1
Vernacular Chinese name: 凹赤翅甲属

**Type species.** *Oblatopyrochroa bellula*, new species, by monotypy and present designation.

**Diagnosis.** This new genus is easily distinguished from other pyrochroine genera by the combination of following characters: frons with a single, large transverse concavity between compound eyes (Fig. 1B); eyes of moderate size, transverse width of an eye less than width between eyes, dorsally (Fig. 1B); antennal pedicel long, approximately 0.8× length of scape, dorsal face slightly concave (Fig. 1D); parameres of a male genitalia fused along approximately basal 2/3 and lacking recurved apical hooks (Fig. 1F, G).

**Description. Male: _head_** (Fig. 1B) subtriangular, widest at level of eyes, abruptly constricted behind compound eyes, forming conspicuous “neck”. Temples strongly reduced, not prominent. Frons with a large, transverse concavity, flat anteriad cranial excavation, between antennal insertions. Eyes of moderate size, separated dorsally by more than dorsal width of an eye, narrowly separated ventrally. Clypeus flat, frontoclypeal suture not obvious; labrum subsemicircular; mandibular apices acutely bidentate; maxillary cardo well developed, articulating distally with subrectangular basistipes; galea apically fan-shaped, surface with dense, brush-shaped, yellow setae; maxillary palpi 4-segmented, palpomere I shortest, followed by III, II, and IV of similar length, IV longest, subcultriform; labial palpi 3-segmented, I longest, II and III subequal in length, approximately half that of I; mentum rectangular; gula narrow, posterior tentorial pits conspicuous. ***Antennae*** (Fig. 1D) pectinate beyond antennomere III; scape widened at apex; pedicel approximately 0.8× length of scape; flagellomere I

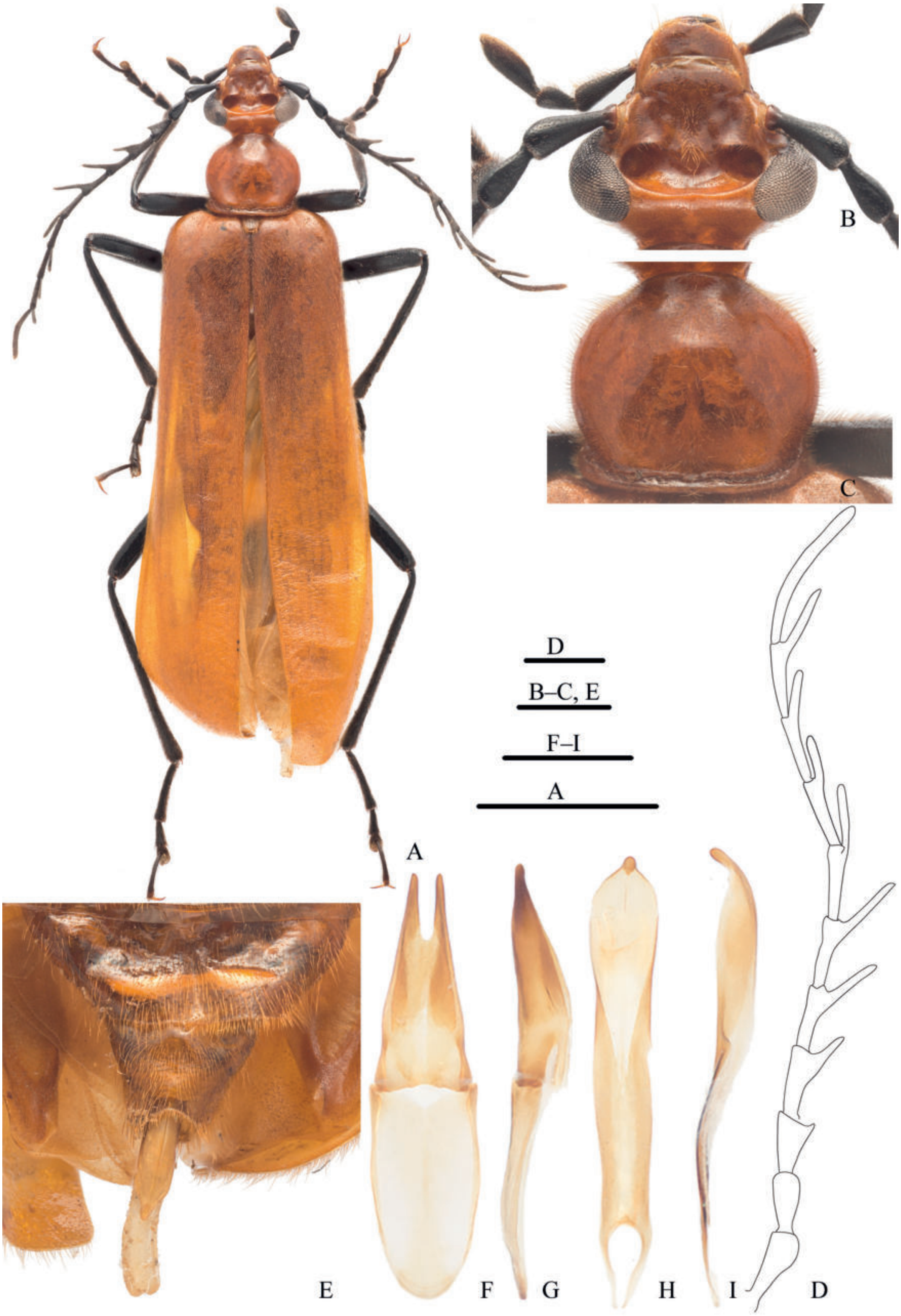

**Figure 1.** *Oblatopyrochroa bellula*, gen. et sp. nov., male, holotype **A** habitus, dorsal view **B** head, dorsal view **C** pronotum, dorsal view **D** antenna, left **E** abdominal sternites VII–VIII, ventral view **F, G** tegmen: **F** dorsal view **G** lateral view **H, I** penis: **H** dorsal view **I** lateral view. Scale bars: 5 mm (**A**); 1 mm (others).

serrate, remaining flagellomeres pectinate with rami cylindrical, less than to approximately as long as respective flagellomere, itself.

***Pronotum*** (Fig. 1C) subcircular, approximately as long as wide; disc shining. Prosternum transverse, with transverse rugosities, middle of posterior margin sharply protruding; prothoracic coxal cavities completely open externally and internally. Mesothorax with scutellum small, widest at base, shield-shaped, slightly longer than wide; mesothoracic coxal cavities not closed outwardly by sterna; mesosternum with posterior margin slightly acuminate mesally. Metathoracic coxal cavities closed externally and internally. Elytra elongate, covering abdomen, longitudinal elytral costae obsolete (Fig. 1A). Legs ambulatorial; tarsal formula 5-5-4; each penultimate tarsomere bilobed; pretarsal claws simple.

Abdominal tergites I–II absent, III–VI poorly sclerotized, VII–VIII lightly sclerotized; sternites I–II absent, III–VI with posterior margins nearly parallel, VIII widest basally, apex acutely emarginate mesally (Fig. 1E). Apex of parameres acuminate, without recurved hooks, basal 2/3 fused, dorsal and terminal parts with scattered yellow setae (Fig. 1F, G); penis broadly flattened, median struts paired, short, narrow, wisest subapically, narrowly nodular at apex (Fig. 1H, I).

**Etymology.** From the Latin root “*oblat*-” for “spread out” and *Pyrochroa*, in reference to the single, large transverse concavity on the frons, putatively diagnostic for the genus. This generic name is feminine.

**Distribution.** China: SE Xizang.

### ***Oblatopyrochroa bellula*** Gao, Young & Pan, sp. nov.

https://zoobank.org/38C0977F-0DB3-4847-9E1D-1DFD7059E068
Fig. 1
Vernacular Chinese name: 秀凹赤翅甲

**Diagnosis.** This species, the only known member of *Oblatopyrochroa*, can be recognized by the generic diagnosis given above.

**Description. Male: *body*** (Fig. 1A) orange-yellow, except labial palpi, antennae, and legs black; mandibular apices dark brown. Body densely covered with short, fine, orange-yellow setae; dorsal surface of head sparsely setose except for patch of moderately long, mostly retrorse setae along meson of frons and along anterior rim of cranial excavation. Body length: 19.8 mm; humeral width: 4.8 mm.

***Head*** (Fig. 1B) with dense, small punctures, diameter of punctures less than spacing of punctures, each inside with a very fine, medium-length seta. Dorsal distance between compound eyes wide (OI = 49.4). Clypeus and labrum flattened; labrum with anterior margin slightly emarginate. Frons with widely U-shaped, sub-reniform concavity, shallowly excavate mesally and more deeply so on sides near compound eyes, posterior margin complete, anterior margin obsolete mesally. ***Antennae*** (Fig. 1D) extending back to near middle of elytra; flagellomere I shortest; II–IV subequal in length, approximately as long as pedicel.

***Pronotum*** (Fig. 1C) widest in middle, approximately as wide as head, length 0.87× width; disc shining, densely covered with small punctures, each side of base with inconspicuous protuberance; basal marginal bead complete. Scutellar shield densely covered with small punctures. Leg slender; prothoracic tarsomere V longest, I second longest, II–IV gradually shorter; mesothoracic

**Figure 2.** Habitat of *Oblatopyrochroa bellula* **A** general habitat **B** specific site (indicated by arrow) **C** microhabitat (the beetle inside is the holotype of *O. bellula*). Photographed from China, Xizang, Pai Town-Mêdog County Highway 42 km, elev. 1991 m (type locality), by Quan-Yu Ji.

tarsomere I subequal in length to V, II–IV gradually shorter; metathoracic tarsomere I longest, IV second longest, II–III gradually shorter.

Posterior margins of abdominal sternites III–VII subparallel, VIII with posterior margin shallowly, acutely emarginate mesally (Fig. 1E). In dorsal view, parameres subequal in length to phallobase, basal 2/3 of parameres fused (Fig. 1F). Penis broadly flattened, proximal part abruptly narrowed toward apex, apex nodular-shaped and curved ventrally (Fig. 1H, I).

**Type material.** ***Holotype*:** ♂, with the following labels: “2023.V.16 // 西藏派墨公路42 km [China, Xizang, Pai Town-Mêdog County Highway 42 km] // 季权宇采 [Quan-Yu Ji leg.] // 河北大学博物馆 [Museum of Hebei University]”, “29.358986°N // 95.134955°E // elev. 1991 m // 河北大学博物馆 [Museum of

Hebei University]", "HOLOTYPE // *Oblatopyrochroa bellula* n. sp. // Det. Gao, Young & Pan" (MHBU).

**Etymology.** The specific epithet comes from the Latin adjective root "*bellula-*" meaning "pretty" or "elegant", in reference to the beauty of the species.

**Collecting habitat.** The holotype was collected in May on the side of a stretch of road from Pai Town to Mêdog County, at a relative low elevation compared to the average elevation in Xizang, with cool temperatures but moist air (Fig. 2A). Specifically, it was found on a dying tree, parts of which had decayed and died (Fig. 2B, C).

**Distribution.** China: SE Xizang.

## Discussion

*Oblatopyrochroa* differs from all known pyrochroine taxa and shows a mixed distribution of character states. The three most diagnostic characters of *Oblatopyrochroa* are the shape of the male antennal pedicel, the configuration of the male cranial apparatus (sensu Young 2004b), and the male genitalia. The antennal pedicel of male pyrochroines is subject to significant variation at the generic and specific levels. In *Oblatopyrochroa*, it is elongate and approximately 0.8× the length of the scape, although its shape approached slightly in *Phyllocladus kasantsevi* Young, 2005 (see Young 2013: fig. 13) and *Frontodendroidopsis gibbiceps* Young, 2006.

The head of male pyrochroines usually bears one or two pits or depressions that represent important diagnostic features of genera and species. Like several genera and species, *Oblatopyrochroa* has only one cranial pit. However, it is distinctly different from the modifications in *Neopyrochroa* (see Young and Caterino 2007: figs 1C, 2, 3a, 4) and *Phyllocladus* (see Young 2013: figs 2, 3, 8, 9, 12, 14, 15). In genera with a single cranial pit, for example *Eupyrochroa* (Fig. 3A) and *Pyrochroa*, the temples are prominent and the pit is quite shallow.

The male genitalia of Pyrochroinae have the parameres fused for most of their length, for example *Dendroidopsis*, *Eupyrochroa* (Fig. 4A), *Pseudopyrochroa*

**Figure 3.** Head of two pyrochroine species, males, dorsal view **A** *Eupyrochroa insignita* (Fairmaire, 1894) **B** *Pseudopyrochroa carinifrons* Kôno, 1929. Scale bars: 1 mm.

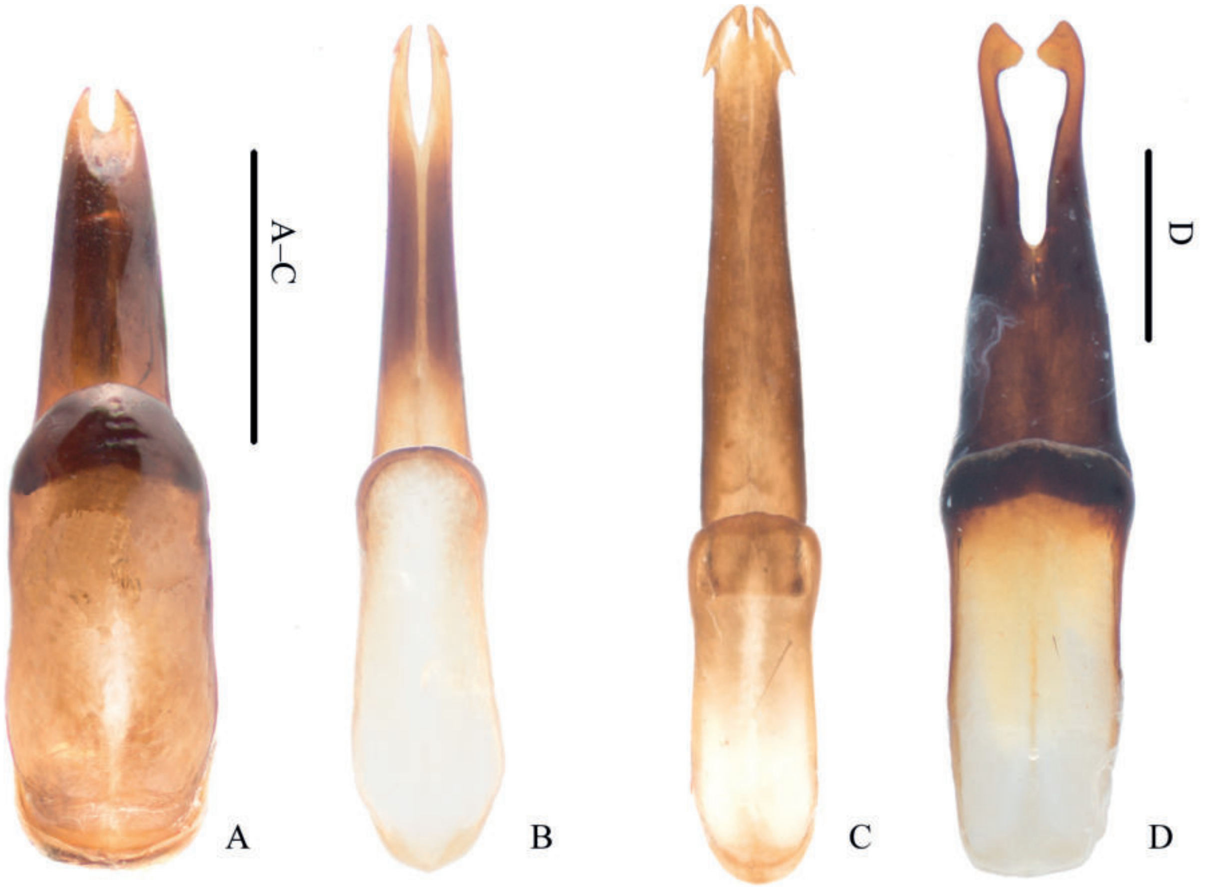

**Figure 4.** Tegmen of pyrochroine species, dorsal view **A** *Eupyrochroa insignita* (Fairmaire, 1894) **B** *Frontodendroidopsis pennyi* Young, 2017 **C** *Pseudopyrochroa carinifrons* Kôno, 1929 **D** *Phyllocladus grandipennis* (Pic, 1906). Scale bars: 1 mm.

(Fig. 4C), *Pyrochroa*, and *Schizotus*, or fused only along the basal half, for example *Himalapyrochroa* and *Phyllocladus* (Fig. 4D). In comparison, the parameres of *Oblatopyrochroa* are fused along the basal 2/3, close to those of *Frontodendroidopsis* (Fig. 4B) but without apically recurved hooks or teeth. The structure of the parameres in *Oblatopyrochroa* is most similar to that of *Eupyrochroa* and *Pyrochroa*. The shape of the penis of *Oblatopyrochroa*, conspicuously widening distally then abruptly “nodular” apically, differs significantly from that of other genera.

Flagellar rami III–IX of *Oblatopyrochroa* are short and thin, similar to *Himalapyrochroa* (Gao et al. 2023; Young 2004a, 2005), not long and almost thread-like, as in most males of *Dendroides*, *Frontodendroidopsis*, and *Sinodendroides*.

The temples of *Oblatopyrochroa* are strongly reduced and not prominent, similar to some species of *Dendroidopsis*, *Frontodendroidopsis*, *Neopyrochroa*, and *Pseudopyrochroa* (Fig. 3B). However, *Dendroidopsis* and *Frontodendroidopsis* usually have large eyes, and the distance between eyes is distinctly less than the dorsal transverse width of each eye in males, which differs from *Oblatopyrochroa*.

Although the observations above clearly support generic recognition, the relationship between the new genus and other pyrochroine genera remains difficult to determine at this time. We anticipate that the relationships will become better resolved by the discovery of larvae and females of *O. bellula*. Additional specimens, together with more material of other genera and species, will enable a more robust molecular phylogenetic analysis of Pyrochroinae as well.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Resources: ZP. Validation: ZP. Visualization: QG. Writing – original draft: QG. Writing – review and editing: DKY, ZP.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

# Review of *Anaka* Dworakowska & Viraktamath, 1975 (Hemiptera, Cicadellidae, Typhlocybinae) with the descriptions of five new species from China

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## Abstract

The dikraneurine leafhopper genus *Anaka* is reviewed based on a comparative morphological study. Five new species, *Anaka auricula* **sp. nov.**, *Anaka cruciata* **sp. nov.**, *Anaka curvata* **sp. nov.**, *Anaka rosacea* **sp. nov.**, and *Anaka spiralis* **sp. nov.** from China are described and illustrated in detail. Additionally, a key to known *Anaka* species is provided along with a checklist of all species and their distributions.

**Key words:** Auchenorrhyncha, Dikraneurini, leafhopper, morphology, taxonomy

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## Introduction

The typhlocybine leafhopper genus *Anaka* Dworakowska & Viraktamath, 1975 belonging to the tribe Dikraneurini was erected by Dworakowska and Viraktamath (1975) with *Anaka colorata* from India as the type species. Thapa and Sohi (1986) added *A. nepalica* and *A. spinosa* from Nepal. Dworakowska (1993) added *A. blada* (India), *A. sumatrana* (Indonesia), *A. shashidhari* (India), *A. burmensis* (Upper Burma), and *A. roryi* (China). Thus, eight species of the genus have been reported to date. Here, we review the previously known species and describe five new species, *Anaka auricula* sp. nov., *Anaka cruciata* sp. nov., *Anaka curvata* sp. nov., *Anaka rosacea* sp. nov. and *Anaka spiralis* sp. nov. from China. We also provide a key to males of all recognized species of the genus.

## Material and methods

All specimens identified in this study were collected by net trapping in southern China and are housed at the Institute of Entomology, Guizhou University, Guiyang, Guizhou, P. R. China (**GUGC:10657**).

Dry specimens were used for preparing descriptions and illustrations. External morphology was observed under a stereoscopic microscope. Body length was measured with an ocular micrometer, in millimeters, from the apex of the head to the apex of the forewing in repose. The genital segments of the specimens examined were macerated in 10% NaOH, washed in water and transferred to glycerin. Male specimens were dissected under a MOTIC B1 SMS-168 SERIES microscope. Figures were made using an OLYMPUS CX41 compound microscope. Photographs were taken with Keyence VHX-1000 and an Olympus E-520 digital camera. The digital images were then imported into Adobe Photoshop CS6 for labeling and figure composition.

## Taxonomic account

### Genus *Anaka* Dworakowska & Viraktamath, 1975

*Anaka* Dworakowska & Viraktamath, 1975: 521.

**Type species.** *Anaka colorata* Dworakowska & Viraktamath, 1975 (type locality: India).

**Description.** Vertex rounded, coronal suture distinct. Face rounded gradually to vertex, flat, lorum broad. Ocelli vestigial. Pronotum ~ 3× longer than head in dorsal view, as broad as head with eyes. Scutum with scutellum distinctly shorter than pronotum. Forewing broad, 3rd apical cell stalked. Hind wing veins RP and MA confluent in male. Hindwing narrow, membrane smoked, veins dark, area bordered.

Abdominal apodemes well developed, reaching caudal margin of 4th abdominal sternite. Pygofer side dark, well sclerotized, dorsal lobe the darkest, hind and ventral margins not pigmented, row of microsetae caudad. Subgenital plate has group of few big macrosetae at approximately mid-length, numerous thin short microsetae present at apical 1/3, several small rigid setae near macrosetae, and a row of thin long setae on basal 1/2 of ventral margin. Paramere hooked at apex, strongly attached to subgenital plate. Connective fused with aedeagus (Dworakowska and Viraktamath 1975). Aedeagus tubular, with basal or apical processes. Dorsoatrium well developed. Gonopore apical.

**Distribution.** China (Guizhou, Guangdong, Guangxi, Yunnan, Sichuan, Chongqing, Hunan, Zhejiang, Fujian, Taiwan), India, Nepal, Sumatra, Indonesia, Burma.

### Checklist of *Anaka* Dworakowska & Viraktamath, 1975

#### 1. *Anaka auricula* sp. nov.

**Distribution.** China (Guizhou).

#### 2. *Anaka blada* Dworakowska, 1993

*Anaka blada* Dworakowska, 1993a: 161.

**Distribution.** India.

#### 3. *Anaka burmensis* Dworakowska, 1993

*Anaka burmensis* Dworakowska, 1993a: 163.

**Distribution.** China (Guizhou, Sichuan, Yunnan, Chongqing, Guangdong, Fujian), India.

### 4. *Anaka colorata* Dworakowska & Viraktamath, 1975

*Anaka colorata* Dworakowska & Viraktamath, 1975a: 523.

**Distribution.** India.

### 5. *Anaka cruciata* sp. nov.

**Distribution.** China (Yunnan).

### 6. *Anaka curvata* sp. nov.

**Distribution.** China (Guangdong, Guangxi).

### 7. *Anaka nepalica* Thapa & Sohi, 1986

*Anaka nepalica* Thapa & Sohi, 1986a: 54.

**Distribution.** Nepal.

### 8. *Anaka roryi* Dworakowska, 1993

*Anaka roryi* Dworakowska, 1993c: 116.

**Distribution.** China (Taiwan).

### 9. *Anaka rosacea* sp. nov.

**Distribution.** China (Guizhou).

### 10. *Anaka shashidhari* Dworakowska, 1993

*Anaka shashidhari* Dworakowska, 1993a: 162.

**Distribution.** India.

### 11. *Anaka spinosa* Thapa & Sohi, 1986

*Anaka spinosa* Thapa & Sohi, 1986a: 56.

**Distribution.** India, Nepal.

### 12. *Anaka spiralis* sp. nov.

**Distribution.** China (Yunnan).

### 13. ***Anaka sumatrana*** Dworakowska, 1993

*Anaka sumatrana* Dworakowska, 1993a: 162.

**Distribution.** Sumatra.

## Key to males of the genus *Anaka* Dworakowska & Viraktamath, 1975

1 Aedeagus with processes basally .......... **2**
– Aedeagus with processes apically .......... **8**
2 Aedeagal processes extended beyond apex of shaft .......... **3**
– Aedeagal processes shorter than or equal to shaft .......... **5**
3 Aedeagal processes sculptured .......... **4**
– Aedeagal processes smooth .......... ***A. sumatrana***
4 Aedeagal processes with areolate sculpture distally and parallel grooves basally .......... ***A. roryi***
– Aedeagal processes with distal areolate sculpture only .......... ***A. nepalica***
5 Aedeagal shaft with minute corrugation on ventral side .......... ***A. shashidhari***
– Aedeagal shaft without minute corrugation on ventral side .......... **6**
6 Apices of aedeagal processes twisted .......... ***A. spiralis* sp. nov.**
– Apices of aedeagal processes straight .......... **7**
7 Aedeagal stem straight, close to basal appendages .......... ***A. burmensis***
– Aedeagal stem curved, well separated from to basal appendages .......... ***A. colorata***
8 Aedeagus with one pair of apical processes .......... **9**
– Aedeagus with two pairs of apical processes .......... ***A. cruciata* sp. nov.**
9 Apex of aedeagal stem not curved .......... **10**
– Apex of aedeagal stem curved .......... **11**
10 Apices of aedeagal processes long and sculptured .......... ***A. rosacea* sp. nov.**
– Apices of aedeagal processes short and not sculptured .......... ***A. spinosa***
11 Aedeagal apical processes unbranched .......... **12**
– Aedeagal apical processes branched .......... ***A. auricula* sp. nov.**
12 Aedeagal apical processes broadly curved .......... ***A. blada***
– Aedeagal apical processes narrowly curved .......... ***A. curvata* sp. nov.**

### ***Anaka auricula*** **sp. nov.**

https://zoobank.org/FFD18D4F-C13E-4AA9-9327-72711E53EE19
Fig. 1A–L

**Type material.** ***Holotype***, 1♂, China: Guizhou Province, Daozhen. 28.1892°N, 107.4294°E, H, 1700 m, 14.V.2006, collected by Yang Zaihua.

**Description.** ***Length***: male 4.2 mm. ***Body*** (Fig. 1A, B) sandy beige. ***Crown*** (Fig. 1C) with two black patches. ***Face*** (Fig. 1D, E) yellowish, frontoclypeal area protuberant, anteclypeus broad. Pronotum yellowish brown, wider than crown. Scutellum yellowish with two blackish patches at lateral corner. ***Forewing*** (Fig. 1F) infuscate 3rd apical cell stalked, hind wing (Fig. 1G) transparent.

***Male abdomen*** (Fig. 1H) well developed and reaching 4th abdominal sternite. ***Pygofer side*** (Fig. 1I) broad, single row of thin setae on central and apical parts.

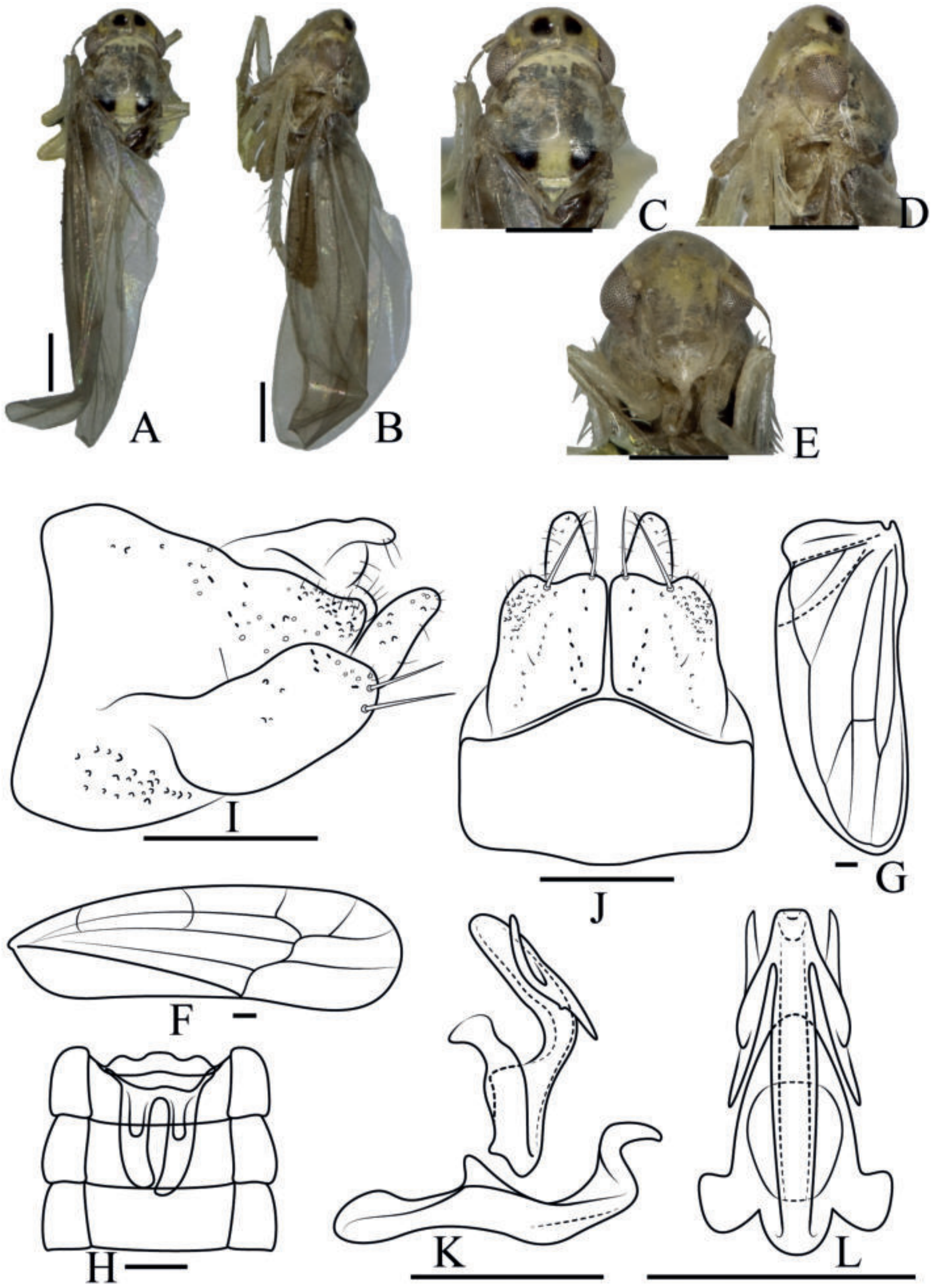

**Figure 1.** *Anaka auricula* sp. nov. **A** male body, dorsal view **B** male body, lateral view **C** head and thorax, dorsal view **D** head and thorax, lateral view **E** face **F** forewing **G** hindwing **H** abdominal apodeme **I** male pygofer, lateral view **J** subgenital plate, ventral view **K** aedeagus, connective, and paramere, lateral view **L** aedeagus and connective, ventral view. Scale bars: 0.5 mm (**A–E**); 0.1 mm (**F–L**).

Basal 1/2 of subgenital plate (Fig. 1J) broad, distal 1/2 slender in lateral view, two large macrosetae at approximately mid-length, several small setae near macrosetae, and scattered setae on distal 1/2. ***Paramere*** (Fig. 1K) hooked at apex. ***Aedeagus*** (Fig. 1K, L) tubular in lateral view, stem curved at middle, apical processes auricle-shaped with small spine at middle. Gonopore apical.

**Etymology.** The specific epithet is derived from the Latin word *auricula* (an ear) referring to the shape of the aedeagal processes.

**Remarks.** This species has an aedeagus very similar in form to that of *A. blada*, but it differs from that species in having elongated apical processes.

### ***Anaka cruciata* sp. nov.**

https://zoobank.org/71769A36-C830-407C-8082-E4575284A965
Fig. 2A–M

**Type material. *Holotype***, 1♂, China: Yunnan Province, Pingbian. 22.9101°N, 103.7008°E, H, 2084 m, 22.V.2015, collected by Yan Bin.

**Description. *Length*:** male 4.2 mm. ***Body*** (Fig. 2A, B) yellowish. ***Crown*** (Fig. 2C) obtuse. Coronal suture distinct. ***Face*** (Fig. 2D–F) white, frontoclypeal area protuberant, anteclypeus broad. Pronotum yellowish, wider than crown. Scutellum small. ***Wings*** (Fig. 2G, H) without patches.

***Male abdomen*** (Fig. 2I) reaching 4th abdominal sternite. ***Pygofer side*** (Fig. 2J) broad, with a small extension and thin setae on central and apical parts. Basal 1/2 of subgenital plate (Fig. 2K) broad, distal 1/2 slender in lateral view, one large macroseta at approximately midlength, several small setae near macrosetae, and scattered setae on distal 1/2. ***Paramere*** (Fig. 2L, M) hooked at apex.

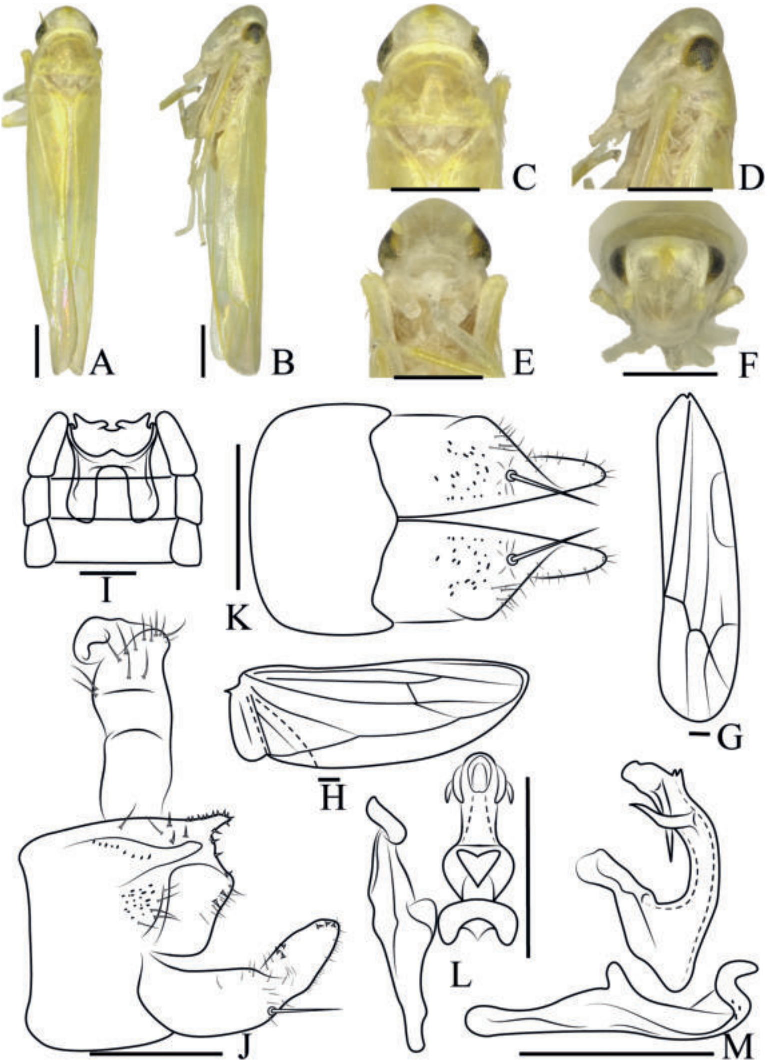

**Figure 2.** *Anaka cruciata* sp. nov. **A** male body, dorsal view **B** male body, lateral view **C** head and thorax, dorsal view **D** head and thorax, lateral view **E** face **F** head, frontal view **G** forewing **H** hindwing **I** abdominal apodeme **J** male pygofer, lateral view **K** subgenital plate, ventral view **L** aedeagus, connective, and paramere, dorsal view **M** aedeagus, connective, and paramere, lateral view. Scale bars: 0.5 mm (**A–F**); 0.1 mm (**G–M**).

Connective fused with aedeagus. ***Aedeagus*** (Fig. 2L, M) tubular, curved, with two pairs of apical processes, of which each pair are crossed. Gonopore apical.

**Etymology.** The specific epithet is derived from the Latin word *cruciatus* (marked by a cross) referring to the shape formed by the two pairs of aedeagal processes.

**Remarks.** This species with two pairs of aedeagal processes differs from all other species of *Anaka*, and two pairs of processes originate from subapical of stem, but in different positions.

### ***Anaka curvata*** sp. nov.

https://zoobank.org/2B819388-B5DB-4879-948A-162E2242B86B
Fig. 3A–L

**Type material.** ***Holotype***, 1♂, China: Guangdong Province, Nanling National Natural Reserve, 24.8796°N, 113.0137°E, H, 1340 m. 4.VIII.2006, collected by

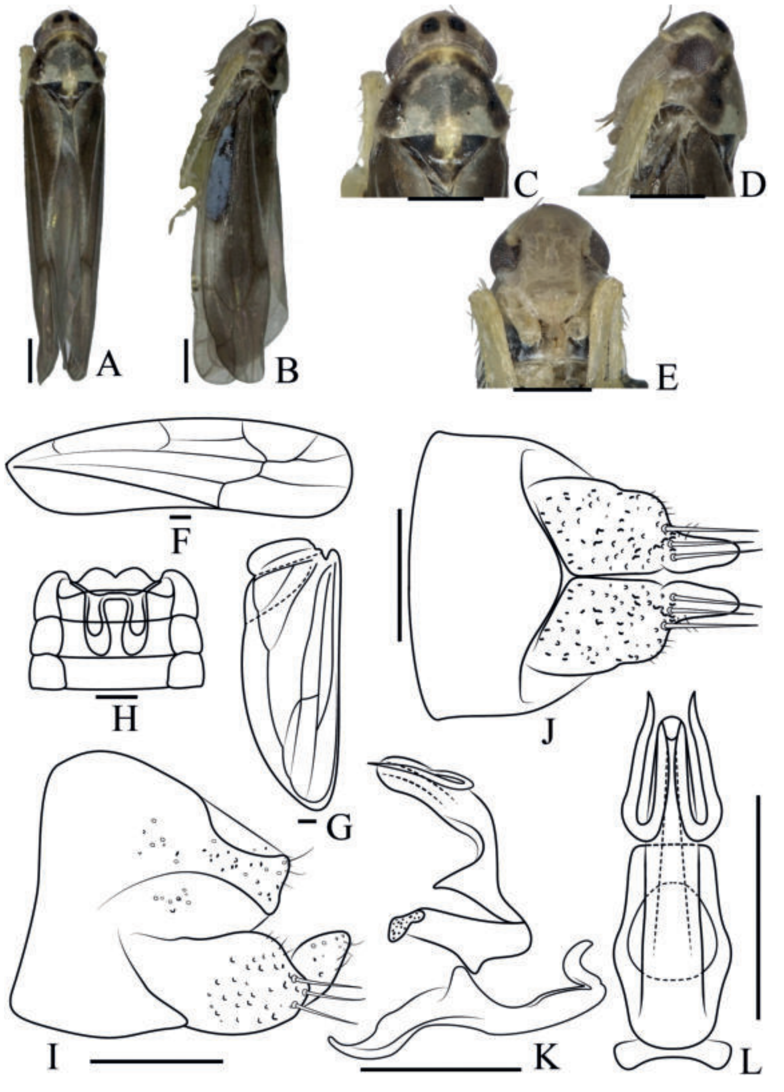

**Figure 3.** *Anaka curvata* sp. nov. **A** male body, dorsal view **B** male body, lateral view **C** head and thorax, dorsal view **D** head and thorax, lateral view **E** face **F** forewing **G** hindwing **H** abdominal apodeme **I** male pygofer, lateral view **J** subgenital plate, ventral view **K** aedeagus, connective, and paramere, lateral view **L** aedeagus, connective, ventral view. Scale bars 0.5 mm (**A–E**); 0.1 mm (**F–L**).

Zhou Zhonghui. ***Paratypes***, 4♂♂, China: Guangxi Province, Damingshan National Natural Reserve, 23.5049°N, 108.4153°E, H, 1290 m. 15.IV.2012, collected by Long Jiankun; 6♂♂, China: Guangxi Province, Damingshan National Natural Reserve, 23.4898°N, 108.4411°E, H, 1250 m. 14.V.2012, collected by Huang Rong and Yu Xiaofei.

**Description. *Length*:** male 4.4–4.5 mm. ***Body*** (Fig. 3A, B) brown. ***Crown*** (Fig. 3C) with two black patches. Coronal suture distinct. ***Face*** (Fig. 3D, E) yellowish brown, frontoclypeal area protuberant, anteclypeus broad. Pronotum brown, wider than crown. Scutellum with a vertical yellow stripe in the median. ***Forewing*** (Fig. 3F) infuscate, 3rd apical cell stalked, hind wing transparent (Fig. 3G).

***Male abdomen*** (Fig. 3H) reaching 4th abdominal sternite. ***Pygofer side*** (Fig. 3I) broad, thin setae on central and apical parts. Basal 1/2 of subgenital plate (Fig. 3G) broad, distal 1/2 slender in lateral view, three large macrosetae at approximately mid-length, several small setae near macrosetae, and scattered setae on distal 1/2. ***Paramere*** (Fig. 3K) hooked at apex. Connective fused with aedeagus. ***Aedeagus*** (Fig. 3K, L) tubular, curved, with a pair of apical processes, which are curved like a paper clip. Gonopore apical.

**Etymology.** The specific epithet is derived from the Latin word *curvatus* (curved) referring to the shape of the aedeagal processes.

**Remarks.** This species is similar to *A. blada*, but it differs in having the aedeagus processes more strongly curved and less divergent from the stem.

### ***Anaka rosacea*** **sp. nov.**

https://zoobank.org/43F14E58-F199-4013-86FB-2ED54327CB64
Fig. 4A–M

**Type material. *Holotype***, 1♂, China: Guizhou Province, Jinsha, 27.4553°N, 106.2667°E, H, 1300 m, 5.VIII.2015, collected by Zhang Yaowen. ***Paratypes***, 3♂9♀, same data as holotype.

**Description. *Length*:** male 4.4–4.5 mm. ***Body*** (Fig. 4A, B) white with red patches. ***Crown*** (Fig. 4C) obtuse, yellowish white. Coronal suture distinct. ***Face*** (Fig. 4D, E) red, frontoclypeal area protuberant, anteclypeus broad, yellowish. Pronotum yellowish, with red patches in the central part, wider than crown. Scutellum yellowish. ***Forewing*** (Fig. 4F) white with red patches along inside margin, hind wing transparent (Fig. 4G).

***Male abdomen*** (Fig. 4H) weakly developed and reaching 4th abdominal sternite. ***Pygofer side*** (Fig. 4I) broad, apical part elliptical. Basal 1/2 of subgenital plate (Fig. 4J) broad, distal 1/2 slender in lateral view, one large macroseta at approximately midlength. ***Paramere*** (Fig. 4K) hooked at apex. Connective fused with aedeagus. ***Aedeagus*** (Fig. 4L, M) tubular, stem inflated at apex, with one pair of apical processes, apical processes straight and sculptured, oriented basad. Gonopore apical.

**Etymology.** The specific epithet is derived from the Latin word *rosaceus* (rose-colored) referring to the color of the head.

**Remarks.** This species marked with rose-red spots. The aedeagal processes are similar to *A. blada* and *A. spinosa* but differs in having the aedeagus with two long apical processes and the processes straight with spiral pattern.

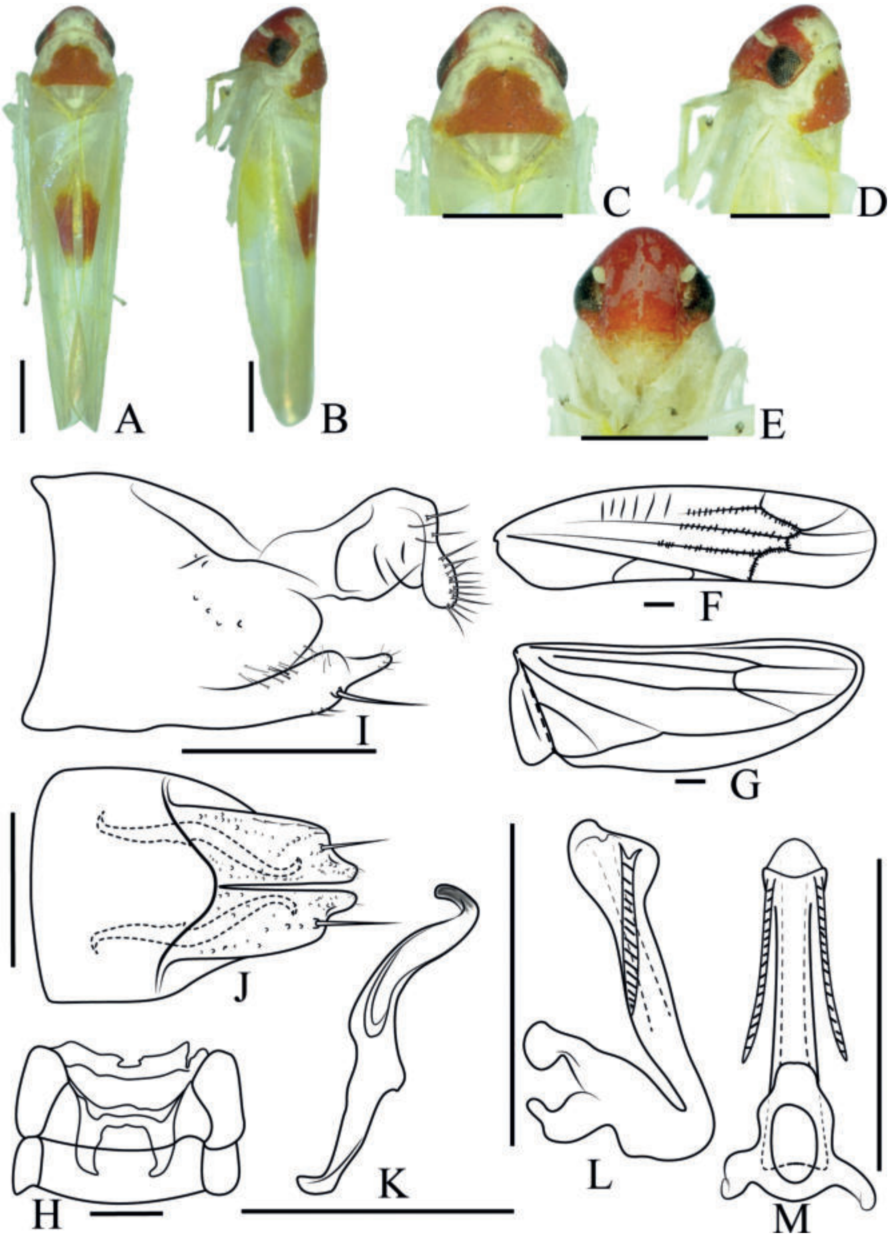

**Figure 4.** *Anaka rosacea* sp. nov. **A** male body, dorsal view **B** male body, lateral view **C** head and thorax, dorsal view **D** head and thorax, lateral view **E** face **F** forewing **G** hindwing **H** abdominal apodeme **I** male pygofer, lateral view **J** subgenital plate, ventral view **K** paramere, lateral view **L** aedeagus and connective, lateral view **M** aedeagus and connective, dorsal view. Scale bars 0.5 mm (**A–E**); 0.1 mm (**F–M**).

### *Anaka spiralis* sp. nov.

https://zoobank.org/FAB85DAA-EBFE-4621-ADED-BBB32FFD5514
Fig. 5A–N

**Type material.** ***Holotype***, 1♂, China: Yunnan Province, Baoshan, 25.1581°N, 99.0814°E, H, 1500 m, 14.V.2016, collected by Li Bin and Ren Guoru. ***Paratypes***, 3♂4♀, same data as holotype.

**Description.** ***Length***: male 4.4–4.5 mm. ***Body*** (Fig. 5A, B) yellow. ***Crown*** (Fig. 5C) obtuse. Coronal suture distinct. ***Face*** (Fig. 5D–F) white, frontoclypeal area protuberant, anteclypeus broad. Pronotum yellow, wider than crown. ***Forewing*** (Fig. 5G) yellow with apical part white, hind wing (Fig. 5H) transparent.

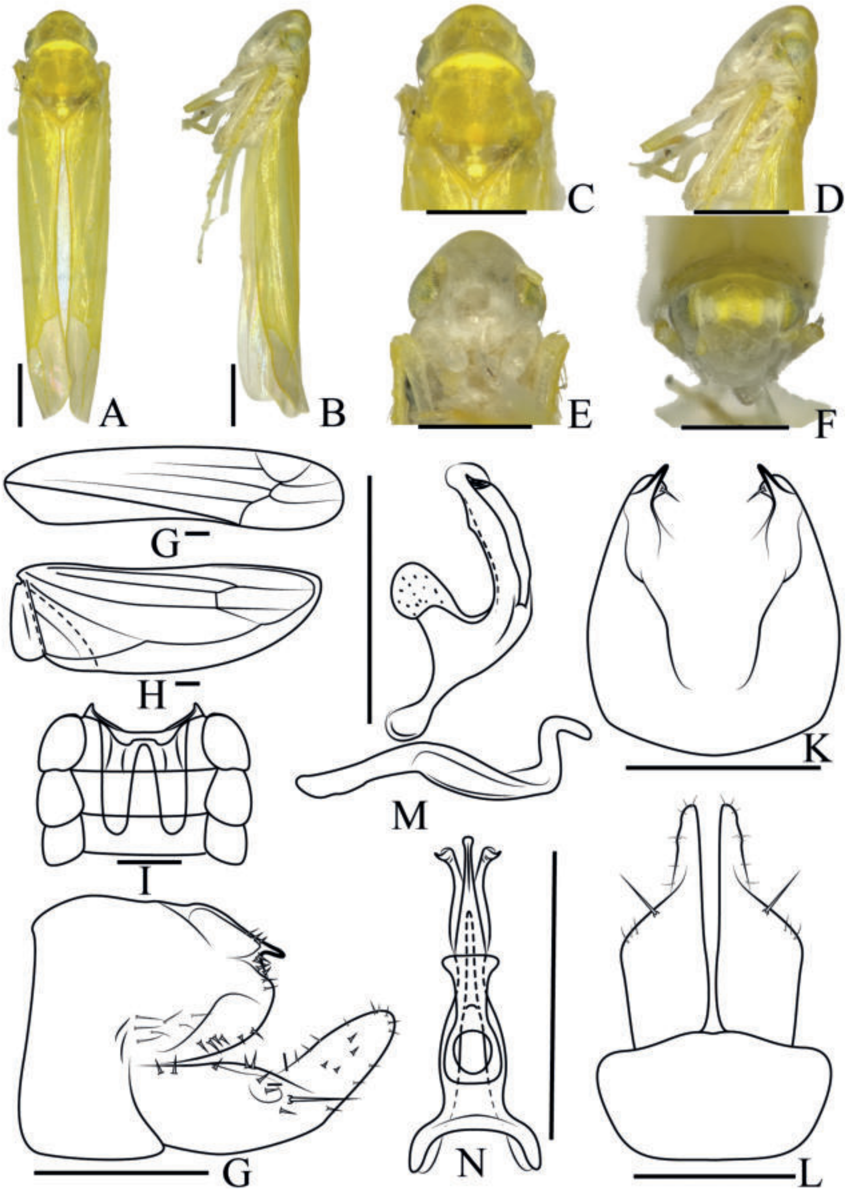

**Figure 5.** *Anaka spiralis* sp. nov. **A** male body, dorsal view **B** male body, lateral view **C** head and thorax, dorsal view **D** head and thorax, lateral view **E** face **F** head, frontal view **G** forewing **H** hindwing **I** abdominal apodeme **J** male pygofer, lateral view **K** male pygofer lobe, dorsal view **L** subgenital plate, ventral view **M** aedeagus, connective and paramere, lateral view **N** aedeagus and connective, dorsal view. Scale bars 0.5 mm (**A–F**); 0.1 mm (**G–N**).

***Male abdomen*** (Fig. 5I) well developed and reaching 5th abdominal sternite. ***Pygofer side*** (Fig. 5J, K) broad, with small extension on superior margin, setae along periphery. Basal 1/2 of subgenital plate (Fig. 5L) broad, distal 1/2 slender in lateral view, one large macroseta at approximately mid-length. ***Paramere*** (Fig. 5M) hooked at apex. Connective fused with aedeagus. ***Aedeagus*** (Fig. 5M, N) tubular, with one pair of basal processes, apical part of processes spiral and not exceeding the stem. Gonopore apical.

**Etymology.** The specific epithet is derived from the Latin word *spiralis* (spiraling) referring to the shape of the aedeagal processes.

**Remarks.** In this species the aedeagus has a pair of basal processes like *A. burmensis* and *A. shashidhari*, but these basal processes have spiral-shaped top, and do not exceed the stem. These features are also not as long as in *A. nepalica*.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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Thapa VK, Sohi AS (1986) A review of Dikraneurini (Homoptera, Cicadellidae) of Nepal. Colemania 3: 53–60.

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Research Article

# Description of a new species of the *Petrolisthes galathinus* complex from the Caribbean Sea, and resurrection of *Petrolisthes occidentalis* from the East Pacific (Crustacea, Anomura, Porcellanidae)

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## Abstract

The *Petrolisthes galathinus* complex currently consists of six American species distributed in the West Atlantic, including the amphi-American *P. galathinus*. All species in the complex are similar in their adult morphology but differ in colour, size, larval morphology, and shape of the adult sternal plate. The West Atlantic species have different geographic ranges, which overlap in the southern Caribbean. Previously published molecular data support the monophyly of the complex, and the reciprocal monophyly of each described species and further clades corresponding to different colour morphs. Here, the morph *P. caribensis* "Blue" is described as *Petrolisthes coeruleus* **sp. nov.**, and *Petrolisthes occidentalis* is formally resurrected for the Pacific individuals of *P. galathinus*. By adding these two species to the *P. galathinus* complex, this now consists of eight species. Colour illustrations of all species and colour morphs are provided and their geographic distributions and ecological ranges are discussed and updated.

**Key words:** Caribbean, colour morphs, ecological range, geographical range, *Petrolisthes coeruleus* sp. nov., *Petrolisthes occidentalis*

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## Introduction

*Petrolisthes galathinus* (Bosc, 1802) is an American species, described as *Porcellana galathina* because of the transverse piliferous ridges covering carapace and extremities resembling those of the galatheid genus *Galathea* (Fig. 1). For more than two centuries the species remained subject of taxonomic conflict for three main reasons: Bosc´s ambiguous description failed to mention a type locality, which was declared as unknown ("on ignore son pays natal"; Bosc 1802: 233), the drawing depicting his holotype specimen consists of a crude sketch (see Fig. 2), and type material does not seem to be traceable. This ambiguous description prompted a labyrinthic path to recreate the morphology and origin of Bosc´s *P. galathinus*. Gibbes (1854), amongst others, criticized Bosc´s drawing because it exhibited "dots instead of stripes", a pattern which did not correspond to observations by earlier authors (e.g., Benedict 1901). Gibbes´ remarks also alluded to different colour patterns, morphologically matching

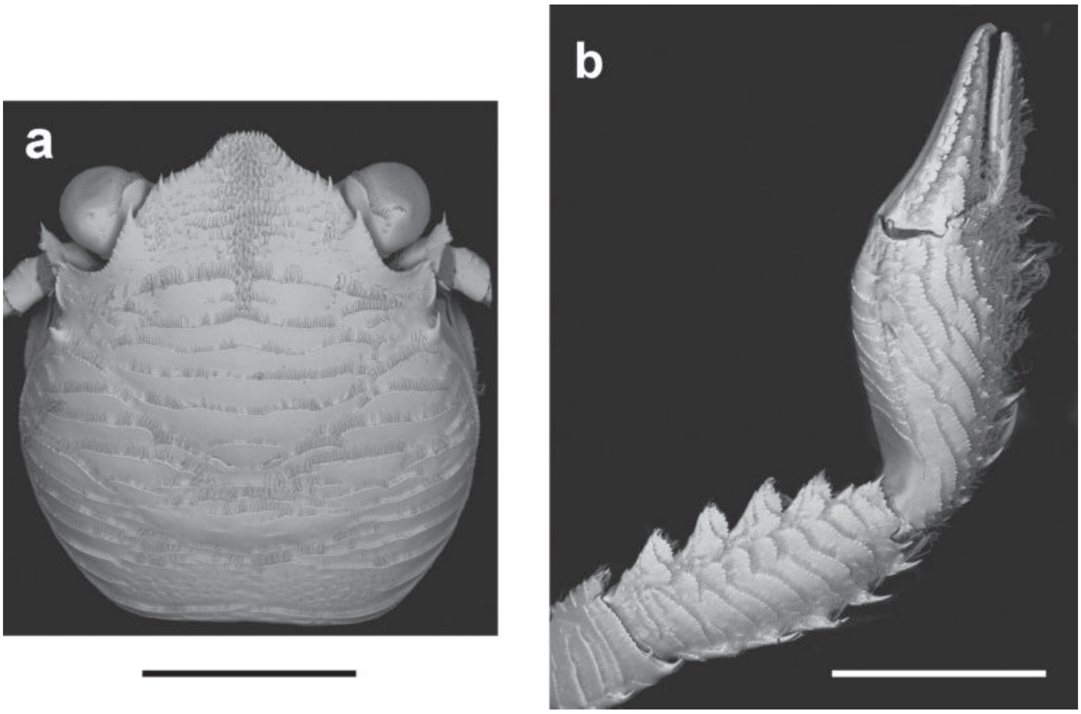

**Figure 1.** Scanning Electron Microscopy (SEM) image of **a** carapace and **b** right cheliped of *Petrolisthes caribensis* Werding, a member of the *Petrolisthes galathinus* complex. Scale bars: 0.2 cm.

**Figure 2.** *Petrolisthes galathinus* (Bosc), original drawing by Bosc (1802: pl. 6, fig. 2).

Bosc´s description. Based on specimens from Puerto Rico, Benedict (1901) described two colour varieties, one with purple stripes matching Gibbes´ (1854) specimens, and another with a double white cross on the carapace. Decades later, Rickner (1975) emphasised the considerable colour variation of specimens from the eastern coast of Mexico, and Williams (1984) reconstructed the history of different colour forms described by previous authors.

Regarding the possible type locality of *P. galathinus*, Latreille (1803: 76) declared the Antilles as the original locality of the species: “Elle se trouve aux Antilles”. Later mentions further referred to its provenance: Desmarest (1825) mentioned Georgia and Florida, and Gray (1831) reported specimens from the British Museum as coming from “North America”. Gibbes (1850) described *Porcellana sexspinosa*, and in a later study (Gibbes 1854), based on own collections from Key West, Florida, concluded that his species was synonymous with Bosc´s, and that it also occurred further north, up to South Carolina. In this study Gibbes (1854) reviewed the literature, acknowledging two western Atlantic species with the typical transverse piliferous rugae: *Porcella galathina* Bosc from the southern Atlantic coast of the United States, and *Porcellana boscii*? Savigny sensu Dana (1852) from Brazil. Gibbes concluded that the specimens from Brazil were different from Savigny´s *P. boscii* Audouin, 1826 from Egypt (de Savigny 1809) and described *Porcellana danae* Gibbes, 1854. *Porcellana boscii* was only listed by de Savigny (1809) but was later described by Audouin (1826). The species is currently accepted as *Petrolisthes boscii* (Audouin) from the Indo-West Pacific (see Werding and Hiller 2007).

In the decades following Bosc´s description, West Atlantic species of *Petrolisthes* with piliferous transverse ridges on carapace and extremities were reported as *P. galathinus* from localities throughout the Caribbean and southwards to Brazil. The eastern Pacific individuals, morphologically matching *P. galathinus*, were described as *Petrolisthes occidentalis* Stimpson, 1859, based on specimens collected in Panama. However, Boone (1931) and Schmitt (1935) reported specimens from the East Pacific under the name *P. galathinus*.

In her study on the Porcellanidae of the western North Atlantic, Haig (1956) extensively reviewed the literature and synonymy of *Petrolisthes galathinus*, concluding that West Atlantic and East Pacific specimens should be considered as one species. As a consequence, all subsequent authors (e.g. Chace 1956; Haig 1962, 1966; Fausto-Filho 1968; Gore 1970, 1974; Rouse 1970; Coelho and Ramos 1972; Rickner 1975; Gore and Abele 1976; Hiller et al. 2004) treated *P. galathinus* as a single widespread species distributed throughout the western Atlantic from North Carolina (U.S.A.) to Santa Catarina (Brazil), and in the eastern Pacific from Jalisco (Mexico) to Ecuador (Hiller et al. 2004).

Werding (1977) recognised different species in the Colombian Caribbean, later describing *P. rosariensis* Werding, 1982 (Fig. 3a). Werding (1983) concluded that *P. galathinus* comprised a complex of several species and described *P. columbiensis* Werding (1983) (Fig. 3b) and *P. caribensis* Werding (1983) (Fig. 3c, d), only distinguishable from *P. galathinus* by their different colouration and two discrete morphological characters (Table 1). Later collections in the Colombian Caribbean revealed the presence of other colour types, described as *P. sanmartini* Werding & Hiller (2002) (Fig. 4a) and *P. bolivarensis*, Werding & Kraus (2003) (Fig. 4b), reaching a total of six species, including *P. galathinus*. Hiller et al. (2006) reconstructed the phylogenetic history of the complex based on mitochondrial DNA sequences and concluded that all species were reciprocally monophyletic, and that further clades, taxonomically matching *P. galathinus* (Fig. 5a–e), supported the presence of new species.

Here, we describe *P. coeruleus* sp. nov. (Figs 6a–c, 7, 8a), which corresponds to the “Blue” morph revealed in the phylogeny by Hiller et al. (2006),

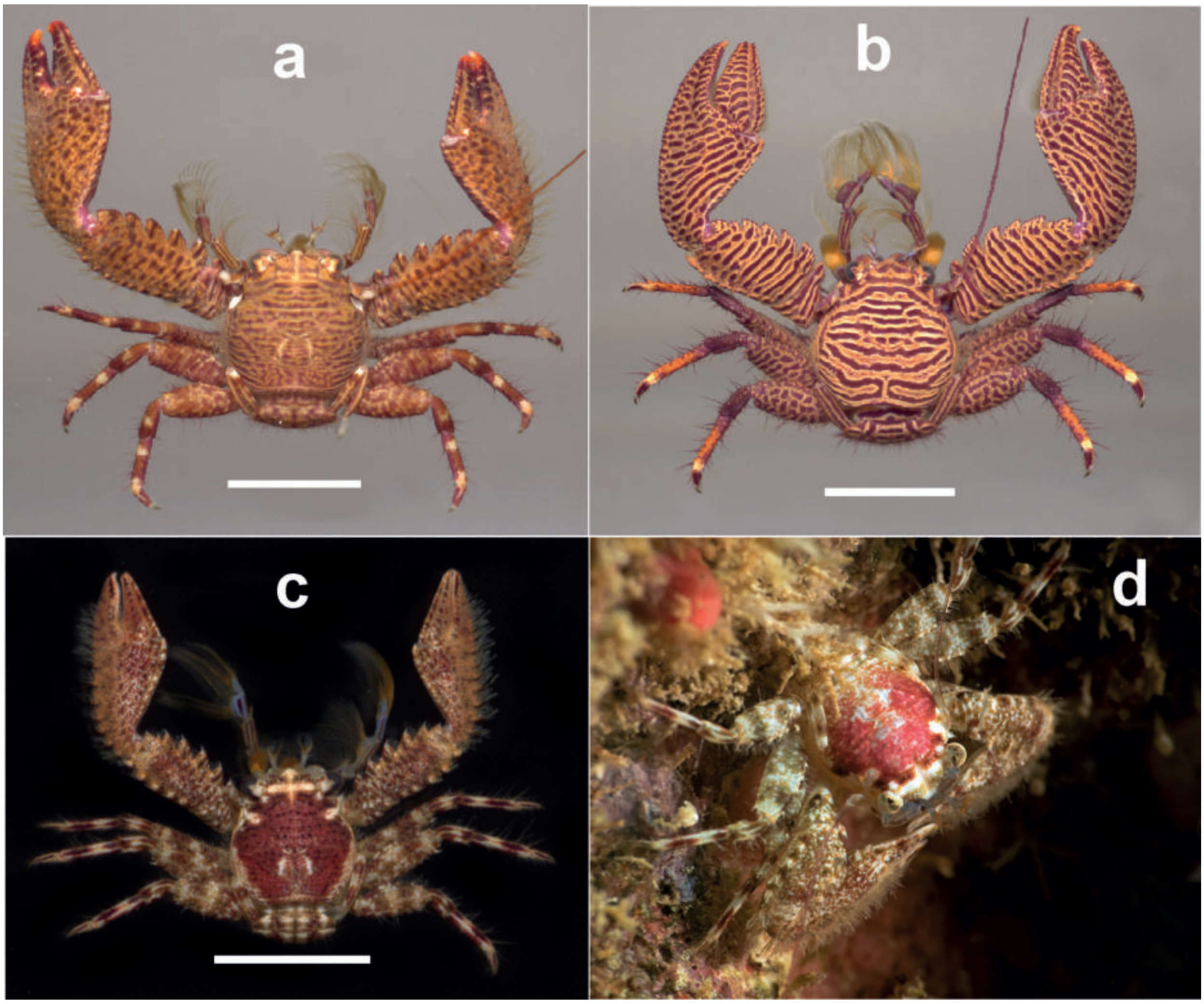

**Figure 3.** Dorsal view of **a** *Petrolisthes rosariensis*, male, Islas del Rosario, Colombian Caribbean **b** *P. columbiensis*, female, Islas del Rosario, Colombian Caribbean **c** *P. caribensis*, male, Islas del Rosario, Colombian Caribbean **d** *P. caribensis*, Roatán, Honduras, photo courtesy of M. Charteris. Scale bars: 0.6 cm (**a**); 0.8 cm (**b**); 0.3 cm (**c**).

**Table 1.** Morphotypes and distinguishing characters of the *Petrolisthes galathinus* complex.

| Species | Number of epibranchial spines | Number of spines on inner border of dactylus of all walking legs | Maximum size of male adults (carapace width in mm) |
|---|---|---|---|
| *P. bolivarensis* Werding & Kraus | 1 | 3 | > 15.0 |
| *P. caribensis* Werding | 1 | 4 | 9.4 |
| *P. coeruleus* sp. nov. | 1 | 4 | 12.4 |
| *P. columbiensis* Werding | 2 | 4 | 7.2 |
| *P. galathinus* (Bosc) “Stripes–Spots” | 1 | 3 | > 14.0 |
| *P. galathinus* (Bosc) “White Teeth” | 1 | 3 | > 15.0 |
| *P. occidentalis* Stimpson | 1 | 3 | > 17.0 |
| *P. rosariensis* Werding | 2 | 4 | 6.0 |
| *P. sanmartini* Werding & Hiller | 1 | 5 | 6.5 |

and resurrect *P. occidentalis* Stimpson, 1859 (Fig. 5a) for the Eastern Pacific individuals of *P. galathinus*. We update the ecological and geographic information of all members of the complex and address the most plausible identity of Bosc´s *P. galathinus*.

**Figure 4.** Dorsal view of **a** *Petrolisthes sanmartini*, male, Islas del Rosario, Colombian Caribbean **b** *P. bolivarensis*, male, Islas del Rosario, Colombian Caribbean. Scale bars: 0.6 cm (**a**); 1.7 cm(**b**).

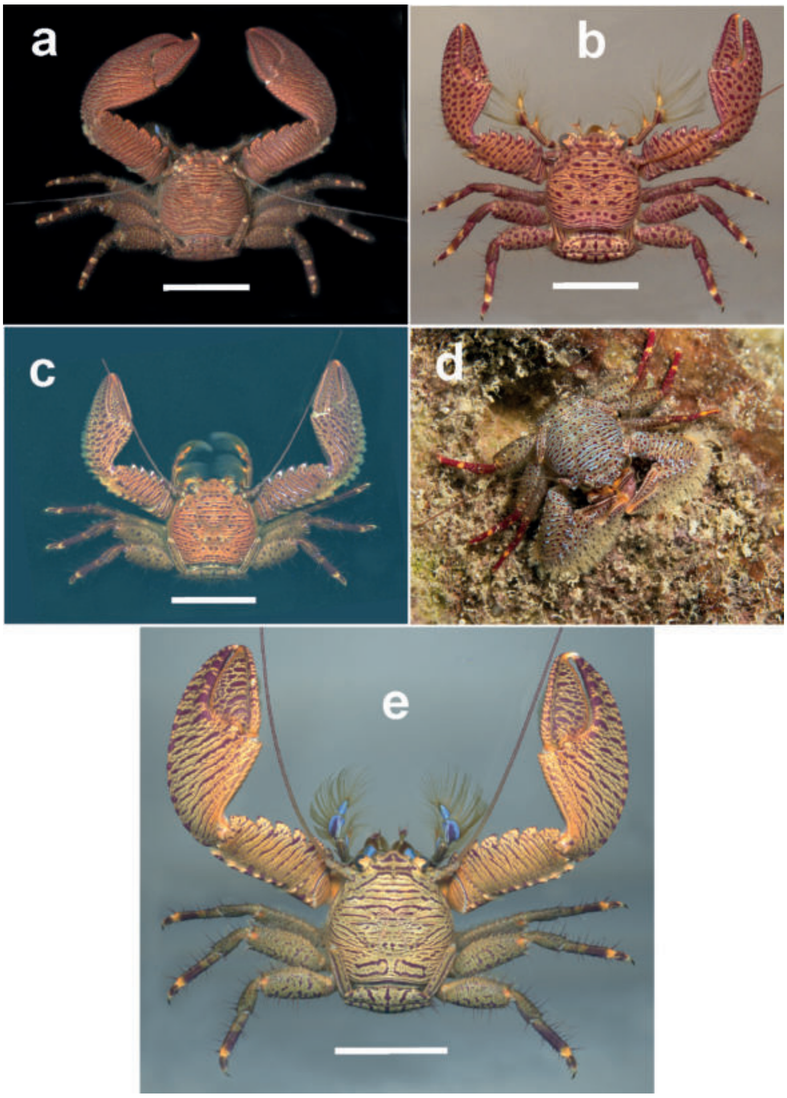

**Figure 5.** Dorsal view of colour morphs within *Petrolisthes galathinus*, as designated by Hiller et al. (2006) **a** East Pacific morph, here resurrected as *P. occidentalis* Stimpson, male, Naos Island, Panamanian Pacific **b** *P. galathinus* “Spots”, male, Islas del Rosario, Colombian Caribbean **c** *P. galathinus* “White Teeth”, female (ov), Isla Cubagua, Venezuela **d** “White Teeth”, Roatán, Honduras, photo courtesy of M. Charteris **e** *P. galathinus* “Stripes”, male, Gulf of Morrosquillo, Colombian Caribbean. Scale bars: 1.65 cm (**a**); 0.71 cm (**b**); 1.36 cm(**c**); 1.35 cm(**e**).

## Material and methods

Material of *Petrolisthes coeruleus* sp. nov. collected in Belize and the Panamanian and Colombian Caribbean, and of *P. occidentalis* collected in the Panamanian East Pacific, was used for morphological examination. Type material of the new species was deposited in the Senckenberg Naturmuseum Frankfurt (**SMF**), Germany, and the Museo de Peces de Agua Dulce e Invertebrados (**MUPADI**) de la Universidad Autónoma de Chiriquí, Panamá (**UNACHI**). Type specimens of *P. occidentalis* are deposited in the Museum of Comparative Zoology (**MCZ**), Harvard University, USA. Additional material of the new species and of *P. occidentalis* was deposited in the collections of the MUPADI in Panama. We updated the geographic and ecological ranges of all species of the *P. galathinus* complex based on new records of material collected by the authors and material found in the Florida Museum of Natural History (**FMNH**). Measurements of specimens are given in mm and correspond to carapace length, followed by carapace width.

## Results

### Systematic account

**Family Porcellanidae Haworth, 1825: 184.**
**Genus *Petrolisthes* Stimpson, 1858: 227.**

***Petrolisthes coeruleus* sp. nov.**
https://zoobank.org/1E5A0FF9-CD71-425D-87BB-439771E73B59
Figs 6a–c, 7, 8a

*Petrolisthes galathinus* Werding, 1982: 443 (part, Islas del Rosario).
*Petrolisthes caribensis* “Blue”: Hiller et al. 2006: 552.

**Type material examined. *Holotype*:** Male, MUPADI–Crus–14, West Atlantic, Panamá, Colón, Punta Galeta, 9°24.161'N, 79°51.634'W; in *Porites porites* (Pallas, 1766), 0.5 m, leg. A Hiller, 12 Apr. 2021; 9.53 × 8.98 mm; female (ov) 8.83 × 7.78 mm; female 7.65 × 7.22 mm. ***Paratypes*:** MUPADI–Crus–02–16, same data as holotype; female (ov) 8.83 × 7.78 mm; female 7.65 × 7.22 mm. SMF57499, West Atlantic, Colombia, Bolívar, Islas del Rosario, Isla San Martín de Pajarales, 10°10.637'N, 75°46.234'W; in coral gravel, 1–2 m, leg. B. Werding, Sep. 2001; female (ov) 7.0 × 6.8 mm; male 7.3 × 7.0 mm; male 7.7 × 7.6 mm; male 5.4 × 5.2 mm; female (ov) 7.7 × 7.4 mm; female (ov) 7.6 × 7.6 mm; male 6.1 × 5.8 mm; female (ov) 7.5 × 7.7 mm; female (ov) 6.4 × 6.5 mm; male 5.4 × 5.3 mm; female 6.1 × 6.2 mm.

**Other material examined (personal collections by the authors).** West Atlantic, Belize, Carrie Bow Cay, 16°48.188'N, 88°5.067'W; under blocks of dead elkhorn coral, 1–2 m, leg. A. Hiller, Jun. 2016; male 5.1 × 4.9 mm; female 5.3 × 5.0 mm.

**Description.** Carapace slightly longer than broad, evenly rounded along branchial margins, broadest on midbranchial level. Surface with transverse, piliferous plications, one epibranchial spine present. Front sinuously triangular with a longitudinal depression, its borders fringed by a row of spinules, giving a serrated aspect; orbitae moderately deep, supraocular spine strong, postorbital angle produced into a spine-tipped tooth. Eyes moderately large, dorsal extension onto

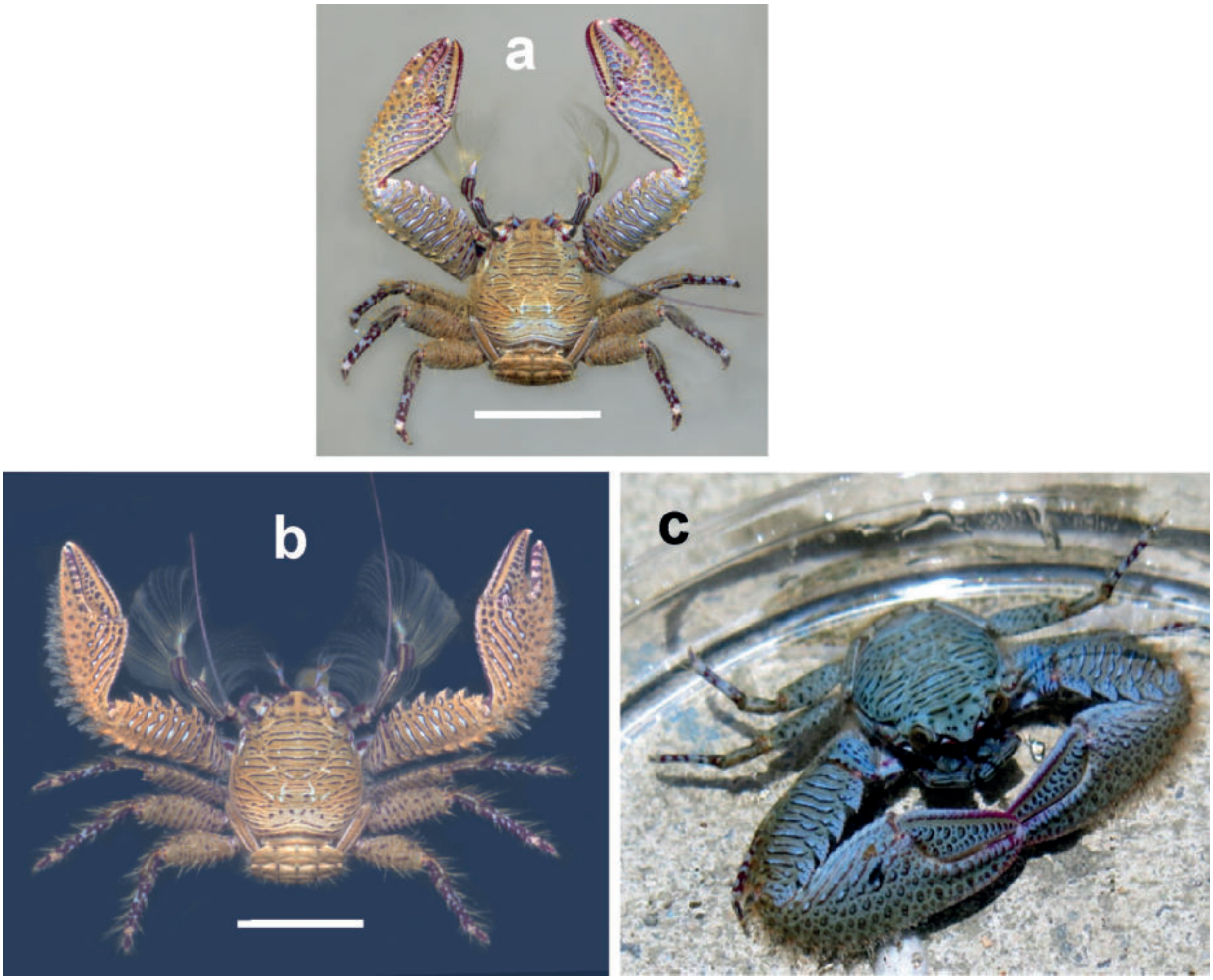

**Figure 6.** Dorsal view of *Petrolisthes coeruleus* sp. nov. **a** male, Islas del Rosario, Colombian Caribbean **b** male, Islas del Rosario, Colombian Caribbean **c** Bocas del Toro, Panamanian Caribbean, photograph courtesy of T. Deuss. Scale bars: 0.5 cm (**a**); 0.65 cm (**b**).

cornea narrow. Basal segment of antennulae with some transverse rugae, anterior margin with teeth. First movable segment of antennae with a serrated, spine-tipped lamellar lobe; second and third segments slightly rugose, flagellum naked.

Chelipeds sub-equal, surface with piliferous striations, merus rugose with serrated, spine-tipped lobe on anterior margin; carpus about two times as long as broad, armed on anterior margin with four, seldom five broad, serrated teeth; posterior margin slightly convex, armed with a row of strong, forwardly directed curved spines. Palm of manus broad with an inconspicuous longitudinal ridge ending at angle between fixed finger and pollex. Lateral surface of dactylus with interrupted transverse, piliferous striations; lateral surface of pollex with rough, conical protuberances extending to fixed finger; outer margin of palm convex, with row of strong, forwardly directed spines, frequently fringed with feathered setae. Gape of fingers with extended ventral pubescence covering proximal portions of pollex and dactylus. Walking legs rugose; anterior margin of merus with fringe of plumose setae, all segments covered with irregularly, wide-set, simple setae; anterior margin of merus with row of spines; large posterodistal spine on merus of walking legs 1 and 2, frequently a smaller one on leg 3; carpus of all walking legs with anterodistal spine; propodus with termi-

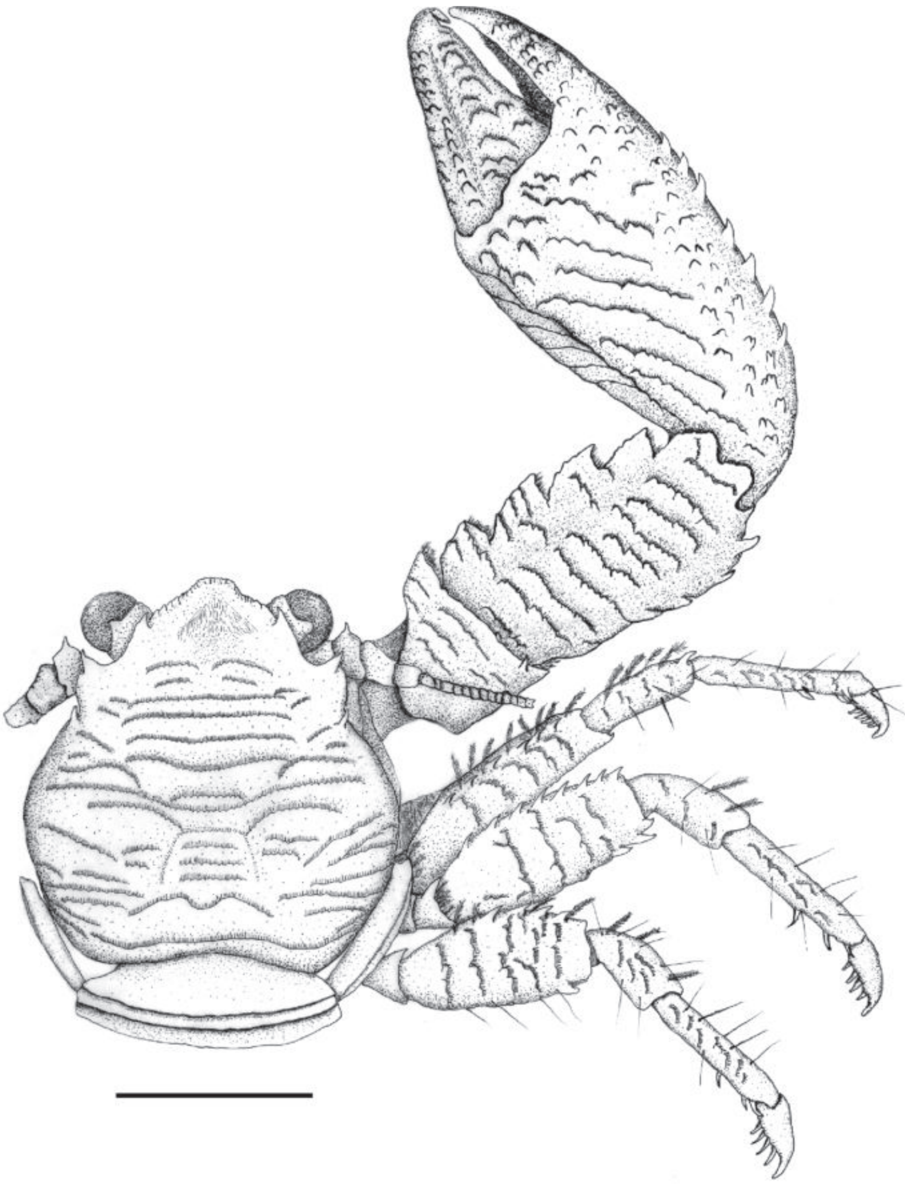

**Figure 7.** Dorsal view of *Petrolisthes coeruleus* sp. nov., male, Punta Galeta, Colón, Panamanian Caribbean. Setae on outer margin of cheliped manus omitted to depict spines. Scale bar: 0.4 cm.

nal triplet of movable spines on ventral border, with one or two additional ones; dactylus large, with four movable spinules on inner margin.

Telson seven-plated with a few short, transverse, piliferous ridges.

**Colouration.** The overall colouration of most specimens consists of a brownish beige background, partly overlaid with iridescent blue tones towards the posterior part of the carapace and on the chelipeds; the transverse ridges of carapace and extremities are marked by blue stripes delineated by narrow dark purple lines. The distal articulations of the walking legs are spotted with blue and purple (Fig. 6a, b). Other specimens show an entirely blue background with similar dark purple delineations of transverse ridges and granules (Fig. 6c).

The new species was first perceived as a different colour morph of *P. caribensis*, as they are not distinguishable through the two main diagnostic traits (Table 1): both bear one pair of epibranchial spines and four movable spines on the dactylus of all walking legs. However, while adult males and females of *P. caribensis* are relatively small, with carapace lengths of up to 9.4 mm in males and 7.5 mm in females, those of *P. coeruleus* sp. nov. reach significantly larger sizes, with carapace lengths of up to 12.4 mm in males, and 12.0 mm in females. The chelipeds in the new species have a more compact aspect, and the dorsal ornamentation on the outer surface of the cheliped's palm is conspicuously more pronounced than in *P. caribensis*, which only bears scattered low granules (Fig. 8a, b).

**Ecology.** While *Petrolisthes caribensis* is a typical inhabitant of shallow-water coralline environments, mostly in the dead bases of the finger coral *Porites porites* (Pallas), *Petrolisthes coeruleus* sp. nov. has a wider habitat spectrum and depth range, as it occurs under boulders in protected sites of the surf zone. The authors found the species on roots of the red mangrove *Rhizophora mangle* L. in a coastal lagoon in the Colombian Gulf of Morrosquillo (9°41.684'N, 75°41.135'W), and also in the furrows of the giant barrel sponge *Xestospongia muta* (Schmidt, 1870) at 8 m depth in the same locality (Table 2). Sequences of the 16S DNA gene previously published by the authors and deposited in the GenBank database (www.ncbi.nlm.nih.gov/Genbank: sequences published as *P. galathinus* "Blue", Accession No. DQ444890–DQ444898) match a sequence from the Yucatán Peninsula collected at 20–29m, published as *P. galathinus* by Bracken-Grissom et al. (2013; accession no. KF182548). This record increases the depth range of the new species, which extends from the upper subtidal at 0.5 m to 29 m depth.

**Distribution.** *Petrolisthes coeruleus* sp. nov. is, so far, known from the Colombian and Panamanian Caribbean, Belize, and the east coast of Mexico. R. Lasley (FMNH; pers. comm. Nov. 2021) confirmed the species to be present in the Bahamas as well. Also, through D. Knott (PoseIDon Taxonomic Services, LLC, Charleston, South Carolina, U.S.A.; pers. Comm. Oct. 2021) we became aware of material of *P. galathinus* collected in South Carolina by SERTC (Southeast Regional Taxonomic Center, South Carolina). Part of the specimens exhibit four spines on the dactylus of the walking legs, thus opening the possibility that the distribution of the new species may reach northern waters along the U.S. western coast. Collections on the coast of South Carolina await further examination to confirm if the new species indeed reaches this northern locality.

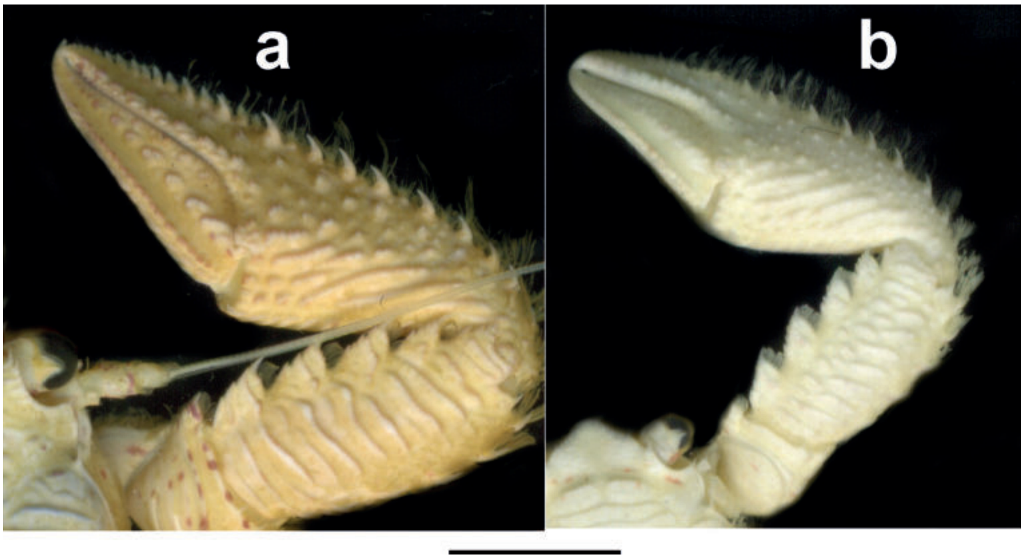

**Figure 8.** Dorsal view of right cheliped of **a** *Petrolisthes coeruleus* sp. nov. and **b** *P. caribensis*. Scale bars: 5 mm (**a, b**). Specimens preserved in ethanol.

**Table 2.** Geographic and ecological range of the species and colour morphs comprising the *Petrolisthes galathinus* complex and allied species. WA = West Atlantic; EP = East Pacific; FMNH = Florida Museum of Natural History.

| Species | Geographic range | Ecology |
|---|---|---|
| *Parapetrolisthes tortugensis* (Glassell, 1945) | WA: Florida, Bahamas, Gulf of Mexico, Belize, Costa Rica, Panama, Colombia, Venezuela, Antilles (Werding et al. 2003; Poupin and Lemaitre 2014; personal records AH and BW) | Coral rubble, from sponges of the genus *Ircinia* Nardo, 1833; pers. comm. F. Sanford), 0.5–54 m (Haig 1956; Werding et al. 2003; Poupin and Lemaitre 2014; personal records AH and BW) |
| *Petrolisthes bolivarensis* | WA: Florida, Panama, Colombia, Venezuela (Werding and Kraus 2003; personal records AH and BW) | Dead part of *Porites porites* (Pallas, 1766), under boulders in protected sites of the surf zone, under dead blocks of *Acropora palmata* (Lamarck, 1816), 0–1.5 m (Werding and Kraus 2003; personal records AH and BW) |
| *Petrolisthes caribensis* | WA: Florida, Bahamas, Gulf of Mexico, Belize, Panama, Colombia, Venezuela, Antilles, (Werding 1983; Werding et al. 2003; Poupin and Lemaitre 2014; FMNH portal; personal records AH and BW) | Dead part of *Porites porites*, under dead blocks of *Acropora palmata*, 0.5–22 m, on coral heads and rubble in shallow waters at 4 m, on outer reef slope ≤11 m (Werding et al. 2003; Poupin and Lemaitre 2014; personal records AH and BW) |
| *Petrolisthes coeruleus* sp. nov. | WA: Bahamas, Gulf of Mexico, Belize, Panama, Colombia (Hiller et al. 2006; FMNH portal; personal records AH and BW). Possibly in Florida up to South Carolina (personal records AH and BW; pers. comm. D. Knott) | Dead part of *Porites porites*, under boulders in protected sites of the surf zone, under dead blocks of *Acropora palmata*, on roots of *Rhizophora mangle* Linnaeus, 1753, in the furrows of *Xestospongia muta* (Schmidt, 1870), 8 m (Quiceno–Cuartas 2012); 0.5–29 m (Bracken–Grissom et al. 2013; personal records AH and BW) |
| *Petrolisthes columbiensis* | WA: Colombia, Cuba (Werding et al. 2003) | Dead part of *Porites porites*, 1–6 m (Werding et al. 2003; Hiller et al. 2006; personal records AH and BW) |
| *Petrolisthes galathinus* “Stripes–Spots” | WA: Panama, Colombia, Guyana, Brazil (Hiller et al. 2006; personal records AH and BW) | Dead part of *Porites porites*, in reef of *Agaricia* Lamarck, 1801, under boulders in protected sites of the surf zone, 0.5–3 m (Hiller et al. 2006; personal records AH and BW) |
| *Petrolisthes galathinus* “White Teeth” | WA: Florida, Gulf of Mexico, Belize, Panama, Colombia, Venezuela, Antilles, possibly along the east coast of Florida (Hiller et al. 2006; Rodríguez et al. 2006; Poupin and Lemaitre 2014; personal records AH and BW) | Dead part of *Porites porites*, under dead, large blocks of *Acropora palmata*, under boulders in protected sites of the surf zone, on coral heads, 0.5–6 m (Hiller et al. 2006; Poupin and Lemaitre 2014; personal records AH and BW) |
| *Petrolisthes occidentalis* | EP: Mexico (Cuastecomate Bay, Jalisco), El Salvador, Costa Rica, Panama, Colombia, Ecuador (Haig 1960; Moran 1984; Hiller et al. 2004, 2006; Ferreira and Anker 2021; personal records AH and BW) | Under boulders at 0–2 m; dredged from sand and sand-shell bottoms at 7.2 and 18 m; among rocks with oysters (Haig 1960; Moran 1984; Hiller et al. 2004; personal records AH and BW) |
| *Petrolisthes rosariensis* | WA: Bahamas, Gulf of Mexico, Belize, Panama, Colombia, Venezuela, Antilles, Brazil (Werding et al. 2003; Poupin and Lemaitre 2014; FMNH portal; personal records AH and BW) | Dead part of *Porites porites*, under dead, large blocks of *Acropora palmata*, under boulders in protected sites of the surf zone, on coral heads, in *Agaricia* coral reef framework, under boulders (Hiller et al. 2006; FMNH portal); 0.5–35 m (Poupin and Lemaitre 2014; personal records AH and BW) |
| *Petrolisthes sanmartini* | WA: Bahamas, French Antilles, Colombia (Werding and Hiller 2002; Werding et al. 2003; FMNH portal; personal records AH and BW) | Dead part of *Porites porites*, in coral rubble; subtidal to 18 m (Werding and Hiller 2002; Werding et al. 2003; FMNH portal; personal records AH and BW) |

**Etymology.** The name *coeruleus* alludes to the blueish tone of carapace and extremities, which comprises a reliable diagnostic character to distinguish this species from *P. caribensis*.

### ***Petrolisthes occidentalis* Stimpson, 1859**

Fig. 5a

*Petrolisthes occidentalis* Stimpson, 1858: 227 (nomen nudum; listed); Stimpson 1859: 73 (description); Streets 1871: 240; Lockington 1878: 395; Faxon 1893: 175; Faxon 1895: 69; Ferreira and Anker 2021: 107.

*Petrolisthes galathinus* Ortmann, 1897: 284; Schmitt 1935: 186; Haig 1960: 36; Haig 1962: 176 (part); Gore and Abele 1976: 21; Gore 1982: 13; Moran 1984: 78; Hiller et al. 2004: 5; Hiller et al. 2006: 548.

**Type material examined.** ***Syntypes*:** MCZ:IZ:CRU–1401, East Pacific, Panama, 1 male, 3 females (ov).

**Other material examined.** MUPADI–Crus–02–17, East Pacific, Panamá, Panama City, Punta Culebra, under large boulders, low intertidal, leg. A. Hiller, 21 Feb. 2015; male, 12.8 × 13.5 mm; male, 12.9 × 13.4 mm.

**Diagnosis.** *Petrolisthes occidentalis* morphologically resembles the other members of the *P. galathinus* complex. An extensive description was given by Haig (1960). The species shares with most members of the group the presence of one epibranchial spine and three movable spines on the ventral side of the dactylus of the walking legs. *P. caribensis*, *P. columbiensis*, and *P. coeruleus* sp. nov. bear four such spines, and *P. sanmartini* bears five (see Table 1). The borders of the carpus of the chelipeds tend to be subparallel in *P. occidentalis* giving the carpus a straight and slender look. In the Atlantic forms, the anterior margin is more convex. *Petrolisthes occidentalis* reaches larger sizes than all Atlantic forms, with carapace lengths of more than 16 mm.

**Colouration.** The transverse ridges and tubercles, which are typical of the members of the *Petrolisthes galathinus* species complex, are bordered with purplish red bands, the intervening grooves are yellowish, the yellow colour prevailing on the carpus teeth. The merus of the walking legs is irregularly spotted with purplish dots, the carpus and propodus show three broad, purplish bands alternating with paler yellowish ones (Fig. 5a).

**Remarks.** *Petrolisthes occidentalis* was listed by Stimpson (1858), and one year later it was described by the same author (Stimpson 1859) from the Pacific coast of Panama. In the description he stated that the species is “scarcely to be distinguished from *P. sexspinosus* Stimpson, 1858”, an older synonym of the western Atlantic *P. galathinus*. In the decades after Stimpson´s studies, various authors referred to the Pacific populations as *P. occidentalis* (see Streets 1871; Faxon 1893, 1895). Ortmann (1897) emphasised the lack of differences between specimens from western India and Pacific Panama, stating that since *P. galathinus* occurred likewise on the east and west of tropical America, *P. occidentalis* should be treated as a synonym of *P. galathinus* (arguments reviewed by Haig 1960).

Hiller et al. (2006) postulated that the Eastern Pacific *P. galathinus* deserves specific status, given the relatively large genetic distances between the Pacific and the most closely related Atlantic clades, which comprised the “Spots” and “Striped” morphs. The East Pacific species differs in colour and size from all Atlantic forms. In a local catalogue of the Porcellanidae of Panama, Ferreira and Anker (2021) published a short note suggesting the need to resurrect the species, based on the recommendations by Hiller et al. (2006).

**Geographic range.** Haig (1960) highlighted the discontinuous distribution of the species in the East Pacific, with a concentration near Panama City, and only few findings from Isla San Lucas, Costa Rica, and off La Libertad, Ecuador. Based on new records of the species in the Panamanian and Colombian East Pacific, Hiller et al. (2004) confirmed that *P. occidentalis* seems to have a continuous distribution from Jalisco, south side of Cuastecomate Bay, Mexico, throughout Central America and Colombia, reaching Salinas and La Libertad in Ecuador.

## Discussion

For more than two centuries *Petrolisthes galathinus* has been viewed as a widely dispersed species in the West Atlantic and East Pacific, with a broad ecological range, inhabiting a variety of substrates like rocks, corals, and sponges, and from the upper subtidal down to 50 m depth. This species turned out to be a complex of morphologically similar species; so far, the *P. galathinus* complex encompasses eight species, including *P. coeruleus* sp. nov. and the resurrected *P. occidentalis*. Each species is supported by distinctive mitochondrial DNA sequences, colouration, adult size, larval morphology, and shape of the sternal plate. All species, except *P. rosariensis*, share a most recent common ancestor (MRCA), which started diverging into different Atlantic and Pacific lineages before the Central American Isthmus finished rising and interrupted gene flow between populations from each ocean (Hiller et al. 2006).

*Petrolisthes galathinus* still needs more revision, as it is unclear which of the molecular clades, designated in the phylogeny by Hiller et al. (2006) as "White Teeth", "Stripes", and "Spots", corresponds to Bosc´s (1802) description. The three variants have different geographic distributions, overlapping in the southern Caribbean. However, while the "Stripes" and "Spots" morphs appear to have a southern distribution reaching Brazil (Hiller et al. 2006), the "White Teeth" morph extends to the Gulf of Mexico, up to the Florida Keys (pers. obs.). Since the "White Teeth" morph extends its range from the southern Caribbean to Florida, it is probable that this is the morph reported from Cape Hatteras, North Carolina by Haig (1960).

The *P. galathinus* complex poses an interesting case to study speciation within allopatric and sympatric scenarios, as it comprises closely related species on either side of the Isthmus of Panama. Such a unique assemblage allows assessing the relationship between genetic divergence and reproductive isolation, given the background of a relatively recent and well dated geological barrier that resulted in sister lineages on each side of the Americas (Hiller and Lessios 2017, 2019).

The evolutionary, ecological, and geographic processes that gave rise to the formation of different West Atlantic species with similar geographic ranges and ecologies remains to be explained in the light of a multigene phylogeographic approach of the species complex. The overlapping geographic and ecological ranges in the southern Caribbean (Table 2) are suggestive of ecological speciation driven by different microhabitats offered by coral reefs, where all species occur.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

Both authors have contributed equally.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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