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Phylogenetic relationships and subgeneric classification of European *Ephedrus* species (Hymenoptera, Braconidae, Aphidiinae)

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Abstract

In this study two molecular markers were used to establish taxonomic status and phylogenetic relationships of *Ephedrus* subgenera and species distributed in Europe. Fifteen of the nineteen currently known species have been analysed, representing three subgenera: *Breviephedrus* Gärdenfors, 1986, *Lysephedrus* Starý, 1958 and *Ephedrus* Haliday, 1833. The results of analysis of COI and EF1α molecular markers and morphological studies did not support this classification. Three clades separated by the highest genetic distances reported for the subfamily Aphidiinae on intrageneric level. *Ephedrus brevis* is separated from *persicae* and *plagiator* species groups with genetic distances of 19.6 % and 16.3 % respectively, while the distance between *persicae* and *plagiator* groups was 20.7 %. These results lead to the conclusion that the traditional subgeneric classification of *Ephedrus* needs revision. Species from *persicae* species group are raised to subgenus level as *Fovephedrus* Chen, 1986 and *Lysephedrus* **syn. nov.** is assigned as a junior synonym of subgenus *Ephedrus*. Key for identification of *Ephedrus* subgenera is provided. *Ephedrus hyadaphidis* Kocić & Tomanović **sp. nov.** is described and several species are confirmed as valid species for the first time. Furthermore, two species are synonymised: *E. dysaphidis* **syn. nov.** as a junior synonym of *E. cerasicola* and *E. blattnyi* **syn. nov.** as a junior synonym of *E. plagiator*.

Keywords

molecular phylogeny, *Ephedrus* subgenera, *Ephedrus hyadaphidis* sp. nov.

Introduction

Members of the subfamily Aphidiinae (Hymenoptera, Braconidae) display a fascinating life cycle as obligatory koinobiont parasitoids of aphids, regulating host population size and density and therefore they are considered as a beneficial insect group. Due to their importance in biological control of aphids, this is one of the most extensively investigated groups within the family Braconidae (Quicke 2015), yet their phylogeny and taxonomy still remains unresolved.

Approximately 40 species worldwide belong to the genus *Ephedrus* (Akhtar et al. 2011); however, this number is continuously changing with the description of new species and synonyms of already described species. In Europe, this genus is represented with 19 valid species: *Ephedrus blattnyi* Starý, 1973, *E. brevis* Stelfox, 1941, *E. cerasicola* Starý, 1962, *E. chaitophori* Gärdenfors, 1986, *E. dysaphidis* Tomanović, Kavallieratos & Starý, 2005, *E. helleni* Mackauer, 1968, *E. koponeni* Halme, 1992, *E. lacertosus* Haliday, 1833, *E. laevicollis* Thomson, 1895, *E. longistigmus* Gärdenfors, 1986, *E. lonicerae* Tomanović, Kavallieratos & Starý, 2009, *E. nacheri* Quilis Perez, 1934, *E. niger* Gautier, Bonnamour & Gaumont, 1929, *E. persicae* Froggatt, 1904, *E. plagiator* Nees, 1811, *E. prociphili* Starý, 1982, *E. vaccinii* Gärdenfors, 1986, *E. validus* Haliday, 1833 and *E. tamaricis* Tomanović & Petrović, 2016. Although there are three more species which apparently inhabit Europe, *E. angustithoracicus* Kiriyak, 1977, *E. hyaloptericolus* Kiriyak, 1977 and *E. mandjuriensis* Kiriyak, 1977, these cannot be treated as valid species in absence of available type material and with species descriptions corresponding to *E. nacheri*, *E. niger* and *E. plagiator*, respectively. The distribution patterns of *Ephedrus* species are very diverse: some being distributed throughout the continent like *E. persicae* or *E. plagiator* or some being restricted to certain microhabitats, for instance, *E. lonicerae* (Tomanović et al. 2007). Furthermore, specialisation to a certain aphid host ranges from strict specialists that parasitise only one species or genus (e.g., *E. prociphili*, specialised parasitoid of the genus *Prociphilus* Koch, 1857) to broadly oligophagous (or polyphagous) species such as *E. persicae* and *E. plagiator*. Both species have been found to attack more than 100 aphid species (each) belonging to different tribes (Starý 1981, Gärdenfors 1986, Žikić et al. 2009, 2017a). Several recent studies suggest that generalist Aphidiinae species might actually not be that broadly oligophagous, but instead composed of cryptic species complexes (Mitrovski-Bogdanović et al. 2013, Derocles et al. 2016, Petrović et al. 2016).

Several species from this genus were implemented in biological control programs, and some of them are commercially produced and packed as part of the cocktails containing different parasitoid agents (Menten 2011). Two of *Ephedrus* species are commercially sold in great numbers, *E. cerasicola* (hundreds of thousands to one million of specimens per week) and somewhat less *E. plagiator* (ten thousand to hundred thousand per week) (van Lenteren et al. 2018). Moreover, there have been attempts of *Ephedrus* species introductions to different continents in order to control alien aphid species with the same geographical origin (Autrique et al. 1989, Carver 1989, Starý 1993, Elliott et al. 1995, Ripa et al. 1995, Armstrong and Peairs 1996). Unfortunately, in the majority of these introductions, *Ephedrus* populations were not established.

Systematic position of *Ephedrus* within the subfamily Aphidiinae is still uncertain. There have been numerous hypotheses about which genus or group is most related to *Ephedrus*. Based on wing venation and several other symplesiomorphic characters, the genera *Toxares* Haliday, 1833 and *Ephedrus* were classified within the tribe Ephedrini (Mackauer, 1968), yet studies on larval morphology showed that they differ significantly (Finlayson 1990). Furthermore, morphological examination of the first instar larvae indicated great morphological similarity between *Ephedrus* and *Praon* Haliday, 1833 (O'Donnell 1989). The genus *Parephedrus* Starý & Carver, 1971 from Australia is considered related to *Ephedrus* (Starý and Carver 1971; Mackauer and Finlayson 2012), sharing similar wing venation and 11 segmented antennae in both sexes. Although Schlinger (1974) positioned *Pseudephedrus* Starý, 1972 and *Parephedrus* within the subfamily Ephedrinae (now tribe Ephedrini), these two archaic genera together with *Vanhartenia* Starý and van Harten, 1974 and *Choreopraon* Mackauer, 2012 are considered to form a separate branch in the phylogeny of Aphidiinae (Starý 1976).

The second uncertainty about the systematic position of the genus *Ephedrus* is whether or not it represents the basal group within the subfamily Aphidiinae. There are some, mostly molecular, studies which consider the tribe Praini as basal within the subfamily (Smith et al. 1999), while some others listed *Aclitus* (Kambhampati et al. 2000) or even *Pseudephedrus* (Žikić et al. 2017b) as basal genera. On the other hand, numerous molecular and morphological studies suggest that *Ephedrus* is the most likely candidate for taking a basal position (Gärdenfors 1986, Belshaw and Quicke 1997, Sanchis et al. 2001, Shi and Chen 2005). Species of this genus possess a range of plesiomorphic characters, such as forewing with fully developed braconid venation, 11-segmented antennae in both sexes, existence of central areola of propodeum, shape of ovipositor sheaths, short petiole and several more (Gärdenfors 1986). Additional evidence that goes into favour of its basal position is the discovery of fossil specimens resembling species of this genus, namely *Ephedrus mirabilis* Timon-David, 1944 and *Ephedrus primordialis* Brues, 1933 (Starý 1973, Ortega-Blanco et al. 2009).

Until now, species of *Ephedrus* have only been used for molecular studies on the subfamily level (Belshaw and Quicke 1997, Smith et al. 1999, Kambhampati et al. 2000, Sanchis et al. 2001, Žikić et al. 2017b), while taxonomic status of its subgenera and relationships between species have never been tested with molecular markers. Currently, genus *Ephedrus* comprises three subgenera: *Lysephedrus* (*E. validus*), *Breviephedrus* (*E. brevis*) and *Ephedrus* (all other species), and the third is divided into three species groups (*plagiator*, *lacertosus*, *persicae*) (Gärdenfors 1986). Based on the presence of fovea on mesoscutum, Chen (1986) described the genus *Fovephedrus* Chen, which was later synonymised with *Ephedrus*, but proposed as a separate subgenus (van Achterberg 1997). However, position of *Fovephedrus* within genus *Ephedrus* was completely unclear.

We decided to investigate the taxonomic status and phylogenetic relationships of *Ephedrus* subgenera and species with European origin, with the combination of nuclear and mitochondrial markers and morphology. Here we propose a new subgeneric classification. Several species in this study are confirmed by molecular approach for the first time and phylogenetic relationships among European species of genus *Ephedrus*

are presented. We describe *Ephedrus hyadaphidis* sp. nov., an additional member of the *plagiator* group, parasitoid of *Hyadaphis foeniculi* Passerini, 1860 on several plant species. Furthermore, we synonymise *E. dysaphidis* as a junior synonym of *E. cerasicola* and *E. blattnyi* as a junior synonym of *E. plagiator*.

Materials and methods

Sample collection and morphological analysis

Parasitoid specimens were sampled throughout Europe during the past two decades. Sampling was conducted in two ways, by net sweeping and by rearing of the parasitoids. The second method was preferred as rearing provides important data on their tri-trophic interactions. Parts of the plants infested with aphid colonies were stored in plastic containers with the lid openings covered with mesh. The samples were transported to laboratory and kept under controlled conditions until the emergence of the parasitoids. Aphids stored in 70% ethanol and plant samples were also collected and identified to species or genus level. Unfortunately, all specimens of *E. lonicerae* were slide mounted and thus couldn't be used for molecular analyses (Žikić et al. 2009) and after a thorough search, we were not able to locate and acquire specimens of *E. vaccinii* or *E. longistigmus*.

Each specimen was examined under the ZEISS Discovery V8 stereomicroscope (Carl Zeiss MicroImaging GmbH, Gottingen, Germany). After DNA extractions, samples were dissected and slide-mounted in Berlese medium. When available, specimens were studied using the Jeol JSM–6460LV scanning electron microscope (Jeol USA, Inc., Peabody, MA, USA). Measurements for new species description were obtained using ImageJ software (Schneider et al. 2012) based on photographs taken with Leica DM LS phase contrast microscope (Leica Microsystems GmbH, Wetzlar, Germany). Morphological terminology follows Sharkey and Wharton (1997).

The examined material is deposited in the Insitute of Zoology, Faculty of Biology, University of Belgrade (Serbia), except for specimens of *E. validus* and *E. koponeni* that were loaned from the Zoological Museum, University of Helsinki (Finland) and 5♀9♂ of *E. hyadaphidis* paratypes that are deposited in the Croatian Natural History Museum, Zagreb, Croatia. *Ephedrus* specimens analysed in this study are presented in Suppl. material 1.

Molecular analysis

Total genomic DNA was extracted from single individuals using the Qiagen Dneasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA), following the manufacturers' protocol. The extraction method was non destructive in order to preserve whole

specimens that could be used in further studies of external morphology. Two molecular markers were used; mitochondrial cytochrome c oxidase subunit I (COI) and nuclear elongation factor 1 alpha (EF1α). The primers used for amplification of COI and EF1α fragments were LCO1490 and HCO2198 (Folmer et al. 1994) and EFf and EFr (Belshaw and Quicke 1997), respectively. The amplification was carried out in a total volume of 40 µl which contained 2 µl of extracted DNA, 0.4 µl of Taq polymerase, 2 µl of each primer (10 mM), 2.4 µl of dNTPs (0.6 mM), 3.6 µl of $MgCl_2$, 4 µl of buffer and 23.6 µl of nuclease free water. PCR profile for COI was: 5 minutes of initial denaturation followed by 35 cycles of 60 second denaturation (94 °C), 60 second annealing (54 °C) and 90 second extension (72 °C) and 7 minutes of final extension (72 °C). PCR conditions for amplification of EF1α were same as in Belshaw and Quicke (1997). Obtained PCR products were purified with QIAquick PCR Purification Kit (Qiagen, Valencia, CA, USA) and sent to Macrogen Inc. (Seoul, Korea) for sequencing. DNA of dry museum specimens, due to fragmentation of DNA, was amplified by using primers for amplification of short barcoding fragments, following the protocol by Mitrović and Tomanović (2018). For certain specimens the quantity of extracted DNA was too low, so only the COI fragment was obtained. That was the case with *E. brevis* individuals. For others, like *E. chaitophori* and *E. tamaricis*, the amplification of EF1 alpha fragment yielded PCR products of high quality, but the sequencing was unsuccessful. The reason for this might be the interruption of sequencing due to the existence of DNA introns or a deletion along the fragment.

Phylogenetic analysis

The sequences acquired after amplification were checked for pseudogenes, visualised in FinchTV Geospiza Inc. (Seattle, USA) and manually edited and aligned in BioEdit program (Hall 1999). Sequences were trimmed to the same length of 557 and 440 base pair positions for COI and EF1α, respectively. MEGA 6 (Tamura et al. 2013) software was used to estimate the evolutionary divergence between sequences. The analysis for both gene fragments was conducted independently in BEAST 2.5 (Drummond et al. 2012) software platform for Bayesian evolutionary analysis. The initial data file was designed in BEAUti with the Tamura-Nei (Tamura and Nei 1993) model with gamma distributed rates among sites (TN93+G), which MEGA 6 proposed as the most appropriate model. The initial data file conducted the analysis with strict clock type and Yule Process speciation. The species *Venturia canescens* Gravenhorst, 1829, belonging to the sister family Ichneumonidae was used as an outgroup species in all analyses. Obtained phylogenetic trees which contained all sequences visualised by FigTree 1.4.3. software (Rambaut 2009) were large and hard to follow, thus a single sequence of each haplotype was used to present the results.

Results

Phylogenetic analyses of the two molecular markers yielded trees with similar branch topographies (Figs 1, 2). A total of 86 COI sequences was analysed (seven, including outgroup, were mined from GenBank and 18 were used from authors' previous publications), and 58 different haplotypes were detected (Fig. 1). Species *E. brevis*, *E. cerasicola*, *E. laevicollis*, *E. validus*, and *E. prociphili* are confirmed as distinct species for the first time with the barcoding marker. Phylogenetic tree based on COI sequences showed species separation into three main phylogenetic clades, which does not correspond to traditional subgenera delineation (Fig. 1). First clade was formed by species belonging to *persicae* species group (*E. persicae*, *E. chaitophori*, and *E. tamaricis*). Second clade was represented with *E. brevis* and third with all other species (*plagiator* clade). *Ephedrus brevis*, the only representative of *Breviephedrus* subgenus was separated from both *persicae* and *plagiator* clades on the phylogenetic tree with the average genetic distances of 19.6 % and 16.3 %, respectively, while genetic distance between *persicae* clade and *plagiator* clade was 20.7 % (Suppl. material 2).

According to the obtained results, the nominative subgenus *Ephedrus* is paraphyletic, consisting of two independent lineages, *plagiator* and *lacertosus* species groups. In addition to these groups *E. validus*, the only member of the *Lysephedrus* subgenus, also grouped within this clade. Moreover, *E. validus* is nested within the *plagiator* species group, forming a separate clade together with *E. helleni*. The second clade within the *plagiator* species group consists of specimens belonging to ten different species (*Ephedrus blattnyi*, *E. cerasicola*, *E. dysaphidis*, *E. hyadaphidis* sp. nov., *E. koponeni*, *E. laevicollis*, *E. nacheri*, *E. niger*, *E. plagiator*, and *E. prociphili*). One individual determined as *E. blattnyi* grouped with *E. plagiator* specimens, with the genetic distance ranging from 0.2 % to 0.7 %. The same was the case for one *E. dysaphidis* specimen which clustered within the *E. cerasicola* clade (genetic distance 0.0 %–1.6 %). Genetic distances between other species within this group vary greatly ranging from 1.1 % between *E. nacheri* and *E. prociphili* up to 7.6 % between the previous two and *E. laevicollis* (Table 3). *Ephedrus lacertosus* is clearly separated as a distinct group with genetic distances from all other *Ephedrus* species above 8.9 %. The clade consisting of *Ephedrus persicae* species is the oldest within the genus and represents a separate subgenus. Within this clade all three analysed species were confirmed as valid. Additionally, within *E. persicae* two separate phylogenetic lines were determined with average genetic distance of 2.5 % (Fig. 1).

With the second molecular marker EF1α, 14 sequences (four mined from GenBank), belonging to eleven species (*Ephedrus cerasicola*, *E. helleni*, *E. hyadaphidis* sp. nov., *E. lacertosus*, *E. laevicollis*, *E. nacheri*, *E. niger*, *E. persicae*, *E. plagiator*, *E. prociphili*, *E. validus*) were analysed. While the genetic distances between species groups and species were significantly lower than those based on COI sequences, the topography of the phylogenetic three remained similar (Fig. 2). As previously, sequences separated into two groups, the first composed solely out of the representative of *persicae* species group, *E. persicae*, and the second containing species from *lacertosus* and *plagiator*

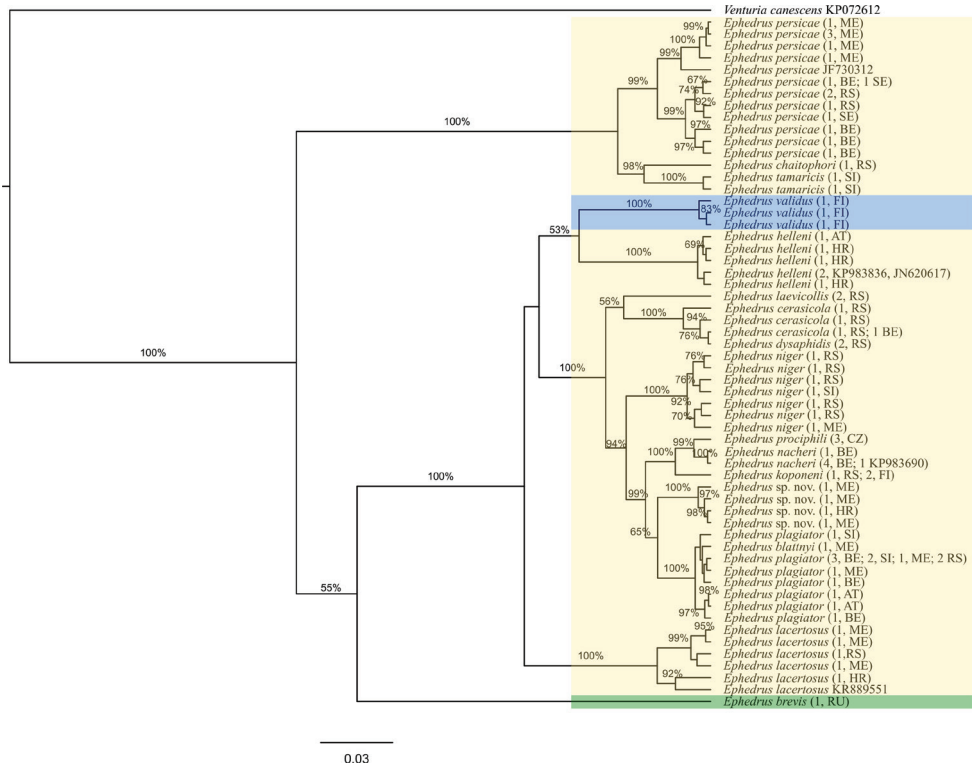

Figure 1. Bayesian inference phylogram for cytochrome oxidase *c* subunit I mitochondrial sequences. Bayesian posterior probabilities above 50 % are shown. The traditional subgenera are marked in different colours: *Lysephedrus* (blue), *Breviephedrus* (green), and *Ephedrus* (yellow). The number of sequences with the same haplotype and countries of origin are presented in brackets. Country abbreviations: AT – Austria, BE – Belgium, CZ – Czech Republic, FI – Finland, HR – Croatia, ME – Montenegro, RS – Republic of Serbia, RU – Russia, SI – Slovenia.

groups. A significant change in relation to the COI phylogenetic tree is clustering of *E. validus* and *E. helleni* together with *E. lacertosus*, species from *lacertosus* group. This topography could be explained by genetic distances: *E. helleni* and *E. validus* show genetic distances of 3.8–7.2 % and 5.7–9.0 %, respectively, when compared to other *plagiator* species, whereas compared to *lacertosus*, these distances are 4.2 % and 5.4 %, respectively. All genetic distances were considerably lower compared to those based on COI, since EF1α is more conservative nuclear molecular marker (see Suppl. material 2). The average genetic distances between *E. persicae* and *lacertosus* and *plagiator* species groups were 7.6 % and 9.0 %, respectively.

The analysis of the COI molecular marker grouped sequences designated as *Ephedrus* sp. nov. into a distinct clade. Genetic distance parameters position sequences of this group as most closely related to *E. plagiator* (2.7 %–3.0 %) and other members of *plagiator* species group (4.3 %–8.0 %). Results of the EF1α phylogenetic analysis confirmed the position of these sequences in relation to other species.

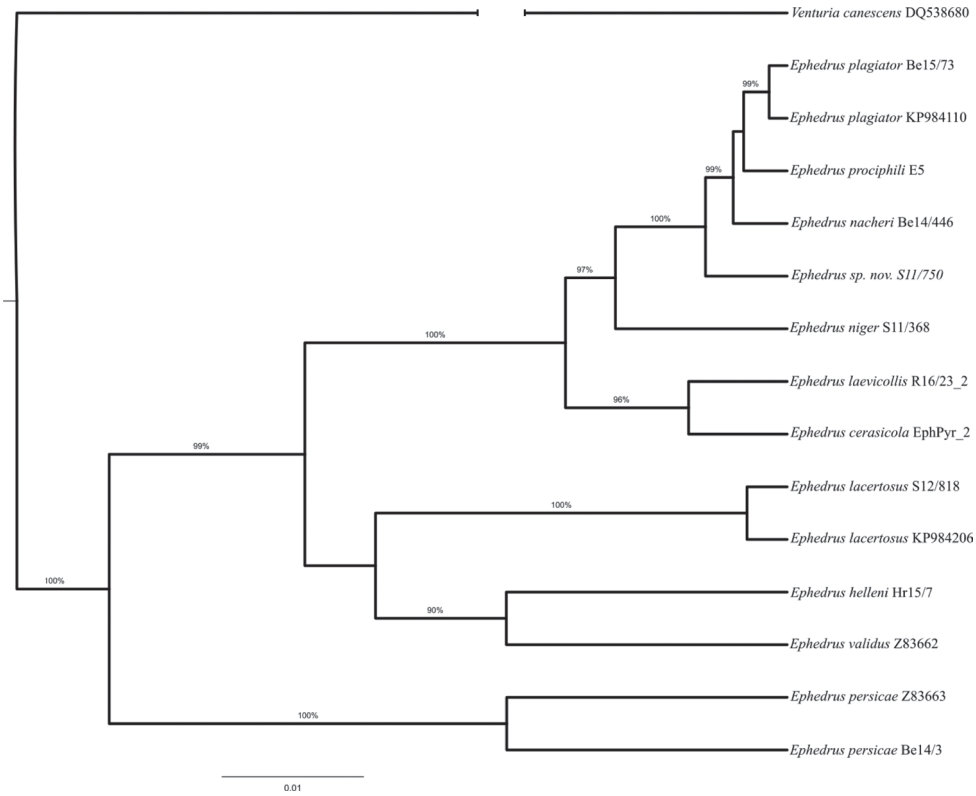

Figure 2. Bayesian inference phylogram for elongation factor 1α nuclear sequences. Bayesian posterior probabilities above 50 % are shown.

Substantial morphological examination of all available specimens of genus *Ephedrus* resulted in discovery of one species new to science, designated as *Ephedrus* sp. nov. in the phylogenetic analysis.

Description of the new species

***Ephedrus hyadaphidis* Kocić & Tomanović, sp. nov.**
http://zoobank.org/92D3A33E-42A9-4177-98DC-40B13653F28D
Fig. 3

Material. Holotype ♀ from Montenegro: Durmitor-Sušica, 27.07.2012, reared from *Hyadaphis foeniculi* on *Sanicula europaea*. Paratypes: 2♂ (slide mounted) from Montenegro: Durmitor-Sušica, 27.07.2012, reared from *Hyadaphis foeniculi* on *Sanicula europaea*. 3♀6♂ from Montenegro: Crno jezero, 20.06.2004, from *Hyadaphis foeniculi* on *Lonicera xylosteum*. 5♂ from Montenegro: Durmitor-Sušica, 22.07.2004, reared from *Hyadaphis foeniculi* on *Sanicula europaea*. 5♀9♂ (2♀ mounted) from

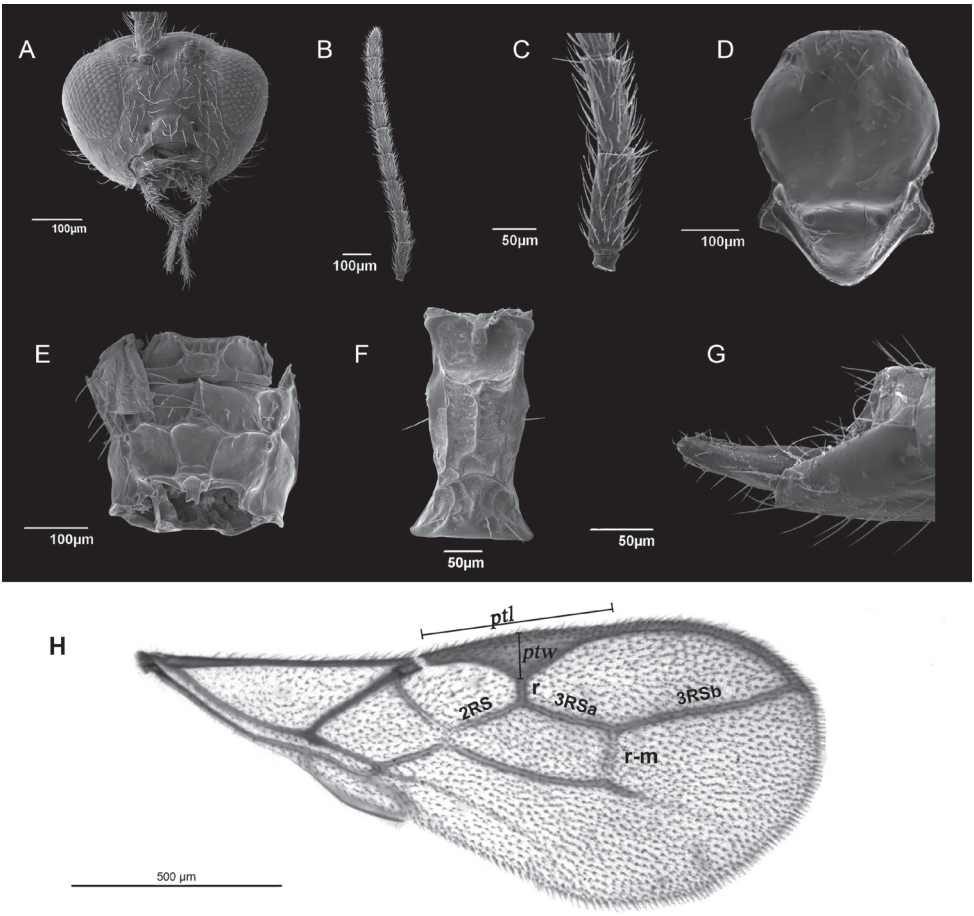

Figure 3. *Ephedrus hyadaphidis* Kocić & Tomanović, sp. nov., female, scanning electron microscopy **A** Head, anterior view **B** Antennae, lateral view **C** First and second antennal segments, lateral view **D** Mesoscutum, dorsal view **E** Propodeum, dorsal view **F** Petiole, dorsal view **G** Ovipositor sheaths, lateral view **H** Forewing, with designated vein terminology. Abbreviations: ptl – pterostigma length, ptw – pterostigma width.

Croatia: Plitvička jezera-Milanovac, 20.06.2015, from *Hyadaphis foeniculi* on *Anthriscus sylvestris*.

Diagnosis. The new species belongs to *E. plagiator* species group, due to fore wing venation. It is differentiated from other *Ephedrus* species by possessing considerably short first flagellar segment; F1 is 2.40–2.65 as long as wide (the closest ratio is in *E. nacheri*, 3.05–3.7). The new species is most closely related to *E. plagiator.* Beside the shorter F1, it can be distinguished from *E. plagiator* by a smaller number of longitudinal placodes on F2 (2–3 compared to 4–6) and wider pterostigma (4.15–4.35 compared to 4.4–4.75 in *E. plagiator*). The new species is a specialised parasitoid of *Hyadaphis foeniculi*, occurring in the Balkan Peninsula.

Description. *Female.* **Head** (Fig. 3A). Eyes medium sized, oval, prominent and sparsely haired. Clypeus somewhat convex, bearing eight long setae. Frons with medium number of setae. Tentorial index 0.6–0.7. Tentorial pits deep. Malar space to longitudinal eye diameter ratio 0.4. Maxillary palps with four palpomeres, labial with two, all of them densely setose. Antennae 11–segmented, filiform, with semi-erect setae that are subequal to 2/3 of the flagellar segment diameter (Fig. 3B). First flagellar segment (F1) 2.41–2.67 times as long as wide, bearing 2–3 longitudinal placodes (Fig. 3C). F2 2.31–2.65 times as long as wide, with 2–3 longitudinal placodes. Number of longitudinal placodes on the remaining seven flagellar segments remains low (F3 2–4, F4 2–4, F5 3–5, F6 3–6, F7 4–6, F8 4–6, F9 4–6). F8 and F9 separated, but due to dense hairs may not seem that visible. **Mesosoma**. Mesoscutum with slightly crenulated notaulices distinct only in anterior part (Fig. 3D). Along mesoscutum two rows of sparse setae present. Propodeum areolated with regular carinae and pentagonal central areola (Fig. 3E). Upper and lower areolae with 2–4 setae. **Forewing** (Fig. 3H). Forewing length 1.6 mm, width 0.6 mm. Pterostigma 4.15–4.35 as long as wide. Pterostigma width to r vein ratio (ptw/r) 1.62–1.87. 3Rsa/r-m and 3Rsb/3Rsa vein ratios 1.62–1.70 and 1.97–2.14, respectively. Vein 2Rsa not visible in first third, therefore may appear shorter than it is. 3Rsa and 2Rsa vein ratio 1.1–1.2. **Metasoma.** Petiole slender, 2.05–2.15 as long as wide at spiracle level (Fig. 3F). Central carina is prominent, while dorso-lateral carinae are slightly distinct. Posterior lateral excavations visible. Ovipositor sheaths elongated, 3.3 times as long as wide, bearing sparse setae along the surface (Fig. 3G). **Colour**. Head and mesoscutum brown, the rest of the mesosoma and petiole yellowish brown. Mouthparts brown. Scape and pedicel brown, F1 with yellow ring at the base, remaining flagellar segments brown. Metasoma and ovipositor sheets brown. Legs yellowish. Body length 1.8 mm. *Male.* Eyes slightly more convex than in female. Head with sparse hairs. Tentorial index 0.45. Malar space to longitudinal eye diameter ratio 0.3. Antennae 11–segmented, with long setae along the surface, almost equal to flagellum diameter. F1 and F2 2.45 times as long as wide, both with 2–3 longitudinal placodes. F2 subequal to F1. Maxillary palps with four palpomeres, labial with two. Mesoscutum like in female. Propodeum with pentagonal central areola and regular carinae. Pterostigma slightly wider than in female, with the length to width ratio 3.8–3.9. Vein ratios Ptw/r, 3Rsa/r-m and 3Rsb/3Rsa are 1.8–1.9, 1.85–1.90 and 1.8–1.95, respectively. 3Rsa to 2Rsa vein ratio is 1.3–1.4. Petiole 2 times as long as wide at spiracle level. Petiole with visible central and lateral carinae. **Colour.** Same as in female.

Etymology. Name of the species is derived from its aphid host, *Hyadaphis foeniculi*.

Distribution. The current species distribution is Balkan Peninsula.

Depositories. Holotype is slide mounted and deposited in the collection of the Institute of Zoology, Faculty of Biology, University of Belgrade. Paratypes collected in National Park Plitvice, Croatia are deposited in the Croatian Natural History Museum, Zagreb, Croatia. The remaining paratypes are deposited at the Institute of Zoology, Faculty of Biology, University of Belgrade.

Synonymies. The molecular phylogenetic analysis clustered *E. dysaphidis* together with *E. cerasicola*, with the genetic distance ranging from 0.0% to 1.6%. We performed a detailed morphological examination of all available material of both species

in order to test the obtained molecular results. *Ephedrus dysaphidis* is a species from *plagiator* species group, described in the study by Tomić et al. (2005). Authors differentiated it from other species in this group by number of longitudinal placodes on F1 (1–2, rarely 3) and F2 (2–3, rarely 4) and shorter petiole (1.94–2.20 times as long as wide). The colour of scapus, pedicel and the ring at the base of F1 is stated as brownish to yellow. It is a parasitoid of aphids from genus *Dysaphis* Börneron on *Malus domestica* Borkh. While studying morphology of many additional populations of *E. dysaphidis* and *E. cerasicola*, we found numerous overlapping characters. In the description of *E. cerasicola*, Starý (1962) states that F1 is more than three times as long as wide, while in the paper of Tomić et al. (2005) the length/width ratio of *E. dysaphidis* is 3.8–4.6. Furthermore, F1/F2 length ratio is also overlapping in both species (in *E. cerasicola* F1 is longer by 1/3 than F2 and in *E. dysaphidis* that ratio is 1.28). Propodeum in both species is with a pentagonal areola, having the same number of setae on upper and lower areolae. Additionally, pterostigma in *E. cerasicola* is more than four times as long as wide; in *E. dysaphidis* this ratio varies between 4.1–4.7. Finally, petiole in *E. cerasicola* is less than twice as long as wide, while in *E. dysaphidis*, according to the authors, this ratio is 1.94–2.20. However, our studied material of both species showed that the length to width ratio at the spiracle level of *E. cerasicola* and *E. dysaphidis* is 1.97–2.1 and 1.90–2.18, respectively, thus also overlapping. The only character that differs in two descriptions of species is the number of longitudinal placodes on F1 and F2 flagellar segments, which is 0 and 2 in *E. cerasicola* and, as mentioned above, 1–2(3) and 2–3(4) in *E. dysaphidis*, respectively. However, we found specimens from the same sample (that were first identified as *E. dysaphidis* based on the aphid host *Dysaphis plantaginea* Passerini, 1860 on *Malus domestica*) having a different number of longitudinal placodes that varied from F1:0, F2:1 to F1:1, F2:3. Moreover, in the revision of the genus *Ephedrus* Gärdenfors (1986) states that the number of longitudinal placodes in F1 and F2 for *E. cerasicola* is 1 and 2–3, respectively. One more distinction between the species was the colour of scape, pedicel and F1 and F2. In *E. cerasicola* scape, pedicel, F1 and part of F2 are yellow brownish (Starý 1962) or can be with scape yellowish to brown, pedicel and at least base or the entire F1 yellow, while F2 is yellowish at base (Gärdenfors 1986). While examining the material of both species we found various gradations of scape, pedicel, F1 and F2 colour, mainly following the description of Starý (1962) and Gärdenfors (1986). Although important morphological variability exists within *E. cerasicola* host associated lineages, after examining all the available data we here synonymise *E. dysaphidis* as a junior synonym of *E. cerasicola*.

Material examined. ***E. dysaphidis***: Holotype ♀ from Serbia: Belgrade, 08.05.1995, reared from *Dysaphis* sp. on *Malus domestica*. Paratypes 3♀ from Serbia: Belgrade, 08.05.1995, reared from *Dysaphis* sp. on *Malus domestica*. 1♀ from Serbia: Belgrade-Radmilovac, 22.04.1992, reared from *Dysaphis* sp. on *Malus domestica*. 3 ♀ Serbia: Belgrade-Zemun, 22.04.2014, from *Dysaphis devecta* Walker on *Malus* sp. 2 ♀ Serbia: Belgrade, 24.04.2014, from *Dysaphis devecta* on *Malus* sp. ***E. cerasicola***: 1♀ from Montenegro: Zminje jezero, 04.08.1982. 1♀ Serbia: Belgrade-Crveni krst, 14.06.1997, from *Myzus cerasi* Fabricius 1775 on *Prunus cerasus* L. 1♀ from Serbia: Mladenovac,

11.06.1990. 1♀ from Serbia: Belgrade-New Belgrade, 17.06.1993, from *Phorodon humuli* Schrank, 1801 on *Prunus cerasifera* 1♀ from Serbia: Kopaonik, 05.07.1997, from *Brachycaudus helichrysi* Kaltenbach, 1843 on *Myosotis* sp. 2♀1♂ from Serbia: Subjel, 01.05.2017., from *Dysaphis pyri* Boyer de Feonscolombe, 1841 on *Pyrus communis*. 4♀ from Belgium: from *Dysaphis plantaginea* on *Malus* sp.

Ephedrus blattnyi is a specialised parasitoid described from one finding in the Czech Republic, reared from *Pterocomma ringadhli* (junior synonym of *Pterocomma rufipes* Hartig, 1841) on *Salix caprea*. Several authors during previous years questioned the validity of *E. blattnyi* species status. After the examination of type specimens Gärdenfors (1986) stated that they are extraordinarily similar to *E. plagiator* and that it is possible that they represent aberrant specimens of *E. plagiator* due to an unusual aphid host. Furthermore, Koponen and Halme (1993) reported that they collected specimens fully corresponding to the *E. blattnyi* redescription (Gärdenfors, 1986). However, the authors didn`t include them in the paper, since the distinguishing characters were not reliable. Finally, Tomanović (2000) states, while reporting the finding of specimens corresponding to *E. blattnyi*, that it is very similar to *E. plagiator* and *E. prociphili*. We analysed specimens from *P. rufipes* which morphologically corresponded to the description of *E. blattnyi* reared from *P. rufipes* aphid host on *Salix retusa*. Molecular analysis of COI clustered *E. blattnyi* within the *E. plagiator*, with the molecular distance ranging from 0.2% to 0.7%. Therefore, we conclude that *E. blattnyi* represents a morphotype of *E. plagiator* and assign it a status of junior synonym.

Subgenera and species groups of the genus *Ephedrus* in Europe

Analysing all obtained results (both molecular and morphological), we concluded that the current subgeneric classification of *Ephedrus* needs revision and here we propose a new one. Subgenus *Lysephedrus* Starý 1958 is synonymised as a junior synonym of the subgenus *Ephedrus* Haliday, 1833 from which *persicae* species group is raised to the level of the subgenus *Fovephedrus* Chen, 1986. The subgenera *Fovephedrus* and *Ephedrus* are redescribed.

Subgenus *Fovephedrus* Chen, 1986

Type species. *Fovephedrus radiatus* Chen, 1986.

Etymology. Name derived from presence of fovea on mesoscutum of type species

Diagnosis. 3Rsa vein shorter than 2Rsa (3Rsa / 2Rsa less than 1), petiole subquadrate.

Description. F1 with smaller number of longitudinal placodes (0–3, rarely 4). Mesoscutum usually with one or two mesoscuteal foveae, sometimes lacking both. Scutellar sulcus always undivided. 3RSa shorter than 2Rsa (0.55–0.95). 3Rsb/3Rsa 2.65–3.4. Petiole short and broad, 1.3–1.5 times as long as wide, lacking post lateral excavations. Ovipositor sheaths varying from stout to slender.

Species in Europe: *Ephedrus persicae* Froggatt, 1904, *Ephedrus chaitophori* Gärdenfors, 1986, *Ephedrus lonicerae* Tomanović, Kavallieratos & Starý, 2009, *Ephedrus tamaricis* Tomanović & Petrović, 2016

Subgenus *Breviephedrus* Gärdenfors, 1986

Notes. For diagnosis and description see Gärdenfors (1986).

Species. *Ephedrus brevis* Stelfox, 1941.

Subgenus *Ephedrus* Haliday, 1833

Lysephedrus Starý, 1958 syn. nov.

Diagnosis. 3Rsa longer or subequal to 2Rsa, petiole more or less elongated.

Description. F1 with variable number of longitudinal placodes (0–5). Mesoscutum without mesoscuteal fovea, except in *E. longistigmus*, and rarely *E. lacertosus*. Scutellar sulcus undivided. 3Rsa varying from almost subequal to considerably longer compared to 2Rsa (1.1–1.5 times). 3Rsb/3Rsa 1.7–2.6. Propodeum and petiole in most species without rugosity, in *E.validus* very rugose. Petiole more or less elongated, with or without post lateral excavations. Ovipositor sheaths commonly slender and elongated, in some species stout and short.

The *plagiator* species group. *Ephedrus cerasicola* Starý, 1962; *Ephedrus helleni* Mackauer, 1968; *Ephedrus koponeni* Halme, 1992; *Ephedrus laevicollis* (Thomson, 1895); *Ephedrus nacheri* Quilis Perez, 1934; *Ephedrus niger* Gautier, Bonnamour & Gaumont, 1929; *Ephedrus plagiator* (Nees, 1811); *Ephedrus prociphili* Starý, 1982; *Ephedrus vaccinii* Gärdenfors, 1986; *Ephedrus validus* Haliday, 1833, *E. hyadaphidis* sp. nov.

The *lacertosus* species group in Europe. *Ephedrus lacertosus* (Haliday, 1833) and *E. longistigmus* Gärdenfors, 1986.

Key to the subgenera of European *Ephedrus*

1 Scutellar sulcus divided into two (Fig. 4A), 3Rsa very long (Fig. 4C) ..... ***Breviephedrus***

– Scutellar sulcus undivided (Fig. 4D, G), 3Rsa longer or shorter than 2RS (Fig. 4F, I) **2**

2 3Rsa visibly or slightly shorter than 2RS (Fig. 4F), petiole subquadrate (Fig. 4E) ..... ***Fovephedrus***

– 3Rsa longer or subequal to 2Rs (Fig. 4I), petiole elongated (Fig. 4H) ..... ***Ephedrus***

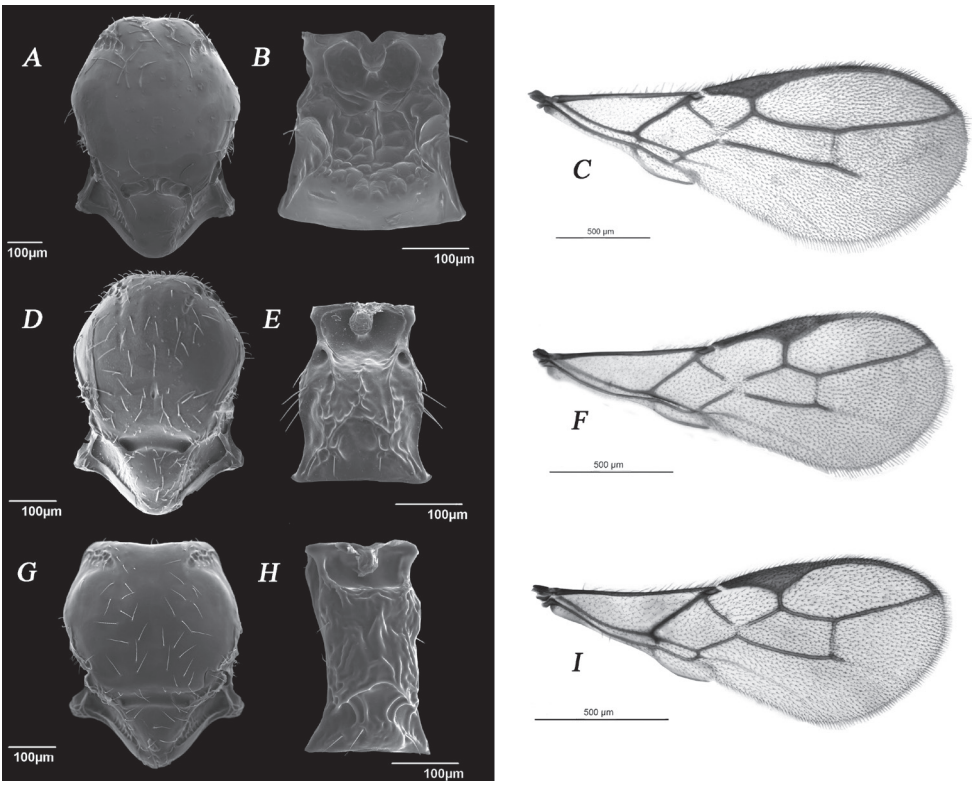

Figure 4. Representative species of the subgenera *Breviephedrus* (*E. brevis*), *Fovephedrus* (*E. persicae*), and *Ephedrus* (*E. plagiator*). **A–C** *Breviephedrus* **A** mesoscutum dorsal view **B** petiole, dorsal view **C** forewing **D–F** *Fovephedrus* **D** mesoscutum dorsal view **E** petiole, dorsal view **F** forewing **G–I** *Ephedrus* **G** mesoscutum, dorsal view **H** petiole, dorsal view **I** forewing.

Discussion

Continuously advancing molecular methods allow us to easily sequence gene fragments of interest and compare them with results of morphological and ecological analyses in order to obtain a clearer picture of phylogenetic relationships and evolution of the group of interest. In this study we used two molecular markers to reveal the taxonomic positions and phylogeny of species within the genus *Ephedrus* in Europe. As proposed by Derocles et al. (2012), we used a combination of both mitochondrial and nuclear markers. The barcoding region of mitochondrial cytochrome c oxidase subunit I proved to be a reliable marker in resolving taxonomic relationships in previous studies of the subfamily Aphidiinae (Folmer et al 1994, Petrović et al. 2016, Tomanović et al. 2018, Mitrović et al. 2019). Furthermore, we conducted an analysis of nuclear EF1α that mostly supported the inter-specific relationships of our taxa previously provided by COI.

Previous studies classified species from genus *Ephedrus* into three subgenera (*Ephedrus*, *Breviephedrus* (*E. brevis*) and *Lysephedrus* (*E. validus*)) based on morphology (Gärdenfors 1986). However, with the combination of molecular and morphologi-

cal approach we here revise the subgeneric classification. All three revised subgenera separated with the highest genetic distances known in Aphidiinae when analysing subgenera, ranging from 16.3 % to 20.7 %. Currently, the only member of the subgenus *Breviephedrus*, *E. brevis*, is at first sight easily distinguished from any other *Ephedrus* species with a very thickset, stocky and black polished body (Stelfox 1941). It is interesting to note that the parasitoid has never been reared from an aphid host (which is still unknown), but is suspected to be from the aphid species associated with *Betula*, since the specimens are found by sweeping or by traps in the vicinity of birch trees. Gärdenfors (1986) states this species as the most primitive within the genus, morphologically similar to *Parephedrus*. Indeed, *E. brevis* possesses a wide range of morphological characters that are also found in *Parephedrus*, thus indicating that these two could be a "connection bridge" in the evolution of ancient genera *Parephedrus*, *Vanhartenia*, *Pseudephedrus*, and *Choreopraon* on one side and the rest of Aphidiinae on the other. In order to uncover phylogenetic relationships between these groups, future studies are needed, especially in the light of our molecular results which do not support previous statements that it is the most primitive species within the genus.

Based on the presence of the fovea on mesoscutum, Chen (1986) described the genus *Fovephedrus*, with the type species *Fovephedrus radiatus* Chen, 1986. Several *E. persicae* morphotypes (*E. persicae*, *E. palaestinensis* (= *E. persicae*, see Gärdenfors (1986)), *E. rugosus*, *E. radiatus*, *E. transversus*) and *E. longistigmus* (member of *lacertosus* species group) were later reclassified to this genus, based on the same morphological character (Chen and Shi 2001). Van Achterberg (1997), synonymised *Fovephedrus* as a synonym of *Ephedrus*, but stated that it could be considered as a valid subgenus. The presence of mesoscutellar fovea is characteristic of several *Ephedrus* species. Even within *E. persicae* its presence is very variable: fovea can be absent, or the specimens can possess one (the most common state) or two foveal pits. Furthermore, this morphological character is shared with the *lacertosus* species group, where it can sometimes be found in *E. lacertosus* specimens, and is always present in *E. longistigmus*. In the end, the existence of the mesoscuteal fovea is not a character specific for species of genus *Ephedrus*, but is also found among *Toxares* (Tomanović et al. 2008). We consider this morphological character to be diagnostically unreliable, especially at the genus level.

The redescribed subgenus *Fovephedrus* is raised from *persicae* species group and its inter-specific relationships are thoroughly discussed in authors' recent study (Petrović et al. 2016). We did not examine type species *E. radiatus* but judging by the description and drawings (Shi and Chen 2001) it obviously belongs to *Ephedrus persicae* species group. The same is the case with Asiatic species *E. rugosus* and *E. transversus* which on the basis of descriptions both belong to *persicae* group. As mentioned earlier, *E. palaestinensis* is synonymised with *E. persicae* (Gärdenfors 1986) and *E. longistigmus* apparently does not belong to subgenus *Fovephedrus*, but *lacertosus* group within the traditional subgenus *Ephedrus*. The subgenus *Ephedrus* holds the remainder of the species and is divided into two species groups, *plagiator* and *lacertosus*. While *E. longistigmus* is reported only two times (see Koponen and Halme 1993, Davidian 2018), *E. lacertosus* is common representative of the lacertosus group in Europe. This species group is considered to be the most phylogenetically advanced within the genus *Ephedrus* (Gärden-

fors 1986), due to several apomorphic morphological traits, like an elongated petiole, flagellomere 1 and pterostigma. Our results confirm the separation of *E. lacertosus* into a distinct clade. Within the *plagiator* group, *E. helleni* and *E. validus* position as most distant phylogenetically from all other *plagiator* species. Both parasitoids are specialists; first one attacking *Cavariella* aphids across its distribution (Koponen and Halme 1993, Kavallieratos et al. 2004, Rakhshani et al. 2007, Starý and Havelka 2008, Tomanović et al. 2009) and additionally *Eumyzus* Shinji, 1929 in Asia (Davidian 2007, Davidian and Gavrilyuk 2014) and the second one parasitising root aphids from the subfamily Eriosomatinae (Gärdenfors 1986). Starý (1958) raised *E. validus* to the subgenus *Lysephedrus*, based on morphological characters, such as very rugose propodeum and petiole, shape of ovipositor sheaths and their heavy pubescence. Davidian considered it as separate genus (Davidian 2007). However, since this species is a parasitoid of waxy root aphids, all those differences could represent adaptations to the specific underground ecological niche (Gärdenfors 1986). It is probable that *E. validus* and *E. helleni* separated from other species early in the evolution of this group, driven by a specialisation for a certain aphid host. The results of molecular analysis of nuclear EF1α grouped *E. lacertosus*, *E. helleni*, and *E. validus* into one clade, separating them from the rest of *plagiator* species.

The fact that revealing new cryptic species within large generalist groups is an ongoing process (Derocles 2016, Petrović et al. 2016) is once again proven by the description of the additional member of *plagiator* group, *E. hyadaphis*. The specimens reared from *Hyadaphis foeniculi* were collected across the Balkans during the period of fifteen years, from different plant hosts (*Lonicera xylosteum*, *Sanicula europaea*, and *Anthriscus sylvestris*), all common for this aphid species. *Ephedrus hyadaphidis* parasitoids were found in the woodland area on higher altitudes (524–1140 meters above sea level). This species might have been noticed earlier: in his revision Gärdenfors (1986) discusses an *Ephedrus* specimen collected in Italy, reared from *Hyadaphis foeniculi* on *Lonicera etrusca*, similar to *E. nacheri*, but with several morphological differences. Along with *E. lonicerae* and *E. tamaricis*, *E. hyadaphis* represents the third recently described species of *Ephedrus* distributed in the Balkan region. Furthermore, *E. persicae* is separated into two clades, one containing Mediterranean taxa, and the other taxa from the rest of Europe. The average genetic distance between these two clades is 2.5 %, suggesting that they have been evolving separately for some time. Thus, both clades require further taxonomic investigation. The richness of species that are distributed only in the Balkan region, as well as richness of haplotype numbers might imply that this area played a significant role for *Ephedrus* species as a refuge during the glacial periods.

Ephedrus koponeni is reported outside its known distribution, northern Europe (Finland and European part of Russia) (Halme 1992, Davidian 2018). One male and one female were reared from *Cinara* sp. on the Balkan pine, *Pinus peuce*, a relict and endemic species with a fragmented distribution in the Balkan Peninsula (in Serbia inhabiting only very southern part). It is possible that the specimens of this species across Europe are, when seldom collected, misidentified as *E. plagiator*. The other probability is that *E. koponeni* possesses an extremely fragmented distribution, restricted only to the secluded areas of its former species range.

The results of this study show close phylogenetic relationships among *E. koponeni*, *E. prociphili*, and *E. nacheri*. All three species are morphologically very similar to *E. plagiator*, distinguished from each other by subtle morphological differences and aphid host range (Gärdenfors 1986). While *E. koponeni* and *E. prociphili* are specialised to coniferous aphid species and *Prociphilus* sp., respectively, *E. nacheri* has a somewhat broader aphid host range, parasitising several species from Aphidini and Macrosiphini tribes. In Europe this species is most frequently reared from the genus *Hayhurstia* Del Guercio, 1917. These species might be quite young in the evolution line of the genus *Ephedrus*, just recently separated from the others in *plagiator* species group, which would explain lower genetic distances and great morphological similarity with *E. plagiator*. Furthermore, our study suggests that *E. cerasicola* (parasitoid of *Myzus* and *Dysaphis*) and *E. laevicollis* (parasitoid of *Chaetosiphon* Mordvilko, 1914), are closely related species.

The results of molecular analyses show that *Ephedrus* species, when multiple sequences for analysis are available, are rich in haplotype variety. *Ephedrus plagiator* is known as a broadly polyphagous species, distributed throughout Europe. Specimens analysed here were collected from various aphid hosts (*Aphis* Linnaeus, 1758, *Brachyunguis* Das, 1918, *Sitobion* Mordvilko, 1914, *Rhopalosiphum* Koch, 1854, *Macrosiphum* Oestlund, 1886, *Anoecia* Koch, 1857, *Linosiphon* Börner, 1944 and *Pterocomma* Buckton, 1879) and plants (*Poa*, *Dactylis*, *Malus*, *Tamarix*, *Triticum*, *Sitobion*, *Galium*, *Salix*, *Prenanthes*, *Abies*, *Vicia*, *Ranunculus*, *Prunus*, *Heracleum*); in 15 sequences eight haplotypes were identified, which all grouped together into one phylogenetic clade. Compared to *E. persicae*, where in 15 specimens 12 haplotypes (forming two clusters) were discovered (Petrović et al. 2016), the genetic variability within *E. plagiator* seems to be somewhat lower. *Ephedrus niger*, an Euroasian species mainly reared from *Uroleucon* Mordvilko, 1914 and *Macrosiphoniella* Del Guercio, 1911 aphid hosts (Gärdenfors 1986, Tomanović et al. 2009) is easily distinguished from the other *Ephedrus* species by dark to black body and longer F1 with a constriction in the basal third. Out of seven analysed specimens we identified seven different haplotypes which all grouped into one separate clade.

In summary, our results show that the phylogeny of *Ephedrus* is more complex than previously thought. It is important to note that European species of *Ephedrus* comprise less than a half of currently described species, so in order to get complete insight into the phylogenetic relationships among species and their evolution, further studies are needed.

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Supplementary material 1

Ephedrus **specimens analysed in this study**

Authors: Korana Kocić, Andjeljko Petrović, Jelisaveta Čkrkić, Milana Mitrović, Željko Tomanović

Data type: specimens data

Link: https://doi.org/10.3897/zookeys.878.38408.suppl1

Supplementary material 2

Estimates of evolutionary divergence between sequences

Authors: Korana Kocić, Andjeljko Petrović, Jelisaveta Čkrkić, Milana Mitrović, Željko Tomanović

Data type: phylogenetic data

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Taxonomic study of the genus *Townesia* Ozols (Hymenoptera, Ichneumonidae, Pimplinae) with description of a new species from China and a key to world species

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Abstract

Five species of the genus *Townesia* Ozols are reported. One, *Townesia sulcata* Sheng & Li, **sp. nov.** collected from Liaoning province, China, is new to science. In addition, digital images and a taxonomic key to the all species of *Townesia* are presented.

Keywords

Ephialtini, host, host plant

Introduction

Townesia Ozols, 1962, belonging to the tribe Ephialtini of the subfamily Pimplinae (Hymenoptera, Ichneumonidae), comprises four species (Yu et al. 2016), of which two are from the Oriental Region (Gupta and Tikar 1976; Liu and He 2012), two from the Palaearctic Region and one from the Nearctic Region (Sheng and Sun 2010; Townes et al. 1960; Yu et al. 2016). Two species of *Townesia* were known from China (He et

al. 1996; Sheng and Li 2006; Liu and He 2012). The diagnostic characters of the genus were most recently revised by Liu and He (2012) and Townes (1969).

Fourteen host species, belonging to Buprestidae and Cerambycidae (Coleoptera); Megachilidae, Siricidae, Sphecidae, and Tenthredinidae (Hymenoptera); and Sesiidae and Tortricidae (Lepidoptera) have been recorded (He et al. 1996; Sheng and Li 2006; Yu et al. 2016).

The aim of this article is to describe a new species and provide a key to the world species.

Materials and methods

Specimens were collected with interception traps (IT) (Li et al. 2012) in Chagou, Haicheng, Liaoning Province, P.R. China. The type locality is a forest comprised of mixed deciduous angiosperms and evergreen conifers, mainly including *Quercus wutaishanica* Mayr, *Quercus* sp., *Larix* sp., *Castanea* spp., and *Pinus tabulaeformis* Carr.

Type specimens are deposited in the Insect Museum, General Station of Forest and Grassland Pest Management (**GSFGPM**), National Forestry and Grassland Administration, China.

The specimens of *Townesia tenuiventris* (Holmgren, 1860), deposited in the Zoologische Staatssammlung München, Germany (**ZSM**) and identified by Bauer, were examined and compared to the new species. The male characters of *T. tenuiventris* mentioned in the following key is based on Zwakhals's (2010) description. The photos of holotype of *Townesia exilis* Gupta & Tikar, 1976, taken by Dr Jonathan Bremer (Florida Department of Agriculture and Consumer Services) was also checked.

Images of the new species were taken using a Stereomicroscope (Leica M205A) with a LAS Montage MultiFocus. Morphological terminology follows Broad et al. (2018).

Taxonomy

Townesia Ozols, 1962

Townesia Ozols 1962: 12. Type species: *Ephialtes tenuiventris* Holmgren.

Diagnosis. Teeth of mandible equal or almost equal. Epomia evidently present. Propodeum elongate, basal portion with median longitudinal impression; pleural carina complete. Areolet subtriangular, receiving *2m-cu* slightly distal of middle. Tarsal claws of female with a large basal lobe. Tergite I 0.6–0.7 times as long as tergite II (*T. exilis* same length), with lateral carina beneath spiracle; basal part of median dorsal carinae distinct. Tergites II to V elongate, with dense punctures. Ovipositor sheath longer than body length, usually about 2.5 times as long as forewing. Apical portion of ventral valve with distinct ridges, subapical portion without or with weak dorsal lobe (Figs 10–14).

Key to world species of *Townesia*

1 Female **2**

– Male **6**

2 Tergite I as long as tergite II. Lateral tubercles of tergites III–V indistinct. Submetapleural carina complete. (Male unknown) ..... ***T. exilis* Gupta & Tikar**

– Tergite I distinctly shorter than tergite II. Tergites III–V with distinct lateral tubercles (except *T. cheni*). Submetapleural carina incomplete, or complete **3**

3 Basal 0.6–0.7 of propodeum (Fig. 7) with median longitudinal furrow. Submetapleural carina complete. Forewing vein 1*cu-a* opposite *1/M*. Basal part of hind tibia (Fig. 1) light brown, subbasal part brownish black, median part unevenly yellowish brown, apically black. Basal parts of hind tarsomeres more or less buff. (Male unknown) ..... ***T. sulcata* Sheng & Li, sp. nov.**

– Propodeum without median longitudinal furrow, or with weak short furrow, not reaching middle of propodeum. Submetapleural carina only present anteriorly; if complete, then metasoma compressed. Forewing vein 1*cu-a* basal or distal of *1/M*. Hind tibia almost with same color, or basal portion slightly buff. Hind tarsomeres with same color **4**

4 Forewing vein 1cu-a distal of *1/M*. Submetapleural carina complete. Third and subsequent tergites compressed. Apical portion of dorsal valve of ovipositor with fine teeth (Fig. 13). Hind coxae brownish black to black ..... ***T. qinghaiensis* He**

– Forewing vein 1cu-a basal of *1/M*. Submetapleural carina only present anteriorly. Metasoma uncompressed. Dorsal valve of ovipositor smooth (Fig. 11) or almost smooth, subbasal portion with two weak small tubercles, without distinct teeth (Figs 10, 14). Hind coxae reddish brown to dark brown **5**

5 Forewing vein radius at middle of pterostigma. Tergites without lateral tubercles. Apical smooth transverse bands of tergites II and III approximately 0.15 times as long as respective length. Fore coxa yellow. Hind coxa dark brown. (Male unknown) ..... ***T. cheni* Liu & He**

– Forewing vein radius distinctly basal to middle of pterostigma. Tergites with distinct lateral tubercles. Apical smooth transverse bands of tergites II and III approximately 0.25 times as long as respective length. All coxae reddish brown ..... ***T. tenuiventris* (Holmgren)**

6 Tergite I 2.3–2.5 times as long as apical width. Hind third tarsomere 1.1 times as long as first flagellomere. Hind fifth tarsomere 1.2–1.3 times as long as third tarsomere. Hind coxa black to brownish black ..... ***T. qinghaiensis* He**

– Tergite I 2.6–2.8 times as long as apical width. Hind third tarsomere 0.9 times as long as first flagellomere. Hind fifth tarsomere 1.0–1.1 times as long as third tarsomere. Hind coxa red ..... ***T. tenuiventris* (Holmgren)**

The species of *Townesia*

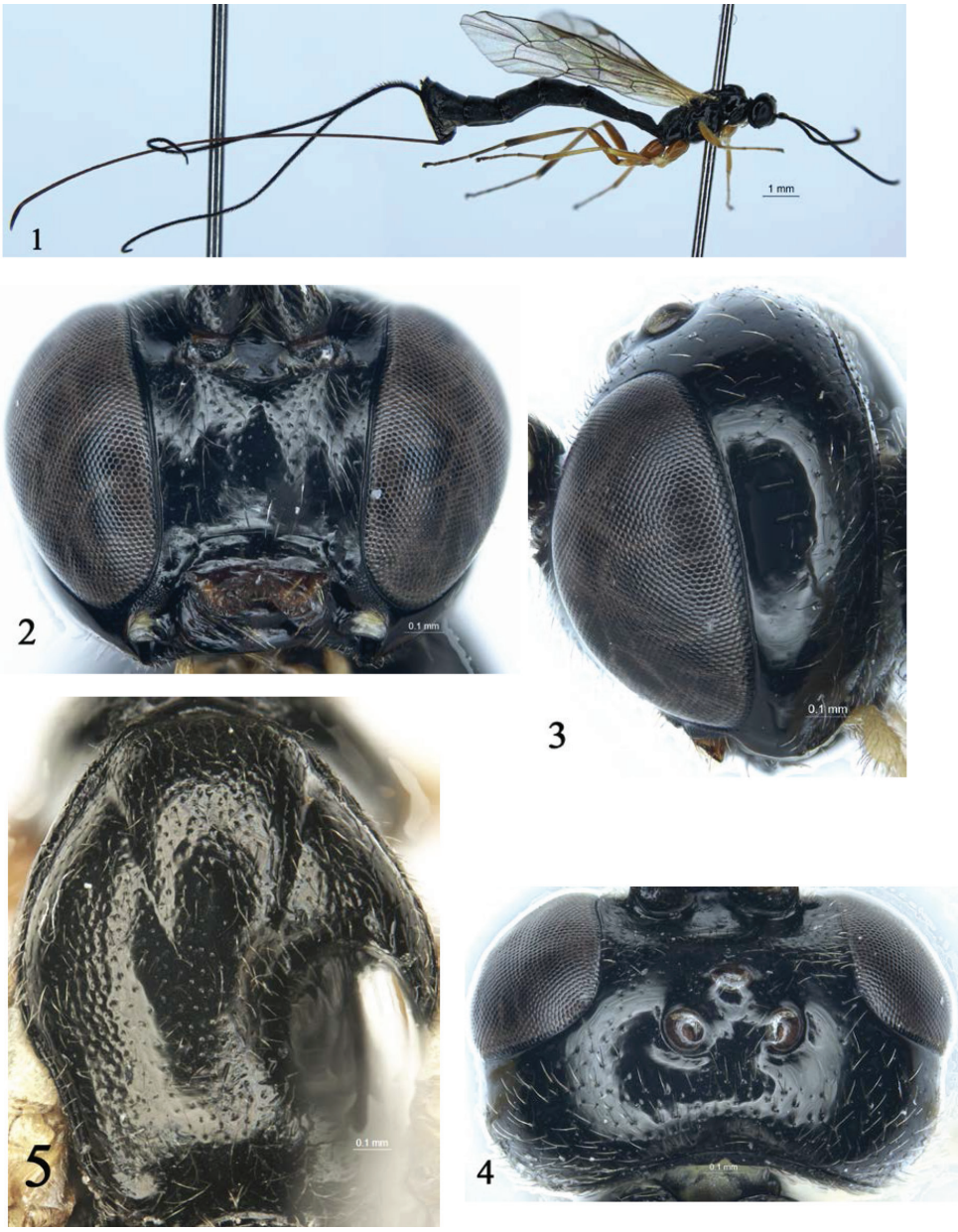
***Townesia sulcata* Sheng & Li, sp. nov.**
http://zoobank.org/B0DBB732-0E3D-4ECC-B9E6-148DD89D21E7
Figures 1–10

Diagnosis. Face (Fig. 2) 1.2 times as wide as long. Malar space approximately 0.3 times as long as basal width of mandible. Postocellar line approximately 0.8 times as long as ocular-ocellar line. Antenna with 24 flagellomeres. Forewing vein *1cu-a* opposite to *1/M*. Areolet receiving *2m-cu* approximately at its posterior 0.2. Hind wing vein *1-cu* about as long as *cu-a*. Basal 0.6–0.7 of propodeum with median longitudinal furrow. Apical portion of ovipositor evenly downcurved.

Description. Female (Fig. 1). Body length approximately 10.4–12.2 mm. Forewing length 7.1–7.8 mm. Ovipositor sheath 11.5–13.1 mm.

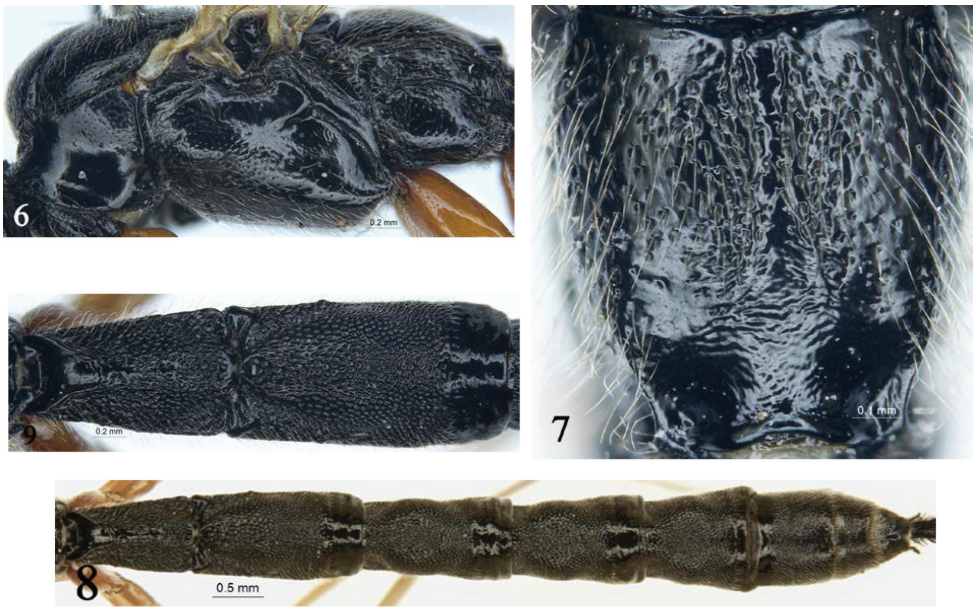
Head. Face (Fig. 2) approximately 1.2 times as wide as long, smooth with sparse, fine punctures and white hairs; median portion slightly convex. Basal portion of clypeus smooth, with sparse, fine punctures and yellowish-brown hairs; apical portion with dense, fine punctures and short, yellowish-brown hairs; apical margin with deep, median concavity. Malar area with finely granulose texture. Malar space approximately 0.3 times as long as basal width of mandible. Inner orbits of compound eyes convergent downwards. Gena smooth (Fig. 3), with fine, sparse punctures and short, yellowish-brown hairs. Vertex (Fig. 4) smooth, laterally with very sparse punctures, hind part with relatively dense punctures and white hairs. Postocellar line approximately 0.8 times as long as ocular-ocellar line. Upper part of frons with evenly dense punctures and short, white hairs; lower portion concave, with weak, fine, transverse wrinkles. Antenna with 24 flagellomeres, ratio of length from first to fifth flagellomeres: 1.2:1.0:1.0:0.9:0.8. Occipital carina complete.

Mesosoma. Pronotum (Fig. 6) smooth; upper and upper-posterior portions with fine punctures and short, white hairs. Mesoscutum (Fig. 5) slightly convex, with dense punctures and yellowish-white hairs, distance between punctures 0.5–3.5 times diameter of puncture, posterior portion distinctly more sparsely punctate than anterior portion. Notaulus evident, reaching about 0.6 the distance to posterior margin of mesoscutum. Scutellum slightly convex, with dense punctures. Posterior portion of postscutellum transversely convex, with sparse punctures; anterior portion oblique concavity. Mesopleuron (Fig. 6) smooth; anterior and lower portions with dense punctures and grey-white hairs. Speculum with few hairs. Metapleuron with sparse punctures. Submetalpeural carina complete. Wings yellowish hyaline; fore wing with vein *1cu-a* opposite to *1/M*. Areolet oblique quadrangle, receiving *2m-cu* approximately at its posterior 0.2. Hind wing vein *1-cu* about as long as *cu-a*. Claws with large basal lobe. Ratio of length of hind first to fifth tarsomeres: 9.5:5.0:3.1:1.0:2.5. Propodeum (Fig. 7) smooth, shiny, with uneven punctures and yellowish-white hairs; apical median portion smooth; basal 0.6–0.7 with median longitudinal furrow; spiracle small, circular.



Figures 1–5. *Townesia sulcata* Sheng & Li, sp.nov. Holotype, ♀ **1** habitus, lateral view **2** head, anterior view **3** head, lateral view **4** head, dorsal view **5** mesoscutum.

Metasoma (Fig. 8). Tergite I (Fig. 9) about 1.7 times as long as apical width; with dense punctures; median portion obviously raised, median longitudinal portion weakly concave; spiracle small, circular, located as basal 0.4 of tergite I. Tergite II (Fig. 9) about 1.9 times as long as apical width; with same texture as that of tergite I, apical



Figures 6–9. *Townesia sulcata* Sheng & Li, sp.nov. Holotype, ♀ **6** mesosoma, lateral view **7** propodeum **8** metasoma, dorsal view **9** tergites I–II, dorsal view.

0.25 glabrous. Tergites III–V with the same texture as that of tergite II, subbasal weakly concave, with lateral tubercles, apical 0.25 glabrous. Tergites VI–VII with dense punctures. Ovipositor slender, apical portion decurved, dorsal valve smooth, ventral valve with 10 or 11 ridges (Fig. 10).

Coloration (Fig. 1). Black, except following. Maxillary and labial palpi, tegula, and basal portion of fore wing, yellow. Clypeus fusco-testaceous. Legs reddish brown. Fore and mid trochanters yellow; tibia yellowish brown; first to fifth tarsi brown; fifth tarsus dark brown. Hind trochantellus yellow; main portion of tibia yellowish brown to brown, apical portion dark brown; tarsus dark brown to black brown. Veins and pterostigma brown.

Male. Unknown.

Etymology. The name of the new species is based on the form of the propodeum which is characterized by having a median, longitudinal groove.

Type material. Holotype: ♀, CHINA, Hongqiling, Chagou, Haicheng City, Liaoning Province, 15 May 2015, leg. Mao-Ling Sheng. Paratypes: 4 ♀♀, same data as holotype except leg. Mao-Ling Sheng, Tao Li.

Host. Unknown.

Distribution. China.

Comments. This new species is similar to *T. qinghaiensis* He, 1996 in having the gena, vertex, mesopleuron (Fig. 6), and propodeum smooth and shiny; propodeum almost without transverse wrinkles; and main portion of hind tibia yellowish brown to brown, with subbasal and apical portion dark brown to black. It can be distin-

guished from the latter by the following combination of characters: forewing vein 1cu-a opposite *1/M* (distal in *T. qinghaiensis*), basal 0.6 to 0.7 of propodeum with median longitudinal furrow (absent in *T. qinghaiensis*), apical portion of ovipositor distinctly curved, dorsal valve smooth, without ridge (Fig. 10), straight and dorsal valve with weak ridges in *T. qinghaiensis* (Fig. 13), hind coxa red-brown (brownish black in *T. qinghaiensis*). The new species can be distinguished from all other species by the key provided above.

Townesia cheni Liu & He, 2012

Figure 11

Diagnosis. Forewing length 9.1 mm. Ovipositor sheath length 18.0 mm. Upper tooth of mandible as long as lower tooth. Propodeum with dense punctures and short hairs, without median longitudinal furrow. Tergite I 2.1 times as long as apical width, 0.77 times as long as tergite II. Tergites II–V almost without lateral tubercles. Tergite II as long as tergite III, apical smooth transverse bands 0.15 times as long as respective length. Apical portion of ovipositor evenly curved. Fore coxa yellow. Hind coxa dark brown.

Male. Unknown.

Host. Unknown.

Material examined. 1 ♀ (Holotype), CHINA: Zhejiang Province, Mt West Tianmu, Laodian-xianrending, 1150–1106 m, 17 May 1988, Xue-Xin Chen leg., coll. no. 882277.

Townesia exilis Gupta & Tikar, 1976

Figure 12

Diagnosis. Female: Forewing length 8 mm. Ovipositor sheath length 15 mm. Face smooth and shiny. Malar space 0.2 times as long as basal width of mandible. Pronotum smooth, upper-posterior corner with sparse punctures. Fore wing with vein 1*cu-a* opposite to *1/M*. Areolet receiving *2m-cu* approximately at its posterior 0.1. Hind wing vein *1-cu* 0.67 as long as *cu-a*. Tergite I as long as tergite II. Tergite II 2.6 times as long as its maximum width, with distinct, dense, fine punctures; apical, smooth, transverse bands 0.25 times as long as length. Tergite III 2.5 times as long as its maximum width. Lateral tubercles of tergites III–V indistinct. Submetapleural carina complete. Tegula, fore, and middle legs yellow to yellow brown; hind coxa, trochanter, and femur red.

Male. Unknown.

Host. Unknown.

Material examined. 1 ♀ (Holotype), INDIA: Kashmir, Gulmarg, 2600 m, 23 June 1966, J.K. Jonathan leg., coll. no. J166.

Distribution. India.

Figures 10–14. Apical part of ovipositor, lateral view **10** *Townesia sulcata* Sheng & Li, sp. nov. **11** *Townesia cheni* Liu & He **12** *Townesia exilis* Gupta & Tikar **13** *Townesia qinghaiensis* He **14** *Townesia tenuiventris* (Holmgren).

Townesia qinghaiensis He, 1996

Figure 13

Diagnosis. Female: Forewing length 6.7–11.5 mm. Ovipositor sheath length 10.0–17.0 mm. Face, gena, and vertex smooth, shiny, with very sparse, fine punctures. Malar space 0.2 times as long as basal width of mandible. Antenna with 22–23 flagellomeres. Propodeum shiny, almost without carina, without median longitudinal furrow. Tergite I 1.7 times as long as apical width, 0.7 times as long as tergite II. Tergite II 1.2 times as long as tergite III, apical smooth transverse bands of tergites II–IV 0.18 times as long as respective length. Apical portion of dorsal valve of ovipositor (Fig. 13) with fine teeth. Maxillary and labial palpi gray-black.

Male: Forewing length 5.5–12.5 mm. Antenna with 22–24 flagellomeres. Fore wing with vein 1*cu-a* slightly distal of or opposite to *1/M*. Hind third tarsomere 0.4 times as long as first tarsomere, 0.75–0.8 times as long as fifth tarsomere. Tergite I 2.3–2.5 times as long as apical width, 0.67–0.7 times as long as tergite II. Hind coxa black to brownish black.

Host. *Cydia strobilella* (Linnaeus, 1758) (Lepidoptera, Tortricidae).

Host plant. *Picea crassifolia* Kom., *P. mongolica* W.D. Xu.

Material examined. 4 ♀♀, 7 ♂♂, CHINA: Qilian, Qinghai Province, 16–26 April 2004, Mao-Ling Sheng. 68 ♀♀, 26 ♂♂, CHINA: Keshiketeng, Inner Mongolia, 6–10 April 2005, Mao-Ling Sheng. 1 ♂, CHINA: Aletai, Xinjiang, 30 March 2007, Mao-Ling Sheng. 1 ♀, CHINA: Mentougou, Beijing, 13 June 2008, Tao Wang.

Distribution. China.

Townesia tenuiventris (Holmgren, 1860)

Figure 14

Diagnosis. Female: Vertex smooth, shiny, lateral part with sparse, fine punctures. Postocellar line approximately 0.8 times as long as ocular-ocellar line. Upper-posterior part of mesopleuron smooth, shiny, without punctures. Forewing vein radius distinctly basal of middle of pterostigma; 1*cu-a* distinctly basal of *1/M*. Areolet receiving *2m-cu* approximately at its posterior 0.3. Tergite II 1.9 times as long as its maximum width, apical smooth transverse bands of tergites II 0.25–2.7 times as long as length. Subapical portion of upper valve of ovipositor with two indistinct tubercles; ventral valve with 10 or 11 ridges, basal 4 ridges strongly inclivous. All coxae, trochanters, and femora reddish brown.

Host. Fourteen host species were recorded (Yu et al. 2016).

Material examined. The specimens, deposited in ZSM and identified by Bauer, were examined.

Distribution. Austria, Belarus, Belgium, Bulgaria, Canada, Denmark, Finland, France, Germany, Hungary, Ireland, Italy, Japan, Latvia, Lithuania, Netherlands, Norway, Poland, Romania, Russia, Serbia, Spain, Sweden, U.S.A., United Kingdom, Yugoslavia.

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RESEARCH ARTICLE

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Extensive sampling and thorough taxonomic assessment of Afrotropical Rhyssinae (Hymenoptera, Ichneumonidae) reveals two new species and demonstrates the limitations of previous sampling efforts

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Abstract

Tropical forest invertebrates, such as the parasitoid wasp family Ichneumonidae, are poorly known. This work reports some of the first results of an extensive survey implemented in Kibale National Park, Uganda. A total of 456 individuals was caught of the subfamily Rhyssinae Morley, 1913, which in the Afrotropical region was previously known from only 30 specimens. Here, the six species found at the site are described and the Afrotropical Rhyssinae are reviewed. Two new species, *Epirhyssa johanna* Hopkins**, sp. nov.** and *E. quagga* **sp. nov.**, are described and a key, diagnostic characters, and descriptions for all 13 known Afrotropical species are provided, including the first description of the male of *Epirhyssa overlaeti* Seyrig, 1937. *Epirhyssa gavinbroadi* Rousse & van Noort, 2014, **syn. nov.** is proposed to be a synonym of *E. uelensis* Benoit, 1951. Extensive sampling with Malaise traps gave an unprecedented sample size, and the method is recommended for other poorly known tropical areas.

Keywords
Africa, Ichneumonidae, Kibale National Park, Uganda Malaise trapping 2014–2015

Introduction

Like many taxa, the parasitoid wasps of the family Ichneumonidae are poorly known in the tropics. So much so, that the family was once assumed to be exceptionally species-poor in the equatorial region and to peak in species richness in mid latitudes (Owen and Owen 1974, Janzen and Pond 1975, but see Morrison et al. 1979). More recent extensive sampling has revealed rich ichneumonid faunas in the tropical forests of Costa Rica and Amazonia (Gauld 1991, Gaston and Gauld 1993, Sääksjärvi et al. 2004), and the family appears to be too poorly sampled in the tropics to allow reliable conclusions as to the distribution of its species richness (Quicke 2012). In Sub-Saharan Africa, only 2097 of an estimated 12,100 species have been described (Townes and Townes 1973, Yu et al. 2016, van Noort 2019), and even sites that have been studied remain strongly under-sampled (e.g., van Noort et al. 2000, van Noort 2004, Hopkins et al. 2018).

The ichneumonid subfamily Rhyssinae is especially poorly known in the Afrotropical region. It was reviewed in 2014 (Rousse and van Noort 2014), resulting in five new species and a total of twelve species for Sub-Saharan Africa. This is very low compared to the currently known (and increasing) 49 Neotropical, 125 Oriental, 23 Australasian, 40 Palaearctic, and 17 Nearctic species (Yu et al. 2016). Insufficient sampling, rather than a genuine scarcity, is presumably the main reason for the low African species count: even after gathering together material from several African and European museums, Rousse and van Noort (2014) were unable to find more than 30 specimens collected from the whole of the Afrotropical region.

One possible reason for the lack of rhyssine specimens is that adequately inventorying tropical ichneumonids appears to need long-term, extensive sampling (for reasons summarised in Hopkins et al. 2019b). Such sampling is laborious and has rarely been done in the tropics. Ichneumonids have been extensively sampled by Malaise traps in Costa Rica (e.g., more than 1200 trap months: Gauld 1991, about 190 trap months: Shapiro and Pickering 2000) and in Amazonia (185 trap months: Sääksjärvi et al. 2004, at least 72 additional trap months: Gómez et al. 2017). For Sub-Saharan Africa, we know of only two large-scale sampling programs, one of which returned an unexpectedly low sample size of ichneumonids (231 trap months using traps smaller than the standard size, Hopkins et al. 2018). The results of the second program have not yet been published (258 trap months conducted by SvN in Hantam National Botanical Garden, South Africa).

In this and a sister paper, we report the first results of an extensive one-year sampling of Afrotropical ichneumonids in Kibale National Park, Uganda. In the sister paper we report the ecological results for the subfamily Rhyssinae, including descriptions of the habitat use and phenology of the species (Hopkins et al. 2019b). Here, we update the taxonomy of the subfamily and describe the new species found at our site, providing a key, diagnostic characters, and updates to descriptions for all known Afrotropical Rhyssinae.

Materials and methods

We sampled ichneumonids with 34 Malaise traps for a full year (2014–2015) in Kibale National Park, Uganda. The traps were placed in a wide variety of habitats ranging from primary forest to clear-cut former plantations and farmland, and the total sampling effort was roughly 382 trap months (11662.13 trap days, of which 271.16 trap days were unrepresentative of a normal catch). We describe the sampling in greater detail in Hopkins et al. (2019b) and its associated dataset (Hopkins et al. 2019a). As well as using Malaise traps, we also collected ichneumonids by hand netting. Hand-netted ichneumonids were stored individually in 96% ethanol.

We processed the samples at the Zoological Museum of the University of Turku, Finland. We separated the ichneumonoid wasps (families Ichneumonidae and Braconidae) from the Malaise samples, then pinned the subfamily Rhyssinae and sorted specimens into species. We did not pin the hand netted rhyssines; instead, we stored these specimens individually in 96% ethanol. The samples are deposited at the Zoological Museum.

Layer photographs were taken using a Canon 7 D mark 2 digital camera, attached to an Olympus SZX 16 stereomicroscope. Photographs were captured using the programmes Deep Focus 3.1 and Quick Photo Camera 2.3. Photographs were finally combined with the program Zerene and edited in Photoshop CC. Additional images were acquired at SAMC with a Leica LAS 4.9 imaging system, comprising a Leica Z16 microscope (using either a 2 × or 5 × objective) with a Leica DFC450 Camera and 0.63 × video objective attached. The imaging process, using an automated Z-stepper, was managed using the Leica Application Suite V 4.9 software installed on a desktop computer. Diffused lighting was achieved using a Leica LED5000 HDI dome. All images presented in this paper, as well as supplementary images, are available at www.waspweb.org.

Because earlier diagnostic characters (Rousse and van Noort 2014) did not work well with our material, we collected a partly new set of nine diagnostic characters for all Afrotropical species (Fig. 1). We retrieved diagnostic characters for the previously known 30 specimens from Rousse and van Noort (2014) if available, or from the specimens themselves if not.

Morphological terminology largely follows Gauld (1991) and body measurements follow Rousse and van Noort (2014). We measured body length from the base of the antennae to the tip of the metasoma. If the metasoma was bent, we measured it in several line segments. We measured the slenderness of tergite 1 by dividing the median length by the apical width. The images used to take the measurements are available in the supplementary material (Hopkins et al. 2019c).

We generated an identification key automatically, based on the nine diagnostic characters (Hopkins et al. 2019c). The diagnostic characters, descriptions, identification key and data for all Ugandan specimens are available in table format in the supplementary material (Hopkins et al. 2019c).

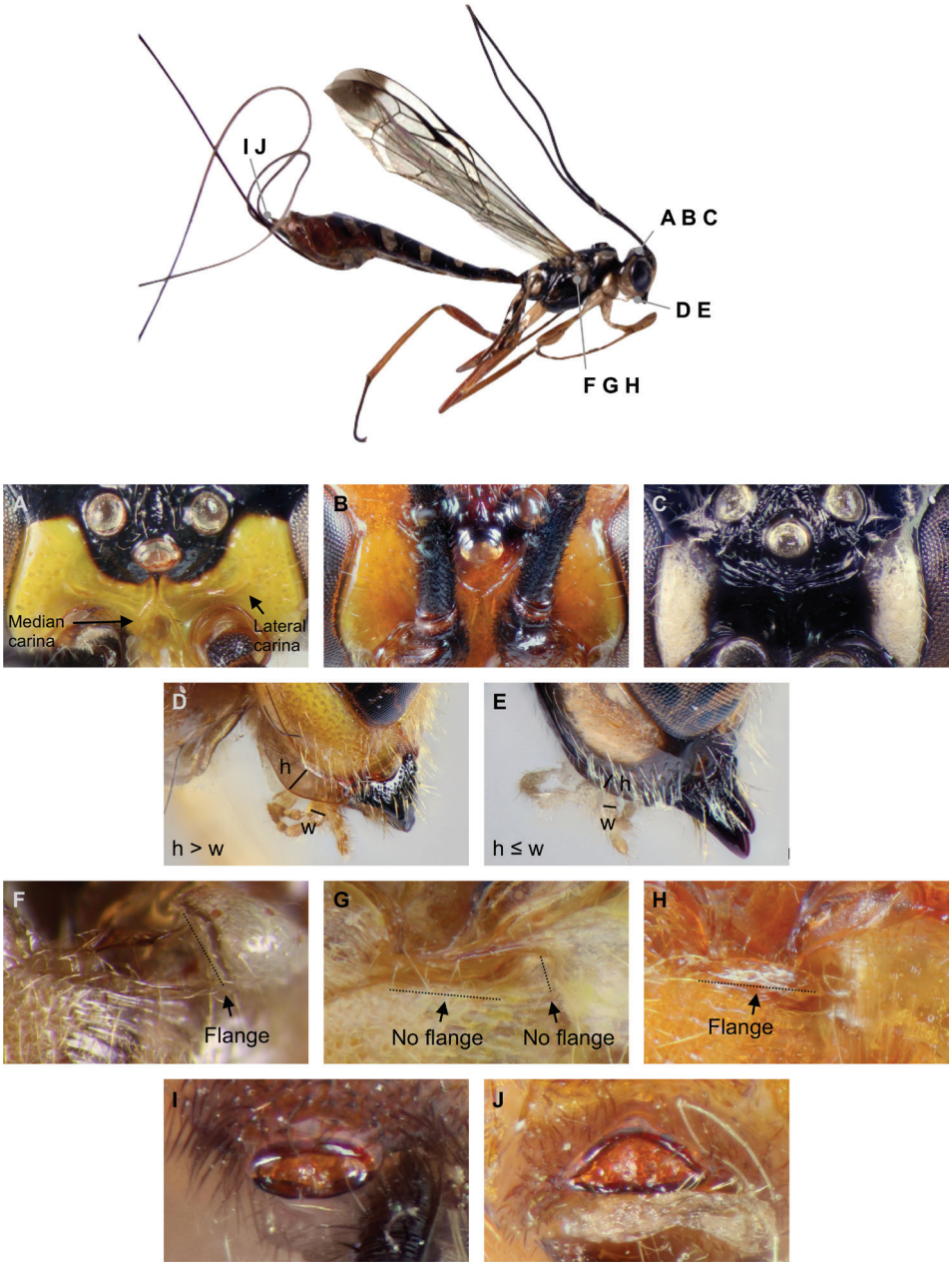


Figure 1. Diagnostic characters for the thirteen known Afrotropical rhyssine species. The figure shows the frons median carinae (**A** converge, **B** diverge, **C** absent), frons lateral carinae (**A** present, **B** absent), hypostomal flange (**D** wider than second maxillary palp, **E** narrower than or comparable to second maxillary palp), subalar prominence (**F** flanged, **G** no flange), mesopleuron margin (**H** flanged, **G** no flange) and female apical horn (**I** ellipse, **J** half-ellipse). Not shown are the epicnemial carina (laterally absent, only just reaches the mesopleuron, reaches high onto the mesopleuron), areolet (present, absent) and tergite 3 structure (mostly striate, mostly punctate, mostly smooth). The images are of http://mus.utu.fi/ZMUT.5766, http://mus.utu.fi/ZMUT.2520 (**A, F**), http://mus.utu.fi/ZMUT.5853 (**B, D, H, J**), http://mus.utu.fi/ZMUT.5788 (**C, E, I**) and http://mus.utu.fi/ZMUT.5663 (**G**). Image **F** has been flipped horizontally.

Repositories

MNHN	Muséum national d'Histoire naturelle, Paris, France (Agnièle Touret-Alby)
NHMUK	Natural History Museum, London, UK (Gavin Broad)
NMSA	KwaZulu-Natal Museum, Pietermaritzburg, South Africa (John Midgley)
RMCA	Royal Museum for Central Africa, Tervueren, Belgium (Stéphane Hanot)
SAMC	Iziko South African Museum, Cape Town, South Africa (Simon van Noort)
ZMUT	Zoological Museum of the University of Turku, Finland (Ilari Sääksjärvi)

Results

We caught 448 rhyssines by Malaise sampling and eight by hand netting. They belonged to six species of which two are new. We provide a key to all 13 known Afrotropical species below. We also provide diagnostic characters and descriptions or updates to descriptions for all species. The key, diagnostic characters, and descriptions are also available in table form in the supplementary material (Hopkins et al. 2019c). Online identification keys are available on www.waspweb.org.

Key to species

1 Fore wing with a closed areolet (Fig. 2A).[Black and orange species with infuscate wings; Fig. 72].....***Megarhyssa babaulti* Seyrig, 1937**

– Fore wing without an areolet (Fig. 2B).....**2**

2 Subalar prominence with a lateral flange (Fig. 2C).[Yellow species with black markings; Fig. 57].....***Epirhyssa uelensis* Benoit, 1951**

– Subalar prominence without a lateral flange (Fig. 2D) **3**

3 Dorsal margin of mesopleuron with a raised flange (Fig. 2D) **4**

– Dorsal margin of mesopleuron without a raised flange (Fig. 2E) **5**

4 Apical horn of metasoma shaped like an ellipse in posterior view (Fig. 2F), frons with median carinae that converge before the ocelli, frons with lateral carinae. [Red, yellow, and black species; Fig. 32] ..... ***Epirhyssa overlaeti* Seyrig, 1937**

– Apical horn of metasoma shaped like a half-ellipse in posterior view (Fig. 2G), frons with median carinae that diverge before continuing towards the lateral ocelli, frons without lateral carinae. [Orange species, sometimes with black markings; Fig. 7]..... ***Epirhyssa ghesquierei* Seyrig, 1937**

5 Epicnemial carina laterally absent, does not reach mesopleuron **6**

– Epicnemial carina present on mesopleuron **7**

6 Frons with median carinae that diverge before continuing towards the lateral ocelli (cf. Fig. 1B). [Yellow species with black on metasoma; Fig. 28]..... .....***Epirhyssa migratoria* Seyrig, 1932**

– Frons smooth, without median carinae (Fig. 2H). [Predominantly orange species; Fig. 14].....***Epirhyssa johanna* sp. nov.**

7 Frons with median carinae that diverge before continuing towards the lateral ocelli (cf. Fig. 1B), frons with lateral carinae. [Black and orange species with infuscate wings; Fig. 68] ..... ***Epirhyssa villemantae*** **Rousse & van Noort, 2014**

– Frons with median carinae that converge before the ocelli or without median carinae (Fig. 2I), frons without lateral carinae (Fig. 2I) **8**

8 Tergite 3 densely striate (Fig. 2J), frons striate but without median carinae. [Black, white and orange species; Fig. 39] ..... ***Epirhyssa quagga*** **sp. nov.**

– Tergite 3 mostly smooth or mostly punctate (Fig. 2K), frons with median carinae **9**

9 Tergite 3 mostly smooth **10**

– Tergite 3 mostly punctate, over 50% of surface (Fig. 2K) **11**

10 Epicnemial carina only just reaches the mesopleuron. [Hypostomal carina raised into a low flange, yellow-orange species with yellow and infuscate wings; Fig. 25] ..... ***Epirhyssa maynei*** **Benoit, 1952**

– Epicnemial carina long, reaches the approximate height of the mesopleural pit. [Hypostomal carina raised into an elevated flange, yellow species with black mesosternum; Fig. 21] ..... ***Epirhyssa leroyi*** **Benoit, 1951**

11 Hypostomal carina raised into an elevated flange (Fig. 2L, see also Fig. 1D). [Black and white species; Fig. 3] ..... ***Epirhyssa brianfisheri*** **Rousse & van Noort, 2014**

– Hypostomal carina raised into a low flange (Fig. 2M, see also Fig. 1E) **12**

12 Apical horn of metasoma shaped like a half-ellipse in posterior view (Fig. 2N). [Yellow species with black markings as in Fig. 50] ..... ***Epirhyssa tombeaodiba*** **Rousse & van Noort, 2014**

– Apical horn of metasoma shaped like an ellipse in posterior view (Fig. 2O). [Yellow species with black markings as in Fig. 46] ..... ***Epirhyssa shaka*** **Rousse & van Noort, 2014**

Taxonomic descriptions

Family Ichneumonidae Latreille, 1802
Subfamily Rhyssinae Morley, 1913

Diagnosis. The subfamily Rhyssinae can be recognised by a combination of the transverse rugae covering much of the mesoscutum; the short, broad mandibles and small, rectangular clypeus; the long ovipositor; and the female 8th metasomal tergite being produced posteriorly as a truncate horn-like projection. Other genera that present a potential confusion risk, such as *Pseudorhyssa* Merril (Pimplinae), *Certonotus* Kriechbaumer, and *Apechoneura* Kriechbaumer (Labeninae) are not present in the Afrotropical region.

Figure 2. Diagnostic character traits used in the identification key. **A** Areolet (*Megarhyssa babaulti* holotype) **B** open areolet (http://mus.utu.fi/ZMUT.5788) **C** subalar prominence flange (http://mus.utu.fi/ZMUT.2520) **D** subalar prominence without flange and dorsal margin of mesopleuron with flange (http://mus.utu.fi/ZMUT.5853) **E** dorsal margin of mesopleuron without flange (SAMC SAM–HYM–P048018) **F** elliptical apical horn of metasoma (http://mus.utu.fi/ZMUT.5766) **G** half-elliptical apical horn of metasoma (http://mus.utu.fi/ZMUT.5853) **H** frons without carinae (http://mus.utu.fi/ZMUT.4920) **I** frons without lateral carinae (http://mus.utu.fi/ZMUT.3234) **J** striate tergite 3 (http://mus.utu.fi/ZMUT.5788) **K** punctate tergite 3 (http://mus.utu.fi/ZMUT.5663) **L** hypostomal carina raised into elevated flange (SAMC SAM–HYM–P048018) **M** hypostomal carina raised into low flange (*E. shaka* holotype) **N** half-elliptical apical horn of metasoma (http://mus.utu.fi/ZMUT.5663) **O** elliptical apical horn of metasoma (*E. shaka* holotype). Image **A** is from van Noort (2019). Image **D** has been flipped horizontally.

Genus *Epirhyssa* Cresson, 1865

Hierax Tosquinet, 1903: 255.
Rhyssonota Kriechbaumer, 1890: 489.
Sychnostigma Baltazar, 1961: 75.

Diagnosis. The genus *Epirhyssa* is easily recognised in the Afrotropical region as the species lack the fore wing areolet (vein 3rs-m is missing), whereas the areolet is closed by vein 3rs-m in *Megarhyssa* Ashmead, the only other rhyssine genus found in the Afrotropical region.

Epirhyssa can be distinguished from other rhyssine genera by the lack of an areolet (cf. *Rhyssella* Rohwer, *Lytarmes* Cameron), the lack of an anterior glymma on tergite 1 (cf. *Rhyssa* Gravenhorst), the upper tooth being slightly wider than the lower and not subdivided (cf. *Triancyra* Baltazar, *Myllenyxis* Baltazar) and the pterostigma being angled where it meets the metacarpus (compared to gradually merging in *Cyrtorhyssa* Baltazar) (Baltazar 1964, Townes 1969, Porter 2001). Old World *Epirhyssa* have fore wing vein 2rs-m only a little proximal to 2m-cu, unlike New World species. The species are rather heterogeneous, with confusion with other genera particularly likely in the Oriental region, and the genus may well prove not to be monophyletic.

Distribution. Afrotropical region: Central African Republic, Cameroon, Democratic Republic of Congo, Madagascar, Nigeria, South Africa, Uganda.

Australasian region: Papua New Guinea.

Nearctic region: Mexico, U.S.A.

Neotropical region: Argentina, Brazil, Bolivia, Costa Rica, Cuba, Ecuador, Guatemala, Guyana, Nicaragua, Paraguay, Peru, Trinidad.

Oriental region: China, India, Indonesia, Japan, Malaysia, Myanmar, Philippines, Singapore, Vietnam.

Palaearctic region: Russia.

Epirhyssa brianfisheri Rousse & van Noort, 2014

Figs 3–6

Material examined. Type material: CENTRAL AFRICAN REPUBLIC:

• 1 ♀, holotype; Préfecture Sangha-Mbaéré, Réserve Spéciale de Forêt Dense de Dzanga-Sangha (12.7 km, 326 degrees NW of Bayanga); 3°00.27'N, 16°11.55'E; alt. 420 m; 13 May 2001; Simon van Noort leg.; Sweep; CAR01–S158; Lowland rainforest; SAMC SAM–HYM–P048018.

Known material: One specimen (1 ♀, see Rousse and van Noort 2014, data above).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of an elevated hypostomal flange, the absence of a raised flange on the dorsal margin of the mesopleuron, an elliptical apical horn of the metasoma, and a finely punctate (over 50% of surface) tergite 3. In practice its colour pattern makes it instantly recognisable.

Figures 3–6. *Epirhyssa brianfisheri* female (holotype, SAM–HYM–P048018). This species was not found in Uganda. **3** Habitus **4** hypostomal flange **5** mesopleuron dorsal margin **6** apical horn of metasoma. Figure **3** is from van Noort (2019).

Head: frons with median carinae converging before continuing towards median ocellus, without lateral carinae; hypostomal carina raised into an elevated flange, its height greater than the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 punctate.

Distribution. Central African Republic.

Epirhyssa ghesquierei Seyrig, 1937

Figs 7–13

Material examined. Type material: DEMOCRATIC REPUBLIC OF CONGO:

• 1 ♀, holotype; Eala [0°4.22'N, 18°18.15'E]; Nov. 1935; "J. Ghesquière"; "R. Dét. G 3330"; RMCA RMCA-ENT-000017927

• 1 ♂, paratype; Bambesa; Dec. 1946; "P.L. Benoit"; RMCA RMCA-ENT-000017928.

Figures 7–13. *Epirhyssa ghesquierei* female (http://mus.utu.fi/ZMUT.5853), a species found in Uganda. **7** Habitus **8** face and clypeus **9** frons **10** hypostomal flange **11** mesopleuron dorsal margin **12** apical horn of metasoma **13** tergites 1–7. Scale bars: 0.5 mm (**8–13**), 1 mm (**7**).

Non-type material: CAMEROON:

• 1 ♂; Korup; Dec. 1980–Jan. 1981; Mrs D. Jackson leg.; NHMUK

• 1 ♂; Korup; 1981; Mrs D. Jackson leg.; NHMUK.

UGANDA:

• 1 ♀; Kibale National Park, Kanyawara, Site R93, Malaise trap R93T1; 0.5653N, 30.3568E (WGS84); alt. 1510 m (GPS, WGS84); 23 Sep. 2014–7 Oct. 2014; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.53

• 1 ♀; same data as preceding; Site K30S, Malaise trap K30ST4; 0.5414N, 30.3755E (WGS84); alt. 1420 m (GPS, WGS84); 25 Aug. 2015–11 Sep. 2015; ZMUT http://mus.utu.fi/ZMUT.1263

• 1 ♀; same data as preceding; Site K15, Malaise trap K15T2; 0.5843N, 30.3644E (WGS84); alt. 1470 m (GPS, WGS84); 4 May 2015–20 May 2015; ZMUT http://mus.utu.fi/ZMUT.5592

• 1 ♀; same data as preceding; Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 15 Dec. 2014–29 Dec. 2014; ZMUT http://mus.utu.fi/ZMUT.5701

• 1 ♀; same data as preceding; 24 Feb. 2015–10 Mar. 2015; ZMUT http://mus.utu.fi/ZMUT.5737

• 1 ♀; same data as preceding; 13 Jan. 2015–27 Jan. 2015; ZMUT http://mus.utu.fi/ZMUT.5853

• 1 ♂; Kibale National Park, Kanyawara, Site K31, Malaise trap K31T4; 0.5362N, 30.3486E (WGS84); alt. 1460 m (GPS, WGS84); 29 Dec. 2014–16 Jan. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.2300

• 1 ♂; same data as preceding; Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 30 Jun. 2015–14 Jul. 2015; ZMUT http://mus.utu.fi/ZMUT.5610.

Non-type material (only diagnostic characters checked): UGANDA:

• 109 ♀; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1250, http://mus.utu.fi/ZMUT.1251, http://mus.utu.fi/ZMUT.1252, http://mus.utu.fi/ZMUT.1257, http://mus.utu.fi/ZMUT.1258, http://mus.utu.fi/ZMUT.1260, http://mus.utu.fi/ZMUT.1264, http://mus.utu.fi/ZMUT.1269, http://mus.utu.fi/ZMUT.1271, http://mus.utu.fi/ZMUT.1282, http://mus.utu.fi/ZMUT.1335, http://mus.utu.fi/ZMUT.1365, http://mus.utu.fi/ZMUT.1526, http://mus.utu.fi/ZMUT.1695, http://mus.utu.fi/ZMUT.1720, http://mus.utu.fi/ZMUT.2569, http://mus.utu.fi/ZMUT.2799, http://mus.utu.fi/ZMUT.3010, http://mus.utu.fi/ZMUT.3077, http://mus.utu.fi/ZMUT.3095, http://mus.utu.fi/ZMUT.3100, http://mus.utu.fi/ZMUT.3103, http://mus.utu.fi/ZMUT.3104, http://mus.utu.fi/ZMUT.3459, http://mus.utu.fi/ZMUT.3495, http://mus.utu.fi/ZMUT.3496, http://mus.utu.fi/ZMUT.3529, http://mus.utu.fi/ZMUT.3542, http://mus.utu.fi/ZMUT.3611, http://mus.utu.fi/ZMUT.3638, http://mus.utu.fi/ZMUT.4375, http://mus.utu.fi/ZMUT.4738, http://mus.utu.fi/ZMUT.5594, http://mus.utu.fi/ZMUT.5598, http://mus.utu.fi/ZMUT.5599, http://mus.utu.fi/ZMUT.5603, http://mus.utu.fi/ZMUT.5612, http://mus.utu.fi/ZMUT.5615, http://mus.utu.fi/ZMUT.5617, http://mus.utu.fi/ZMUT.5621, http://mus.utu.fi/ZMUT.5624, http://mus.utu.fi/ZMUT.5627, http://mus.utu.fi/ZMUT.5634, http://mus.utu.fi/ZMUT.5636, http://mus.utu.fi/ZMUT.5638, http://mus.utu.fi/ZMUT.5639, http://mus.utu.fi/ZMUT.5649, http://mus.utu.fi/ZMUT.5654, http://mus.utu.fi/ZMUT.5659, http://mus.utu.fi/ZMUT.5661, http://mus.utu.fi/ZMUT.5664, http://mus.utu.fi/ZMUT.5666, http://mus.utu.fi/ZMUT.5667, http://mus.utu.fi/ZMUT.5671, http://mus.utu.fi/ZMUT.5676, http://mus.utu.fi/ZMUT.5677, http://mus.utu.fi/ZMUT.5680, http://mus.utu.

fi/ZMUT.5685, http://mus.utu.fi/ZMUT.5686, http://mus.utu.fi/ZMUT.5691, http://mus.utu.fi/ZMUT.5695, http://mus.utu.fi/ZMUT.5696, http://mus.utu.fi/ZMUT.5706, http://mus.utu.fi/ZMUT.5707, http://mus.utu.fi/ZMUT.5710, http://mus.utu.fi/ZMUT.5711, http://mus.utu.fi/ZMUT.5715, http://mus.utu.fi/ZMUT.5716, http://mus.utu.fi/ZMUT.5718, http://mus.utu.fi/ZMUT.5721, http://mus.utu.fi/ZMUT.5723, http://mus.utu.fi/ZMUT.5724, http://mus.utu.fi/ZMUT.5735, http://mus.utu.fi/ZMUT.5745, http://mus.utu.fi/ZMUT.5747, http://mus.utu.fi/ZMUT.5751, http://mus.utu.fi/ZMUT.5753, http://mus.utu.fi/ZMUT.5756, http://mus.utu.fi/ZMUT.5759, http://mus.utu.fi/ZMUT.5760, http://mus.utu.fi/ZMUT.5761, http://mus.utu.fi/ZMUT.5769, http://mus.utu.fi/ZMUT.5770, http://mus.utu.fi/ZMUT.5776, http://mus.utu.fi/ZMUT.5782, http://mus.utu.fi/ZMUT.5786, http://mus.utu.fi/ZMUT.5796, http://mus.utu.fi/ZMUT.5799, http://mus.utu.fi/ZMUT.5800, http://mus.utu.fi/ZMUT.5802, http://mus.utu.fi/ZMUT.5809, http://mus.utu.fi/ZMUT.5810, http://mus.utu.fi/ZMUT.5812, http://mus.utu.fi/ZMUT.5813, http://mus.utu.fi/ZMUT.5819, http://mus.utu.fi/ZMUT.5826, http://mus.utu.fi/ZMUT.5827, http://mus.utu.fi/ZMUT.5830, http://mus.utu.fi/ZMUT.5837, http://mus.utu.fi/ZMUT.5840, http://mus.utu.fi/ZMUT.5841, http://mus.utu.fi/ZMUT.5842, http://mus.utu.fi/ZMUT.5843, http://mus.utu.fi/ZMUT.5847, http://mus.utu.fi/ZMUT.6015, http://mus.utu.fi/ZMUT.6043, http://mus.utu.fi/ZMUT.6050, http://mus.utu.fi/ZMUT.6051, http://mus.utu.fi/ZMUT.6053

• 47 ♂; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1351, http://mus.utu.fi/ZMUT.1359, http://mus.utu.fi/ZMUT.1588, http://mus.utu.fi/ZMUT.1791, http://mus.utu.fi/ZMUT.2170, http://mus.utu.fi/ZMUT.2505, http://mus.utu.fi/ZMUT.2622, http://mus.utu.fi/ZMUT.2647, http://mus.utu.fi/ZMUT.3098, http://mus.utu.fi/ZMUT.3099, http://mus.utu.fi/ZMUT.3528, http://mus.utu.fi/ZMUT.3684, http://mus.utu.fi/ZMUT.3694, http://mus.utu.fi/ZMUT.4322, http://mus.utu.fi/ZMUT.4514, http://mus.utu.fi/ZMUT.4636, http://mus.utu.fi/ZMUT.4641, http://mus.utu.fi/ZMUT.5588, http://mus.utu.fi/ZMUT.5590, http://mus.utu.fi/ZMUT.5602, http://mus.utu.fi/ZMUT.5611, http://mus.utu.fi/ZMUT.5633, http://mus.utu.fi/ZMUT.5651, http://mus.utu.fi/ZMUT.5656, http://mus.utu.fi/ZMUT.5660, http://mus.utu.fi/ZMUT.5682, http://mus.utu.fi/ZMUT.5700, http://mus.utu.fi/ZMUT.5703, http://mus.utu.fi/ZMUT.5714, http://mus.utu.fi/ZMUT.5730, http://mus.utu.fi/ZMUT.5731, http://mus.utu.fi/ZMUT.5744, http://mus.utu.fi/ZMUT.5746, http://mus.utu.fi/ZMUT.5777, http://mus.utu.fi/ZMUT.5779, http://mus.utu.fi/ZMUT.5795, http://mus.utu.fi/ZMUT.5828, http://mus.utu.fi/ZMUT.5833, http://mus.utu.fi/ZMUT.5848, http://mus.utu.fi/ZMUT.5852, http://mus.utu.fi/ZMUT.5859, http://mus.utu.fi/ZMUT.6046, http://mus.utu.fi/ZMUT.6047, http://mus.utu.fi/ZMUT.6048, http://mus.utu.fi/ZMUT.6049, http://mus.utu.fi/ZMUT.6052, http://mus.utu.fi/ZMUT.6054.

Known material: 168 specimens (164 Ugandan, 4 other):

112 ♀, 44 ♂; Ugandan specimens caught by Malaise trap, data above and also in supplementary material (Hopkins et al. 2019c).

3 ♀, 5 ♂; Ugandan hand-netted specimens, data above and also in supplementary material (Hopkins et al. 2019c).

1 ♀, 3 ♂; see Rousse and van Noort (2014), data above in material examined.

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of a half-elliptical apical horn of the metasoma and a mostly smooth tergite 3.

Head: frons with diverging median carinae, without clear lateral carinae; hypostomal carina raised into an elevated flange, its height greater than the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron with an elevated flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn half-elliptical in posterior view; tergite 3 mostly smooth.

Additional or updated characters. Apart from the diagnosis, we provide the following additional or updated character traits to the description in Rousse and van Noort (2014).

Female. Body length 11.4 mm–17.2 mm. Frons rugulose or smooth, often with more or less distinct rugae that fan out from the median carinae towards the ocelli. Antenna with 32–34 flagellar segments. Tergites mostly smooth, but with variable structure on some tergites (4–7 pubescent and anterior margins of 3–5 slightly punctate or striate in Ugandan specimens, 3–6 shallowly punctate with anterior striations in other specimens), tergite 1 2.2–2.5 times as long as apically wide. The Ugandan specimens are more orange than yellow in colour, generally have no dark spots on the lateral lobes of the mesoscutum, and the colour of their interocellar area varies from orange (most frequent) to black.

Male. Body length 11.5 mm–14.1 mm. Antenna with 31–33 flagellar segments. Anterior margin of tergite 3 sometimes neither punctate nor striate. Tergite 1 2.5–3.0 times as long as apically wide. Males are smaller than females on average.

Distribution. Democratic Republic of Congo, Cameroon. New record: Uganda.

Biology. In Uganda, this species was most abundantly caught in primary forest near decaying wood, during the dry season (Hopkins et al. 2019b). It has not been caught outside the forest. Many of the hand-netted individuals were caught after landing on a fallen tree trunk (*Uvariopsis congensis* Robyns & Ghesq.). The males especially seemed to be repeatedly visiting the tree.

Epirhyssa johanna Hopkins, sp. nov.

http://zoobank.org/67413463-3BD1-4812-B6F5-DA6E768ABE03

Figs 14–20

Material examined. Type material: UGANDA:

• 1 ♀, holotype; Kibale National Park, Kanyawara, Site R03, Malaise trap R03T2; 0.5403N, 30.3608E (WGS84); alt. 1490 m (GPS, WGS84); 7 May 2015–21 May 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.4920.

Known material: One specimen (1 ♀, Ugandan specimen, data above).

Figures 14–20. *Epirhyssa johanna* female (holotype http://mus.utu.fi/ZMUT.4920), a new species from Uganda. **14** habitus **15** face and clypeus **16** frons **17** hypostomal flange **18** mesopleuron dorsal margin **19** apical horn of metasoma **20** tergites 1–7. Scale bars: 0.5 mm (**15–20**), 1 mm (**14**).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of a smooth frons without median carinae and a laterally absent epicnemial carina. No other species has the same colour pattern.

Head: frons without median carinae, without lateral carinae; hypostomal carina raised into a low flange, its height slightly less than or equivalent to the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina laterally absent.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 mostly smooth.

Description (female). Body length 8.4 mm.

Head: Frons without median carinae, without lateral carinae, smooth or very faintly striate. Occipital carina interrupted dorsally and interrupted or extremely faint near hypostomal carina. Hypostomal carina raised into a low flange, its height slightly less than or equivalent to maximum width of second maxillary palp segment. Face smooth or very faintly punctate. Clypeus sparsely punctate, with a median apical tubercle. Antenna with 28 flagellar segments.

Mesosoma: Subalar prominence without a lateral flange. Mesopleuron without a flange along the dorsal margin. Epicnemial carina laterally absent. Fore wing with 2m-cu distal to rs-m.

Metasoma: Tip of apical horn elliptical (flattened ellipse) in posterior view. Tergites mostly smooth, anterior of tergites 2–6 medially striate, tergite 1 1.2 times as long as apically wide.

Colour: General colour orange. Other colour: white face, lower 1/4 of genae, lateral frons, black mandibles, median frons, occiput, upper genae, and median spot on apical half of tergite 6 and entire tergite 7, dark brown hind tarsi. Antennae black. Ovipositor sheaths dark testaceous. Wings hyaline, faintly infuscate near apex.

Male. Unknown.

Etymology. Dedicated to Johanna Hopkins, the first author's wife. This species is known from only one, quite exceptional, female specimen.

Distribution. Uganda.

Remarks. Only one specimen was caught during 382 trap months of sampling, in a habitat (successional forest logged 2002–2004) that generally yielded few rhyssines.

Epirhyssa leroyi Benoit, 1951

Figs 21–24

Material examined. Type material: DEMOCRATIC REPUBLIC OF CONGO:

• 1 ♀, holotype; Bambesa [03°28'N 25°43'E]; Dec. 1933; "J.V. Leroy"; RMCA RMCA-ENT-000017923

• 1 ♀, paratype; Ubangui-Bumba; Dec. 1939; H. de Saeger; RMCA RMCA-ENT-000017924.

Known material: Two specimens (2 ♀, see Rousse and van Noort 2014, data above).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of converging median carinae on the frons, the absence of lateral

Figures 21–24. *Epirhyssa leroyi* female (paratype RMCA-ENT-000017924). This species was not found in Uganda. **21** Habitus **22** hypostomal flange **23** mesopleuron dorsal margin **24** apical horn of metasoma. Scale bars 1 mm (**22–24**), 5 mm (**21**). Figures courtesy of RMCA (Stéphane Hanot).

carinae on the frons, an epicnemial carina that reaches high onto the mesopleuron, and a mostly smooth tergite 3. No other species is known to have a black mesosternum.

Head: frons with median carinae converging before continuing towards median ocellus, without lateral carinae; hypostomal carina raised into an elevated flange, its height slightly greater than the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 mostly smooth.

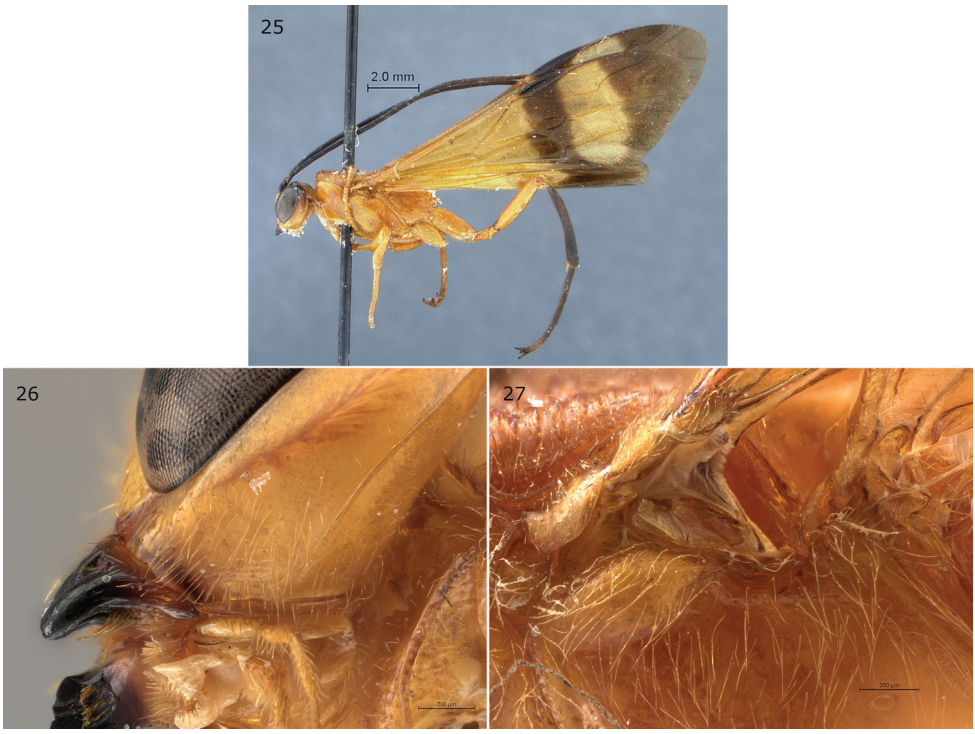
Distribution. Democratic Republic of Congo.

Epirhyssa maynei Benoit, 1952

Figs 25–27

Material examined. Non-type material: CENTRAL AFRICAN REPUBLIC:

• 1 ♂; Préfecture Sangha-Mbaéré, Parc National de Dzanga-Ndoki (38.6 km, 173 degrees S of Lidjombo); 2°21.60'N, 16°09.20'E; alt. 350 m; 27 May 2001;



Figures 25–27. *Epirhyssa maynei* male (**25**: holotype, **26–27**: SAM–HYM–P049437). This species was not found in Uganda. **25** Habitus **26** hypostomal flange **27** mesopleuron dorsal margin. Figure **25** is from van Noort (2019).

Simon van Noort leg.; Handnet; CAR01-H25; Lowland rainforest; SAMC SAM–HYM–P049437.

Known material: Three specimens (0 Ugandan, 3 other):

1 ♂, holotype; see Rousse and van Noort (2014); Democratic Republic of Congo, Albertville [Kalemie, 05°56'N, 29°12'E]; Jul. 1918; "R. Mayné"; MRAC.

1 ♂, paratype; see Rousse and van Noort (2014); Democratic Republic of Congo, Bambesa; Dec. 1946; "P.L. Benoit"; MRAC.

1 ♂; see Rousse and van Noort (2014), data above in material examined.

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the epicnemial carina only just reaching the mesopleuron. The fore wing colour pattern makes it instantly recognisable.

Head: frons with median carinae converging before continuing towards median ocellus, without lateral carinae; hypostomal carina raised into a low flange, its height slightly less than or equivalent to the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina short, barely extending onto mesopleuron.

Metasoma: tip of apical horn of unknown shape (no females are known); tergite 3 mostly smooth.

Distribution. Democratic Republic of Congo, Central African Republic.

Epirhyssa migratoria Seyrig, 1932

Figs 28–31

Material examined. Type material: MADAGASCAR:

• 1 ♀, paralectotype; Rogez, Forêt Cote Est; Mar. 1932; "A Seyrig"; NHMUK.

Known material: Eight specimens (0 Ugandan, 8 other):

1 ♀, lectotype; see Rousse and van Noort (2014); Madagascar, Rogez [18°18'S, 48°32'E]; Sep. 1930; "A. Seyrig"; MNHN EY8815.

3 ♂; see Rousse and van Noort (2014), same label data as lectotype.

1 ♀, paralectotype; previously unpublished specimen, data above in material examined.

1 ♀, 2 ♂; previously unpublished specimens, same data as paralectotype except collection dates Apr. 1931, Sep. 1932, Dec. 1932; NHMUK.

Figures 28–31. *Epirhyssa migratoria* female (holotype). This species was not found in Uganda. **28** Habitus **29** hypostomal flange **30** mesopleuron dorsal margin **31** apical horn of metasoma. Figure **28** is from van Noort (2019).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of diverging median carinae on the frons, the lateral absence of the epicnemial carina, and an open areolet. Its yellow and black colour pattern is distinctive.

Head: frons with median carinae diverging towards ocelli, without lateral carinae; hypostomal carina raised into a low flange, its height slightly less than or equivalent to the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina laterally absent.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 mostly smooth.

Distribution. Madagascar.

Epirhyssa overlaeti Seyrig, 1937

Figs 32–38

Material examined. Non-type material: UGANDA:

• 1 ♀; Kibale National Park, Kanyawara, Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 10 Mar. 2015–24 Mar. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1249

• 1 ♀; same data as preceding; Site K31, Malaise trap K31T4; 0.5362N, 30.3486E (WGS84); alt. 1460 m (GPS, WGS84); 16 Jul. 2015–30 Jul. 2015; ZMUT http://mus.utu.fi/ZMUT.2291

• 1 ♀; same data as preceding; Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 18 Nov. 2014–2 Dec. 2014; ZMUT http://mus.utu.fi/ZMUT.5591

• 1 ♀; same data as preceding; Site R93, Malaise trap R93T2; 0.5654N, 30.3593E (WGS84); alt. 1510 m (GPS, WGS84); 20 May 2015–1 Jun. 2015; ZMUT http://mus.utu.fi/ZMUT.5766

• 1 ♀; same data as preceding; Site HILL, Malaise trap HILLT1; 0.5486N, 30.3614E (WGS84); alt. 1520 m (GPS, WGS84); 30 Jul. 2015–13 Aug. 2015; ZMUT http://mus.utu.fi/ZMUT.6013

• 1 ♂; Kibale National Park, Kanyawara, Site K31, Malaise trap K31T2; 0.5427N, 30.3482E (WGS84); alt. 1460 m (GPS, WGS84); 9 Apr. 2015–23 Apr. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1280

• 1 ♂; same data as preceding; Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 24 Feb. 2015–10 Mar. 2015; ZMUT http://mus.utu.fi/ZMUT.5738

• 1 ♂; same data as preceding; Site K31, Malaise trap K31T3; 0.5360N, 30.3469E (WGS84); alt. 1450 m (GPS, WGS84); 26 Aug. 2015–12 Sep. 2015; ZMUT http://mus.utu.fi/ZMUT.5792.

Non-type material (only diagnostic characters checked): UGANDA:

• 56 ♀; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1261, http://mus.utu.fi/ZMUT.1262, http://mus.utu.fi/ZMUT.1270, http://mus.utu.fi/ZMUT.1336, http://mus.utu.fi/ZMUT.1337, http://mus.utu.

Figures 32–38. *Epirhyssa overlaeti* male (http://mus.utu.fi/ZMUT.1280) and female (**34**: http://mus.utu.fi/ZMUT.2291, **37**: http://mus.utu.fi/ZMUT.5766), a species found in Uganda. **32** Habitus **33** face and clypeus **34** frons **35** hypostomal flange **36** mesopleuron dorsal margin **37** apical horn of metasoma **38** tergites 1–7. Scale bars: 0.5 mm (**33–38**), 1 mm (**32**).

fi/ZMUT.1338, http://mus.utu.fi/ZMUT.1345, http://mus.utu.fi/ZMUT.1364, http://mus.utu.fi/ZMUT.1721, http://mus.utu.fi/ZMUT.1761, http://mus.utu.fi/ZMUT.1762, http://mus.utu.fi/ZMUT.1820, http://mus.utu.fi/ZMUT.2056,

http://mus.utu.fi/ZMUT.2058, http://mus.utu.fi/ZMUT.2161, http://mus.utu.fi/ZMUT.2706, http://mus.utu.fi/ZMUT.2724, http://mus.utu.fi/ZMUT.2856, http://mus.utu.fi/ZMUT.2985, http://mus.utu.fi/ZMUT.3080, http://mus.utu.fi/ZMUT.3092, http://mus.utu.fi/ZMUT.3541, http://mus.utu.fi/ZMUT.3737, http://mus.utu.fi/ZMUT.5595, http://mus.utu.fi/ZMUT.5600, http://mus.utu.fi/ZMUT.5626, http://mus.utu.fi/ZMUT.5630, http://mus.utu.fi/ZMUT.5640, http://mus.utu.fi/ZMUT.5645, http://mus.utu.fi/ZMUT.5658, http://mus.utu.fi/ZMUT.5672, http://mus.utu.fi/ZMUT.5674, http://mus.utu.fi/ZMUT.5675, http://mus.utu.fi/ZMUT.5697, http://mus.utu.fi/ZMUT.5704, http://mus.utu.fi/ZMUT.5720, http://mus.utu.fi/ZMUT.5727, http://mus.utu.fi/ZMUT.5728, http://mus.utu.fi/ZMUT.5729, http://mus.utu.fi/ZMUT.5741, http://mus.utu.fi/ZMUT.5742, http://mus.utu.fi/ZMUT.5749, http://mus.utu.fi/ZMUT.5752, http://mus.utu.fi/ZMUT.5773, http://mus.utu.fi/ZMUT.5781, http://mus.utu.fi/ZMUT.5783, http://mus.utu.fi/ZMUT.5784, http://mus.utu.fi/ZMUT.5789, http://mus.utu.fi/ZMUT.5791, http://mus.utu.fi/ZMUT.5793, http://mus.utu.fi/ZMUT.5798, http://mus.utu.fi/ZMUT.5814, http://mus.utu.fi/ZMUT.5815, http://mus.utu.fi/ZMUT.5818, http://mus.utu.fi/ZMUT.5822, http://mus.utu.fi/ZMUT.5839

• 14 ♂; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.2906, http://mus.utu.fi/ZMUT.3086, http://mus.utu.fi/ZMUT.3089, http://mus.utu.fi/ZMUT.3642, http://mus.utu.fi/ZMUT.5622, http://mus.utu.fi/ZMUT.5652, http://mus.utu.fi/ZMUT.5758, http://mus.utu.fi/ZMUT.5767, http://mus.utu.fi/ZMUT.5771, http://mus.utu.fi/ZMUT.5785, http://mus.utu.fi/ZMUT.5790, http://mus.utu.fi/ZMUT.5832, http://mus.utu.fi/ZMUT.5838, http://mus.utu.fi/ZMUT.5877

• 1 unknown sex; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.6045.

Known material: 81 specimens (79 Ugandan, 2 other):

61 ♀, 17 ♂, 1 U; Ugandan specimens, data above and also in supplementary material (Hopkins et al. 2019c).

1 ♀, holotype; see Rousse and van Noort (2014); Democratic Republic of Congo, Lulua [10°37'S 24°54'E], Kapanga; Apr. 1933; "F.G. Overlaet"; "R. Dét"; MRAC "F 3330".

1 ♀; see Rousse and van Noort (2014); Cameroon, Nkoemvon; Jul. 1980-Aug. 1980; "Ms. D. Jackson"; NHMUK.

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of converging median carinae on the frons, lateral carinae on the frons, and the absence of a lateral flange on the subalar prominence. In practice its unique colour pattern and large size make it instantly recognisable.

Head: frons with strong median carinae converging before continuing towards median ocellus, with lateral carinae curving towards lateral ocelli; hypostomal carina raised into an elevated flange, its height slightly greater than the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron with a raised flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn almost circular in posterior view; tergite 3 mostly smooth.

Description (male). Body length 16.4 mm–25.1 mm. Males seem slightly smaller than females on average.

Head: Frons with strong median carinae converging before continuing towards median ocellus, with lateral carinae curving towards lateral ocelli, often with faint traces of lateral rugae. Occipital carina interrupted dorsally. Hypostomal carina raised into an elevated flange, its height slightly greater than maximum width of second maxillary palp segment. Face punctate. Clypeus punctate, without a clear median apical tubercle. Antenna with 38–40 flagellar segments.

Mesosoma: Subalar prominence without a lateral flange. Mesopleuron with a raised flange along dorsal margin. Epicnemial carina reaches approximate height of mesopleural pit. Fore wing with 2m-cu distal to rs-m.

Metasoma: Tergites 1–5 mostly smooth, 6–7 smooth or sparsely pubescent, tergite 1 1.8–2.2 times as long as apically wide.

Colour: General colour mottled dark testaceous, testaceous and pale yellow, pale yellow patches of tergites 1 and 2 are fused (cf. female). Antennae black. Wings hyaline, infuscate near apex.

Additional or updated characters. Apart from the diagnosis and description of the male, we provide the following additional or updated character traits to the description in Rousse and van Noort (2014).

Female. Body length 14.7 mm–37.8 mm. Frons often with faint traces of lateral rugae. Face punctate, transversely rugulose-punctate or transversely striate. Antenna with 38–43 flagellar segments (38–41 in Ugandan specimens). Tergites 1–5 mostly smooth, 6–7 often pubescent, anterior margins of tergites 3–6 (sometimes only 4–5) sightly striate or punctate, tergite 1 1.4–1.8 times as long as apically wide. The colour patches vary in extent, with the pale yellow patches of tergite 1 fused in small individuals.

Distribution. Democratic Republic of Congo, Cameroon. New record: Uganda.

Biology. In Uganda, this species was mostly caught in primary forest near decaying wood (Hopkins et al. 2019b). It has not been caught outside the forest.

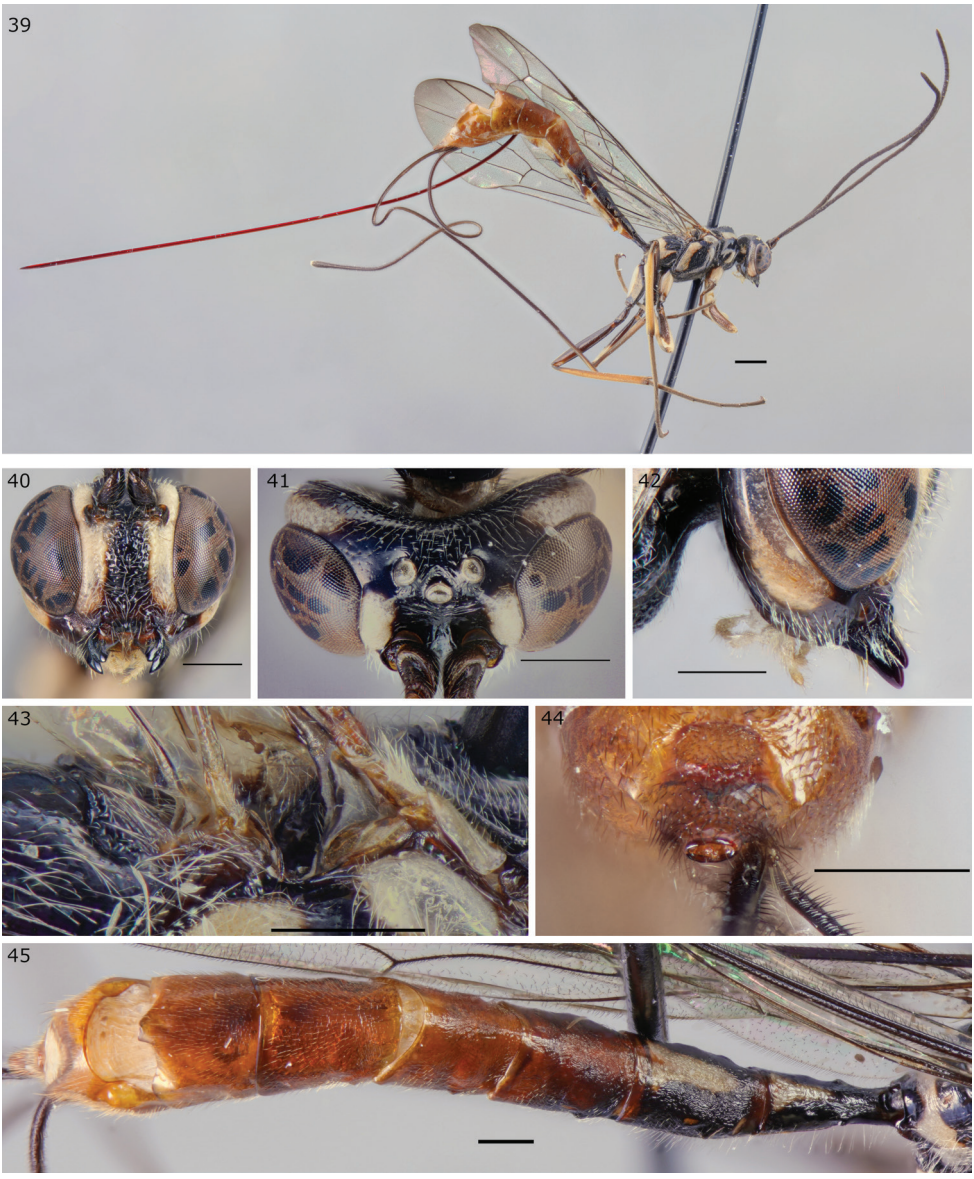
Remarks. *Epirhyssa overlaeti* was earlier known from only two females. We describe the male for the first time.

Epirhyssa quagga sp. nov.

http://zoobank.org/9BABD7C8-7644-45BA-9985-96408F898402
Figs 39–45

Material examined. Type material: UGANDA:

• 1 ♀, holotype; Kibale National Park, Kanyawara, Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 11 Aug. 2015–25 Aug. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.5788



Figures 39–45. *Epirhyssa quagga* female (holotype http://mus.utu.fi/ZMUT.5788), a new species from Uganda. **39** Habitus **40** face and clypeus **41** frons **42** hypostomal flange **43** mesopleuron dorsal margin **44** apical horn of metasoma **45** tergites 1–7. Scale bars: 0.5 mm (**40–45**), 1 mm (**39**).

• 1 ♀, paratype; same data as preceding; Site R03, Malaise trap R03T2; 0.5403N, 30.3608E (WGS84); alt. 1490 m (GPS, WGS84); 21 May 2015–4 Jun. 2015; ZMUT http://mus.utu.fi/ZMUT.1500

• 1 ♀, paratype; same data as preceding; Site K31, Malaise trap K31T3; 0.5360N, 30.3469E (WGS84); alt. 1450 m (GPS, WGS84); 23 May 2015–4 Jun. 2015; ZMUT http://mus.utu.fi/ZMUT.4238

• 1 ♀, paratype; same data as preceding; Site K30S, Malaise trap K30ST4; 0.5414N, 30.3755E (WGS84); alt. 1420 m (GPS, WGS84); 2 Dec. 2014–15 Dec. 2014; ZMUT http://mus.utu.fi/ZMUT.5743

• 1 ♀, paratype; same data as preceding; Site R01, Malaise trap R01T2; 0.5501N, 30.3561E (WGS84); alt. 1600 m (GPS, WGS84); 27 Mar. 2015–10 Apr. 2015; ZMUT http://mus.utu.fi/ZMUT.5801

• 1 ♂, paratype; Kibale National Park, Kanyawara, Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 2 Jun. 2015–17 Jun. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.3074

• 1 ♂, paratype; same data as preceding; Site K30S, Malaise trap K30ST2; 0.5392N, 30.3771E (WGS84); alt. 1480 m (GPS, WGS84); 5 May 2015–19 May 2015; ZMUT http://mus.utu.fi/ZMUT.4000

• 1 ♂, paratype; same data as preceding; Site K15, Malaise trap K15T4; 0.5845N, 30.3674E (WGS84); alt. 1510 m (GPS, WGS84); 4 May 2015–20 May 2015; ZMUT http://mus.utu.fi/ZMUT.5836.

Non-type material (only diagnostic characters checked): UGANDA

• 18 ♀; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1259, http://mus.utu.fi/ZMUT.2057, http://mus.utu.fi/ZMUT.2203, http://mus.utu.fi/ZMUT.2358, http://mus.utu.fi/ZMUT.2627, http://mus.utu.fi/ZMUT.3199, http://mus.utu.fi/ZMUT.3649, http://mus.utu.fi/ZMUT.4866, http://mus.utu.fi/ZMUT.5596, http://mus.utu.fi/ZMUT.5647, http://mus.utu.fi/ZMUT.5679, http://mus.utu.fi/ZMUT.5712, http://mus.utu.fi/ZMUT.5717, http://mus.utu.fi/ZMUT.5736, http://mus.utu.fi/ZMUT.5803, http://mus.utu.fi/ZMUT.5804, http://mus.utu.fi/ZMUT.5805, http://mus.utu.fi/ZMUT.5835

• 20 ♂; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1350, http://mus.utu.fi/ZMUT.1355, http://mus.utu.fi/ZMUT.1401, http://mus.utu.fi/ZMUT.1765, http://mus.utu.fi/ZMUT.2645, http://mus.utu.fi/ZMUT.2657, http://mus.utu.fi/ZMUT.2803, http://mus.utu.fi/ZMUT.3076, http://mus.utu.fi/ZMUT.3081, http://mus.utu.fi/ZMUT.3087, http://mus.utu.fi/ZMUT.3097, http://mus.utu.fi/ZMUT.3761, http://mus.utu.fi/ZMUT.3876, http://mus.utu.fi/ZMUT.4990, http://mus.utu.fi/ZMUT.5143, http://mus.utu.fi/ZMUT.5609, http://mus.utu.fi/ZMUT.5768, http://mus.utu.fi/ZMUT.5787, http://mus.utu.fi/ZMUT.5831, http://mus.utu.fi/ZMUT.6033.

Known material: 46 specimens (23 ♀, 23 ♂, Ugandan specimens, data above).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the distinctive pattern of striation on the frons and the densely striate tergite 3. No other species has the same colour pattern.

Head: frons without median carinae, without lateral carinae; hypostomal carina raised into a low flange, its height slightly less than or equivalent to the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 densely striate.

Description (female). Body length 8.5 mm–14.3 mm (holotype 12.3 mm).

Head: Frons without clear median carinae, without lateral carinae, with faint median rugae that fan out towards ocelli. Occipital carina interrupted dorsally. Hypostomal carina raised into a low flange, its height slightly less than or equivalent to maximum width of second maxillary palp segment. Face densely and deeply punctate. Clypeus with little or no punctation, with a median apical tubercle. Antenna with 30–33 flagellar segments (32 in holotype).

Mesosoma: Subalar prominence without a lateral flange. Mesopleuron without a flange along dorsal margin. Epicnemial carina reaches approximate height of mesopleural pit. Fore wing with 2m-cu varying from clearly distal to opposite rs-m.

Metasoma: Tip of apical horn elliptical in posterior view. Tergites 1–5 with dense, light, predominantly longitudinal striation and punctation, 6–7 smoother and more pubescent, tergite 1 1.9–2.4 times as long as apically wide (1.9 in holotype).

Colour: General colour mottled black and white with metasoma orange testaceous from tergite 3 onwards. Hind tibia dark brown. Antennae black. Ovipositor sheaths black to dark testaceous. Wings hyaline.

Variation: Colour of the dark patches of the legs varies from entirely black to testaceous, the black and white metasomal colour extends onto tergite 3 in some individuals.

Male. Similar to female. Body length 7.9 mm–10.4 mm. T1 3.2–3.6. Antenna with 29–33 flagellar segments. Males are smaller than females on average.

Etymology. Refers to the colour pattern which is reminiscent of the plains zebra, especially its extinct subspecies, the quagga.

Distribution. Uganda.

Biology. In Uganda, this species was most abundantly caught during the dry season (Hopkins et al. 2019b). It has not been caught outside the forest. It appears to be attracted to decaying wood (although the sample size is too small for statistical significance).

Epirhyssa shaka Rousse & van Noort, 2014

Figs 46–49

Material examined. Type material: SOUTH AFRICA:

• 1 ♀, holotype; Natal, 2831 Dd Umlalazi Nat. Res., 1.5 km E of Mtunzini; 28°57'S, 31°45'E; Nov. 1978; R. M. Miller leg.; indigenous forest; Malaise trap; NMSA.

Known material: One specimen (1 ♀, see Rousse and van Noort 2014, data above).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of a low hypostomal flange, an elliptical apical horn of the metasoma, and a punctate (over 50% of surface) tergite 3.

Head: frons with median carinae converging before continuing towards median ocellus, without lateral carinae; hypostomal carina raised into a low flange, its height slightly less than or equivalent to the maximum width of the second maxillary palp segment.

Figures 46–49. *Epirhyssa shaka* female (holotype). This species was not found in Uganda. **46** Habitus **47** hypostomal flange **48** mesopleuron dorsal margin **49** apical horn of metasoma. Figure **46** is from van Noort (2019).

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 punctate.

Distribution. South Africa (KwaZulu-Natal).

Epirhyssa tombeaodiba Rousse & van Noort, 2014

Figs 50–56

Material examined. Non-type material: UGANDA:

• 1 ♀; Kibale National Park, Kanyawara, Site K30, Malaise trap K30T2; 0.5566N, 30.3633E (WGS84); alt. 1490 m (GPS, WGS84); 26 Aug. 2015–9 Sep. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1273

• 1 ♀; same data as preceding; Site K15, Malaise trap K15T1; 0.5850N, 30.3641E (WGS84); alt. 1490 m (GPS, WGS84); 20 Apr. 2015–4 May 2015; ZMUT http://mus.utu.fi/ZMUT.1333

Figures 50–56. *Epirhyssa tombeaodiba* female (http://mus.utu.fi/ZMUT.5663, **52**: http://mus.utu.fi/ZMUT.3234), a species found in Uganda. **50** Habitus **51** face and clypeus **52** frons **53** hypostomal flange **54** mesopleuron dorsal margin **55** apical horn of metasoma **56** tergites 1–7. Scale bars: 0.5 mm (**51–56**), 1 mm (**50**).

• 1 ♀; same data as preceding; Site HILL, Malaise trap HILLT2; 0.5478N, 30.3619E (WGS84); alt. 1510 m (GPS, WGS84); 4 Jun. 2015–18 Jun. 2015; ZMUT http://mus.utu.fi/ZMUT.3234

• 1 ♀; same data as preceding; Site K30S, Malaise trap K30ST3; 0.5378N, 30.3777E (WGS84); alt. 1480 m (GPS, WGS84); 19 May 2015–2 Jun. 2015; ZMUT http://mus.utu.fi/ZMUT.5628

• 1 ♀; same data as preceding; Site K30, Malaise trap K30T3; 0.5590N, 30.3617E (WGS84); alt. 1540 m (GPS, WGS84); 14 Jul. 2015–28 Jul. 2015; ZMUT http://mus.utu.fi/ZMUT.5663

• 1 ♀; same data as preceding; Site R93, Malaise trap R93T2; 0.5654N, 30.3593E (WGS84); alt. 1510 m (GPS, WGS84); 9 Mar. 2015–23 Mar. 2015; ZMUT http://mus.utu.fi/ZMUT.5705.

Known material: 10 specimens (6 Ugandan, 4 other):

6 ♀; Ugandan specimens, data above and also in supplementary material (Hopkins et al. 2019c).

1 ♀, holotype; see Rousse and van Noort (2014); Cameroon, Nkoemvon [02°48'N 11°08'E]; 16 Mar. 1980–4 May 1980; "Ms. D. Jackson"; NHMUK.

1 ♀, paratype; see Rousse and van Noort (2014), same data as holotype.

1 ♀, paratype; see Rousse and van Noort (2014), same data as holotype except 30 Mar. 1980–19 Apr. 1980.

1 ♀, paratype; see Rousse and van Noort (2014), same data as holotype except Korup; 1981; "Mrs D. Jackson"

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of a half-elliptical apical horn of the metasoma and a punctate (over 50% of surface) tergite 3. *Epirhyssa uelensis* is also predominantly yellow with black spots, but its subalar prominence has a lateral flange.

Head: frons with weak median carinae converging before continuing towards median ocellus, without lateral carinae; hypostomal carina raised into a low flange, its height slightly less than or equivalent to the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn half-elliptical in posterior view; tergite 3 densely punctate.

Additional or updated characters. Apart from the diagnosis, we provide the following additional or updated character traits to the description in Rousse and van Noort (2014).

Female. Body length 7.2 mm–12.7 mm. Frons without rugae or with faint lateral rugae curving towards lateral ocelli. Face punctate or transversely rugulose-punctate. Clypeus longitudinally strigose and sparsely punctate. Antenna with 28–29 flagellar segments. Tergites 1 mostly smooth, 2–7 punctate (2 sometimes only punctate laterally), anterior margins of 5–6 often striate, tergite 1 1.2–1.5 times as long as apically wide. The Ugandan specimens have black anterior median spots on tergites 1–7 (ranging from very small on tergite 1 to reaching posterior margin on tergite 7), not just on tergites 4–7.

Distribution. Cameroon. New record: Uganda.

***Epirhyssa uelensis* Benoit, 1951**
Figs 57–63, 64–67

Epirhyssa gavinbroadi Rousse & van Noort, 2014, syn. nov.

Material examined. Type material: CAMEROON:

• 1 ♀, holotype of *E. gavinbroadi*; Nkoemvon [Nko'emvon]; 02°48'N, 11°08'E; 16 Mar. 1980–4 May 1980; NHMUK type number HYM 3b.2832.

Non-type material: UGANDA

• 1 ♀; Kibale National Park, Kanyawara, Site K31, Malaise trap K31T4; 0.5362N, 30.3486E (WGS84); alt. 1460 m (GPS, WGS84); 16 Jul. 2015–30 Jul. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.2292

• 1 ♀; same data as preceding; Site K30, Malaise trap K30T3; 0.5590N, 30.3617E (WGS84); alt. 1540 m (GPS, WGS84); 21 Apr. 2015–5 May 2015; ZMUT http://mus.utu.fi/ZMUT.2520

• 1 ♀; same data as preceding; Site K31, Malaise trap K31T4; 0.5362N, 30.3486E (WGS84); alt. 1460 m (GPS, WGS84); 30 Jan. 2015–13 Feb. 2015; ZMUT http://mus.utu.fi/ZMUT.2878

• 1 ♀; same data as preceding; Site K13, Malaise trap K13T1; 0.5932N, 30.3598E (WGS84); alt. 1460 m (GPS, WGS84); 13 Jul. 2015–27 Jul. 2015; ZMUT http://mus.utu.fi/ZMUT.5665

• 1 ♀; same data as preceding; Site K30, Malaise trap K30T2; 0.5566N, 30.3633E (WGS84); alt. 1490 m (GPS, WGS84); 2 Dec. 2014–15 Dec. 2014; ZMUT http://mus.utu.fi/ZMUT.5689

• 1 ♀; same data as preceding; Site CC, Malaise trap CCT1; 0.5497N, 30.3673E (WGS84); alt. 1450 m (GPS, WGS84); 27 Jan. 2015–10 Feb. 2015; ZMUT http://mus.utu.fi/ZMUT.5732

• 1 ♀; same data as preceding; 24 Feb. 2015–10 Mar. 2015; ZMUT http://mus.utu.fi/ZMUT.5739

• 1 ♀; same data as preceding; Site K30S, Malaise trap K30ST4; 0.5414N, 30.3755E (WGS84); alt. 1420 m (GPS, WGS84); 30 Jun. 2015–14 Jul. 2015; ZMUT http://mus.utu.fi/ZMUT.5844

• 1 ♂; Kibale National Park, Kanyawara, Site R93, Malaise trap R93T2; 0.5654N, 30.3593E (WGS84); alt. 1510 m (GPS, WGS84); 20 May 2015–1 Jun. 2015; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.5765

• 1 ♂; same data as preceding; Site K13, Malaise trap K13T1; 0.5932N, 30.3598E (WGS84); alt. 1460 m (GPS, WGS84); 4 May 2015–20 May 2015; ZMUT http://mus.utu.fi/ZMUT.5807.

Non-type material (only diagnostic characters checked): UGANDA:

• 150 ♀; Kibale National Park, Kanyawara; Tapani Hopkins leg.; ZMUT http://mus.utu.fi/ZMUT.1265, http://mus.utu.fi/ZMUT.1266, http://mus.utu.fi/ZMUT.1267, http://mus.utu.fi/ZMUT.1268, http://mus.utu.fi/ZMUT.1272, http://mus.utu.fi/ZMUT.1334, http://mus.utu.fi/ZMUT.1366, http://mus.utu.fi/ZMUT.1367, http://mus.utu.fi/ZMUT.1375, http://mus.utu.fi/ZMUT.1499,

Figures 57–63. *Epirhyssa uelensis* female (http://mus.utu.fi/ZMUT.2520), a species found in Uganda. **57** Habitus **58** face and clypeus **59** frons **60** hypostomal flange **61** mesopleuron dorsal margin **62** apical horn of metasoma **63** tergites 1–7. Scale bars: 0.5 mm (**58–63**), 1 mm (**57**).

http://mus.utu.fi/ZMUT.1673, http://mus.utu.fi/ZMUT.1677, http://mus.utu.fi/ZMUT.1763, http://mus.utu.fi/ZMUT.1764, http://mus.utu.fi/ZMUT.1807, http://mus.utu.fi/ZMUT.2015, http://mus.utu.fi/ZMUT.2152, http://mus.utu.fi/ZMUT.2162, http://mus.utu.fi/ZMUT.2165, http://mus.utu.fi/ZMUT.2172, http://mus.utu.fi/ZMUT.2299, http://mus.utu.fi/ZMUT.2317, http://mus.utu.fi/ZMUT.2340, http://mus.utu.fi/ZMUT.2361, http://mus.utu.fi/ZMUT.2362,

Figures 64–67. *Epirhyssa gavinbroadi* female (holotype). We treat this species as a synonym of *E. uelensis* in this work. **64** Habitus **65** hypostomal flange **66** mesopleuron dorsal margin **67** apical horn of metasoma. Figure **64** is from van Noort (2019).

http://mus.utu.fi/ZMUT.2364, http://mus.utu.fi/ZMUT.2473, http://mus.utu.fi/ZMUT.2573, http://mus.utu.fi/ZMUT.2640, http://mus.utu.fi/ZMUT.2642, http://mus.utu.fi/ZMUT.2643, http://mus.utu.fi/ZMUT.2644, http://mus.utu.fi/ZMUT.2646, http://mus.utu.fi/ZMUT.2648, http://mus.utu.fi/ZMUT.2887, http://mus.utu.fi/ZMUT.2910, http://mus.utu.fi/ZMUT.3022, http://mus.utu.fi/ZMUT.3090, http://mus.utu.fi/ZMUT.3091, http://mus.utu.fi/ZMUT.3093, http://mus.utu.fi/ZMUT.3094, http://mus.utu.fi/ZMUT.3096, http://mus.utu.fi/ZMUT.3102, http://mus.utu.fi/ZMUT.3106, http://mus.utu.fi/ZMUT.3135, http://mus.utu.fi/ZMUT.3225, http://mus.utu.fi/ZMUT.3259, http://mus.utu.fi/ZMUT.3262, http://mus.utu.fi/ZMUT.3334, http://mus.utu.fi/ZMUT.3438, http://mus.utu.fi/ZMUT.3452, http://mus.utu.fi/ZMUT.3619, http://mus.utu.fi/ZMUT.3698, http://mus.utu.fi/ZMUT.3743, http://mus.utu.fi/ZMUT.3745, http://mus.utu.fi/ZMUT.3747, http://mus.utu.fi/ZMUT.3947, http://mus.utu.fi/ZMUT.4424, http://mus.utu.fi/ZMUT.4512, http://mus.utu.fi/ZMUT.4517, http://mus.utu.fi/ZMUT.5086, http://mus.utu.fi/ZMUT.5315, http://mus.utu.fi/ZMUT.5381, http://mus.utu.fi/ZMUT.5542, http://mus.utu.fi/ZMUT.5589, http://mus.utu.fi/ZMUT.5593, http://mus.utu.fi/ZMUT.5597, http://mus.utu.

fi/ZMUT.5601, http://mus.utu.fi/ZMUT.5605, http://mus.utu.fi/ZMUT.5606, http://mus.utu.fi/ZMUT.5607, http://mus.utu.fi/ZMUT.5608, http://mus.utu.fi/ZMUT.5613, http://mus.utu.fi/ZMUT.5614, http://mus.utu.fi/ZMUT.5616, http://mus.utu.fi/ZMUT.5618, http://mus.utu.fi/ZMUT.5619, http://mus.utu.fi/ZMUT.5620, http://mus.utu.fi/ZMUT.5623, http://mus.utu.fi/ZMUT.5625, http://mus.utu.fi/ZMUT.5629, http://mus.utu.fi/ZMUT.5631, http://mus.utu.fi/ZMUT.5632, http://mus.utu.fi/ZMUT.5635, http://mus.utu.fi/ZMUT.5637, http://mus.utu.fi/ZMUT.5641, http://mus.utu.fi/ZMUT.5642, http://mus.utu.fi/ZMUT.5643, http://mus.utu.fi/ZMUT.5644, http://mus.utu.fi/ZMUT.5646, http://mus.utu.fi/ZMUT.5648, http://mus.utu.fi/ZMUT.5650, http://mus.utu.fi/ZMUT.5653, http://mus.utu.fi/ZMUT.5655, http://mus.utu.fi/ZMUT.5657, http://mus.utu.fi/ZMUT.5662, http://mus.utu.fi/ZMUT.5668, http://mus.utu.fi/ZMUT.5669, http://mus.utu.fi/ZMUT.5670, http://mus.utu.fi/ZMUT.5673, http://mus.utu.fi/ZMUT.5678, http://mus.utu.fi/ZMUT.5681, http://mus.utu.fi/ZMUT.5683, http://mus.utu.fi/ZMUT.5684, http://mus.utu.fi/ZMUT.5687, http://mus.utu.fi/ZMUT.5688, http://mus.utu.fi/ZMUT.5690, http://mus.utu.fi/ZMUT.5692, http://mus.utu.fi/ZMUT.5693, http://mus.utu.fi/ZMUT.5694, http://mus.utu.fi/ZMUT.5698, http://mus.utu.fi/ZMUT.5699, http://mus.utu.fi/ZMUT.5702, http://mus.utu.fi/ZMUT.5708, http://mus.utu.fi/ZMUT.5709, http://mus.utu.fi/ZMUT.5719, http://mus.utu.fi/ZMUT.5722, http://mus.utu.fi/ZMUT.5725, http://mus.utu.fi/ZMUT.5726, http://mus.utu.fi/ZMUT.5733, http://mus.utu.fi/ZMUT.5734, http://mus.utu.fi/ZMUT.5740, http://mus.utu.fi/ZMUT.5748, http://mus.utu.fi/ZMUT.5750, http://mus.utu.fi/ZMUT.5754, http://mus.utu.fi/ZMUT.5755, http://mus.utu.fi/ZMUT.5757, http://mus.utu.fi/ZMUT.5762, http://mus.utu.fi/ZMUT.5763, http://mus.utu.fi/ZMUT.5764, http://mus.utu.fi/ZMUT.5772, http://mus.utu.fi/ZMUT.5774, http://mus.utu.fi/ZMUT.5775, http://mus.utu.fi/ZMUT.5778, http://mus.utu.fi/ZMUT.5780, http://mus.utu.fi/ZMUT.5794, http://mus.utu.fi/ZMUT.5797, http://mus.utu.fi/ZMUT.5806, http://mus.utu.fi/ZMUT.5808, http://mus.utu.fi/ZMUT.5811, http://mus.utu.fi/ZMUT.5816, http://mus.utu.fi/ZMUT.5817, http://mus.utu.fi/ZMUT.5821, http://mus.utu.fi/ZMUT.5823, http://mus.utu.fi/ZMUT.5824, http://mus.utu.fi/ZMUT.5825, http://mus.utu.fi/ZMUT.5829, http://mus.utu.fi/ZMUT.5834, http://mus.utu.fi/ZMUT.5845, http://mus.utu.fi/ZMUT.5846.

Known material: 167 specimens (160 Ugandan, 7 other):

158 ♀, 2 ♂; Ugandan specimens, data above and also in supplementary material (Hopkins et al. 2019c).

1 ♀, holotype of *E. gavinbroadi*; see Rousse and van Noort (2014), data above in material examined.

1 ♀, holotype of *E. uelensis*; see Rousse and van Noort (2014); Democratic Republic of Congo, Haut-Uele, Paulis [Isiro, 03°28'N 25°43'E]; Dec. 1947; "P.L.G. Benoit"; MRAC.

1 ♂, paratype of *E. uelensis*; see Rousse and van Noort (2014); Democratic Republic of Congo, Bambesa; Jul. 1933; "H.J. Bredo"; MRAC.

1 ♀; see Rousse and van Noort (2014); Cameroon, Nkoemvon; 30 Mar. 1980–19 Apr. 1980; "Ms. D. Jackson"; NHMUK.

2 ♀; see Rousse and van Noort (2014), same data as previous except 13 Jul. 1980–4 Aug. 1980.

1 ♀; see Rousse and van Noort (2014), same data as previous except Oct. 1980–Nov. 1980.

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by its subalar prominence having a lateral flange. *Epirhyssa tombeaodiba* is also predominantly yellow with black spots but lacks the flange.

Head: frons with median carinae converging before continuing towards median ocellus, with lateral carinae curving towards lateral ocelli; hypostomal carina raised into an elevated flange, its height greater than the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence with a lateral flange; mesopleuron with a raised flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 mostly smooth.

Additional or updated characters. Apart from the diagnosis, we provide the following additional or updated character traits to the description in Rousse and van Noort (2014).

Female. Body length 9.8 mm–15.7 mm (15.7 mm *E. gavinbroadi* holotype, 9.8 mm–15.1 mm other specimens). Frons with more or less distinct rugae parallel to the lateral carinae, often as distinct as the lateral carinae. Clypeus sparsely punctate or smooth. Antenna with 30–35+ flagellar segments (30–33 in Ugandan specimens, at least 35 in *E. gavinbroadi* type, 30–34 in other specimens). Fore wing with 2m-cu varying from clearly distal to only just distal to rs-m. Tip of apical horn with an extra dorsal projection in one aberrant female (http://mus.utu.fi/ZMUT.5844). Tergites mostly smooth, except with varied amount of punctation on tergites 3–7 (anteriorly punctate 3–6 in many Ugandan specimens, punctate 3–6 in most non-Ugandan specimens, punctate apex of 5 and 6–7 in *E. gavinbroadi* holotype), anterior margins of 3–5 or 3–6 often striate, tergite 1 1.2–1.7 times as long as apically wide (1.7 in *E. gavinbroadi* holotype, 1.2–1.5 in other specimens). The Ugandan specimens have black posterior margins of tergites 2–7 (sometimes faint or patchy, especially on anterior tergites) and median stripes on 4–7 (strongest on 5–6). Non-Ugandan specimens sometimes have black median stripes on 5–7, or 3–6 in the *E. gavinbroadi* holotype.

Male. Body length 8.5 mm–8.7 mm. Antenna with 30 flagellar segments. Tergites 4–7 faintly pubescent, tergite anterior margins smooth, or lightly striate and punctate, tergite 1 1.5–2.0 times as long as apically wide. The two Ugandan males are smaller than females on average.

Distribution. Democratic Republic of Congo, Cameroon. New record: Uganda.

Biology. In Uganda, this species was most abundantly caught in primary forest near decaying wood, during the dry season (Hopkins et al. 2019b). It has not been caught outside the forest.

Remarks. This species is quite variable, but we are unable to find morphological characters that would reliably split it into more than one species. We propose that *Epirhyssa gavinbroadi* (of which there is only one specimen) is a synonym of *E. uelensis*. It was mainly distinguished from *E. uelensis* by the punctate clypeus and slender tergite 1, but the Ugandan specimens generally have a punctate clypeus and a stout tergite 1. These two characters also vary considerably in the Ugandan specimens and seem to represent intraspecific variation. The Ugandan material has a very skewed sex ratio with 158 female specimens collected and only two males.

Epirhyssa villemantae Rousse & van Noort, 2014

Figs 68–71

Material examined. Type material: NIGERIA:

• 1 ♀, holotype; "Ilorin Prov." [06°48'N, 05°18'E]; "18 Jun. 192" [18 Jun 1921?]; "De. G.W.S. Macfie" leg.; "Pres. by Imp. Bur. Ent. 1921–129"; NHMUK.

Known material: One specimen (1 ♀, see Rousse and van Noort 2014, data above).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the combination of lateral carinae on the frons and the absence of a raised flange on the dorsal margin of the mesopleuron. No other species has the same colour pattern.

Head: frons with median carinae diverging towards ocelli, with lateral carinae curving towards lateral ocelli; hypostomal carina raised into an elevated flange, its height greater than the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina reaches the approximate height of the mesopleural pit.

Metasoma: tip of apical horn elliptical in posterior view; tergite 3 mostly smooth.

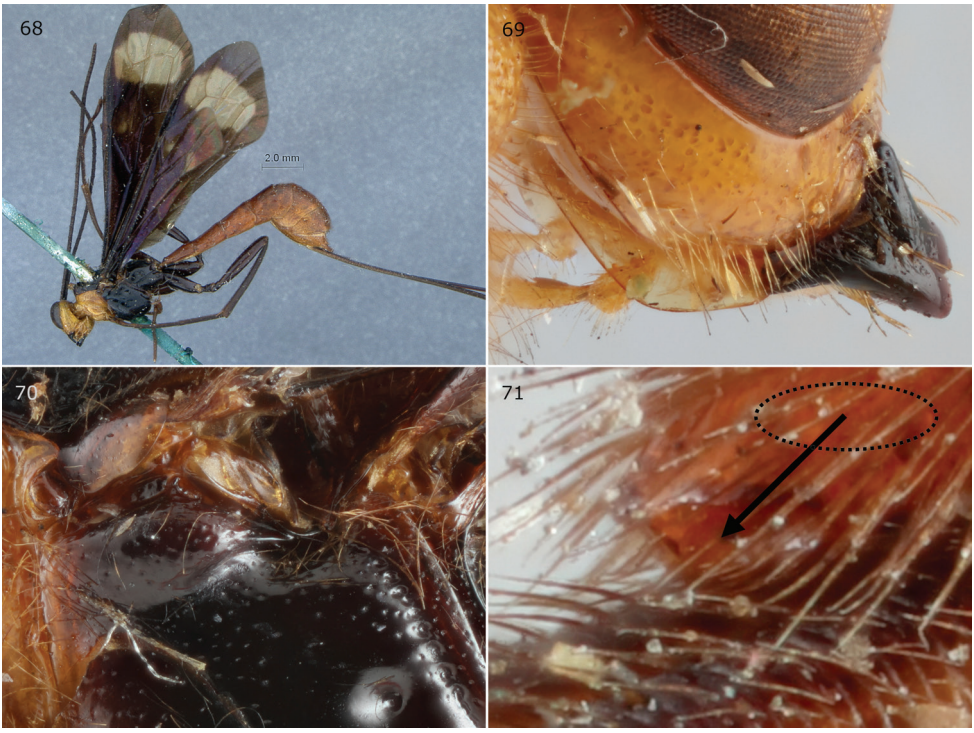
Distribution. Nigeria.

Genus *Megarhyssa* Ashmead, 1900

Thalessa Holmgren, 1859: 122.
Megalorhyssa Shulz, 1906: 115.
Eurhyssa Derksen, 1941: 721.

Diagnosis. The genus *Megarhyssa* is easily recognised in the Afrotropical region by the presence of the fore wing areolet (vein 3rs-m is present), whereas vein 3rs-m is missing in *Epirhyssa*, the only other rhyssine genus found in the Afrotropical region.

Megarhyssa can be distinguished from other rhyssine genera by the presence of an areolet (cf. *Triancyra*), the lack of an anterior glymma on tergite 1 (cf. *Rhyssa*), the upper tooth not being subdivided (cf. *Myllenyxis*), tergite 1 having anterior lateral carinae (cf. *Cyrtorhyssa* which lacks carinae), the occipital carina joining the hypostomal carina



Figures 68–71. *Epirhyssa villemantae* female (holotype). This species was not found in Uganda. **68** Habitus **69** hypostomal flange **70** mesopleuron dorsal margin **71** apical horn of metasoma. Figure **68** is from van Noort (2019).

some distance from the mandible base (cf. *Lytarmes*) and tergites 3–6 not being transversely, non-uniformly aciculate (cf. *Rhyssella*) (Baltazar 1964, Porter 2001). The genus includes the largest species of Rhyssinae.

Distribution. Afrotropical region: Democratic Republic of Congo.

The genus is cosmopolitan with the largest number of species found in the Oriental and Palaearctic regions.

Megarhyssa babaulti Seyrig, 1937

Figs 72–75

Material examined. Type material: DEMOCRATIC REPUBLIC OF CONGO:

• 1 ♀, holotype; "reg. Lac Kivu", "Kadjudju" [Kajuju, 02°09'S, 28°54'E]; 1932; MNHN EY8831.

Known material: One specimen (1 ♀, see Rousse and van Noort 2014, data above).

Diagnosis. This species can be distinguished from other Afrotropical Rhyssinae by the presence of a closed areolet. No other species has the same colour pattern.

Figures 72–75. *Megarhyssa babaulti* female (holotype). This species was not found in Uganda. **72** Habitus **73** mesopleuron dorsal margin **74** hypostomal flange **75** apical horn of metasoma. Figure **72** is from van Noort (2019), **73–75** courtesy of MNHN (Agnièle Touret-Alby).

Head: frons with median carinae diverging towards ocelli, without lateral carinae; hypostomal carina raised into an elevated flange, its height slightly greater than the maximum width of the second maxillary palp segment.

Mesosoma: subalar prominence without a lateral flange; mesopleuron without a flange along the dorsal margin; epicnemial carina laterally absent.

Metasoma: tip of apical horn almost circular in posterior view; tergite 3 mostly smooth.

Distribution. Democratic Republic of Congo.

Discussion

Sampling tropical ichneumonids for a year with numerous Malaise traps gave us an unprecedented sample size. We caught 456 individuals of the subfamily Rhyssinae, which in the Afrotropical region was earlier known from only 30 published specimen records (Rousse and van Noort 2014). This clearly demonstrates the advantage of extensive, long-term sampling in the tropics. Although the method is laborious, involving a full year of sampling and several years processing the samples, it provides much greater sample sizes than the more limited sampling which is often the norm due to logistical constraints (see Owen and Chanter 1970, van Noort et al. 2000, van Noort 2004). We were also able to obtain information on the phenology and habitat use of species, by linking to vegetation and weather data (Hopkins et al. 2019b).

Our results strongly support the idea that the Afrotropical region contains a large number of rhyssine species, most of which have simply not been discovered due to insufficient sampling (Rousse and van Noort 2014). Two of the six species at our site were new to science. New information was also obtained on, for example, the male of *Epirhyssa overlaeti* and the synonymy of *E. gavinbroadi* with *E. uelensis*. It is clear that sampling at other Afrotropical sites would reveal numerous new species, and considerably update our knowledge of described species. Further sampling would likely uncover more species even at our site; we caught only one individual of *E. johanna* sp. nov., for example, which demonstrates that our site is still under-sampled.

Our results also support the claim by Quicke (2012) that it is too early to draw conclusions on how ichneumonid species richness is distributed on our planet. Before this work, no rhyssines were known from our site despite our having sampled there before (Hopkins et al. 2018, SvN pers. obs.). After this work, the species count is six, and further sampling would likely discover more. In such circumstances, any attempt to compare the species richness of different sites may end up merely comparing sample sizes. Of two recent studies that made this attempt, one found the highest rhyssine and pimpline richness at Allpahuayo-Mishana in Amazonia, which may be due to the fact it is also one of the best sampled sites (Gómez et al. 2017). The other study showed that even well sampled sites are so under-sampled that species richness and sample size are interchangeable (Timms et al. 2016, although note that the authors interpret this result differently). Much more sampling, especially in the tropics, will be needed before we can draw conclusions on ichneumonid species richness distributions.

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RESEARCH ARTICLE

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Nine new species groups, 15 new species, and one new subspecies of New Guinea diving beetles of the genus *Exocelina* Broun, 1886 (Coleoptera, Dytiscidae, Copelatinae)

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Abstract

Nine new species groups of *Exocelina* Broun, 1886 from New Guinea are introduced with keys to their representatives. Four groups are monotypic and include three new species: the *E. aipomek* group, the *E. koroba* group: *E. koroba* **sp. nov.**, the *E. mekilensis* group: *E. mekilensis* **sp. nov.**, and the *E. morobensis* group: *E. morobensis* **sp. nov.** The remaining five species groups include 18 species with 12 new species and one new subspecies: the *E. bacchusi* group: *E. akameku* **sp. nov.**, *E. oiwa* **sp. nov.**, *E. oksibilensis* **sp. nov.**, and *E. bacchusi herzogensis* **ssp. nov.**; the *E. jaseminae* group: *E. aseki* **sp. nov.**, *E. kailaki* **sp. nov.**, and *E. pseudojaseminae* **sp. nov.**; the *E. larsoni* group: *E. warahulenensis* **sp. nov.**; the *E. takime* group: *E. mianminensis* **sp. nov.**; and the *E. warasera* group: *E. haia* **sp. nov.**, *E. kobau* **sp. nov.**, *E. pulchella* **sp. nov.**, and *E. warasera* **sp. nov.** Diagnoses of five already described species of these groups are provided, as well as comparatives notes on all species. *Exocelina santimontis* (Balke, 1998) **syn. nov.** is a junior synonym of *E. aipomek* (Balke, 1998). Data on the distribution of the species are given, showing that most of the species of these groups occur in the Papua New Guinea.

Keywords
Australasia, distribution, *Exocelina*, key, new taxa, species delimitation, systematics

Introduction

This paper introduces nine new species groups of *Exocelina* Broun, 1886, completing our assessment of the supraspecific classification of the genus in New Guinea. Four of the species groups here diagnosed are monotypic and include species with distinct morphological characters and which were inferred as separate lineages in our previous molecular phylogenetic analyses (Toussaint et al. 2014, 2015). One of these groups is proposed for the described species, *Exocelina aipomek* (Balke, 1998), and the three remaining for three new species. Five other groups are small and consist of two to five species. Four groups (the *E. bacchusi*, *E. jaseminae*, *E. larsoni* and *E. takime* groups) are proposed for already known species with the addition of eight new species and one new subspecies, and the fourth group, the *E. warasera* group, includes only four new species. We provide a diagnosis for the complex of groups treated herein and notes on their phylogeny, as well as morphological diagnoses for each group separately. All species of the groups are treated, including comparative notes and detailed descriptions for the new species. Identification keys are presented for the groups with more than one species. Including the results of this work, 140 species of *Exocelina* are now described from New Guinea and 195 species worldwide. As in most of our previous papers on the genus (Shaverdo et al. 2012, 2013, 2014, 2016a, b, c, 2017, 2018), all species data will be presented on the species-id.net portal automatically created by ZooKeys with the publication of this paper.

Materials and methods

The present work is based on material from the following collections:

BMNH	The Natural History Museum, London, UK
CGW	Collection of Günther Wewalka, Vienna, Austria
KSP	Koleksi Serangga Papua, at the Biology Department of Universitas Cenderawasih (UNCEN), Waena, Papua, Indonesia
MZB	Museum Zoologicum Bogoriense, Cibinong, Indonesia
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
ZSM	Zoologische Staatsammlung München, Munich, Germany

Our methods follow those described in detail in our previous articles (Shaverdo et al. 2012, 2014; Shaverdo and Balke 2014). The terminology to denote the orientation of the genitalia (ventral for median lobe and dorsal and external for paramere) follows Miller and Nilsson (2003). All specimen data are quoted as they appear on the labels

attached to the specimens. Label text is cited using quotation marks. Comments in square brackets are ours. The following abbreviations were used: TL (total body length), TL-H (total body length without head), MW (maximum body width), and hw (handwritten).

The keys are based mostly on the male characters. In many cases, females cannot be assigned to species due to similarity of their external and internal structures (for female genitalia see Shaverdo et al. 2005: fig. 17a, b). Some species are rather similar in point of external morphology, therefore, in most cases the male genitalia need to be studied for reliable species identification.

Checklist and distribution of the species

Abbreviations: IN – Indonesia; PNG – Papua New Guinea.

***Exocelina aipomek* group**	
1. *Exocelina aipomek* (Balke, 1998)	IN: Papua: Pegunungan Bintang; PNG: Sandaun
***Exocelina koroba* group**	
2. *Exocelina koroba* sp. nov.	PNG: Hela
***Exocelina mekilensis* group**	
3. *Exocelina mekilensis* sp. nov.	PNG: Sandaun
***Exocelina morobensis* group**	
4. *Exocelina morobensis* sp. nov.	PNG: Morobe
***Exocelina bacchusi* group**	
5. *Exocelina akameku* sp. nov.	PNG: Madang
6. *Exocelina bacchusi* (Balke, 1998)	PNG: Madang, Simbu, Eastern Highlands, Morobe, Gulf
6a. *Exocelina bacchusi herzogensis* ssp. nov.	PNG: Morobe, Central
7. *Exocelina erteldi* (Balke, 1998)	IN: Papua: Pegunungan Bintang
8. *Exocelina oiwa* sp. nov.	PNG: Morobe
9. *Exocelina oksibilensis* sp. nov.	IN: Papua: Pegunungan Bintang
***Exocelina jaseminae* group**	
10. *Exocelina aseki* sp. nov.	PNG: Morobe
11. *Exocelina jaseminae* (Balke, 1998)	PNG: Morobe, Eastern Highlands
12. *Exocelina kailaki* sp. nov.	PNG: Central
13. *Exocelina pseudojaseminae* sp. nov.	PNG: Central
***Exocelina larsoni* group**	
14. *Exocelina larsoni* (Balke, 1998)	PNG: Madang, Eastern Highlands
15. *Exocelina nomax* (J. Balfour-Browne, 1939)	PNG: Central, National Capital District
16. *Exocelina warahulenensis* sp. nov.	PNG: Simbu, Eastern Highlands
***Exocelina takime* group**	
17. *Exocelina mianminensis* sp. nov.	PNG: Sandaun
18. *Exocelina takime* (Balke, 1998)	IN: Papua: Pegunungan Bintang
***Exocelina warasera* group**	
19. *Exocelina haia* sp. nov.	PNG: Simbu
20. *Exocelina kobau* sp. nov.	PNG: Morobe
21. *Exocelina pulchella* sp. nov.	PNG: Central
22. *Exocelina warasera* sp. nov.	PNG: Simbu, Eastern Highlands

General diagnostic characters of the treated groups and notes on their phylogeny

Here, we provide general diagnostic characters for all representatives of the groups, which can be used to separate them from some of the previously studied groups. To complete diagnoses, special diagnostic characters for each group, mainly based on shape of the median lobe and shape and setation of the parameres, are provided below, before the species treatments.

- beetles small or medium-sized (TL-H 2.85–4.5 mm);
- habitus elongate to oval, in most species oblong-oval; with rounded pronotal and elytral sides, body outline continuous;
- pronotum short, trapezoidal, with posterior angles not drawn backwards;
- pronotum and elytra without striae or strioles;
- antennomeres not modified, simple;
- male protarsomeres 1–3 not expanded laterally;
- male protarsomere 4 cylindrical, narrow, with a large, hook-like to thin, long, slightly curved anterolateral seta;
- male protarsomere 5 not modified, long and narrow, sometimes slightly concave ventrally;
- median lobe of aedeagus with continuous outline in ventral and lateral view;
- ventral sclerite of median lobe more or less deeply divided apically.

All treated species groups (except for the monotypic *E. koroba* and *E. mekilensis* groups) are separate lineages within a monophyletic complex, including the *E. danae* and *E. monae* groups (Toussaint et al. 2014, 2015). Although altogether they do not form a monophyletic complex, all of them (except one species *Exocelina warahulenensis* sp. nov.) have a character that distinguishes them from the representatives of the *E. danae* and *E. monae* groups – absence of the setation on the median lobe of the aedeagus. *Exocelina koroba* sp. nov. and *E. mekilensis* sp. nov. have a very distinct morphology, especially of the male genitalia, and belong to a completely different clade of New Guinea *Exocelina*. They form separate lineages within a monophyletic complex, which also includes some species of the *E. casuarina* group (Toussaint et al. 2014, 2015; Shaverdo et al. 2018).

Diagnostic characters of the species groups, species descriptions and comparative notes

Monotypic groups
Exocelina aipomek group

This group is characterised by extremely fine, inconspicuous dorsal punctation, pronotum with distinct lateral bead; median lobe of aedeagus without setation, simple,

with rounded apex in ventral view; apexes of ventral sclerites of median lobe almost equal; paramere with distinct dorsal notch and large, long subdistal part with numerous strong setae, proximal setae more or distinct.

1. *Exocelina aipomek* (Balke, 1998)
Figs 1, 5–7

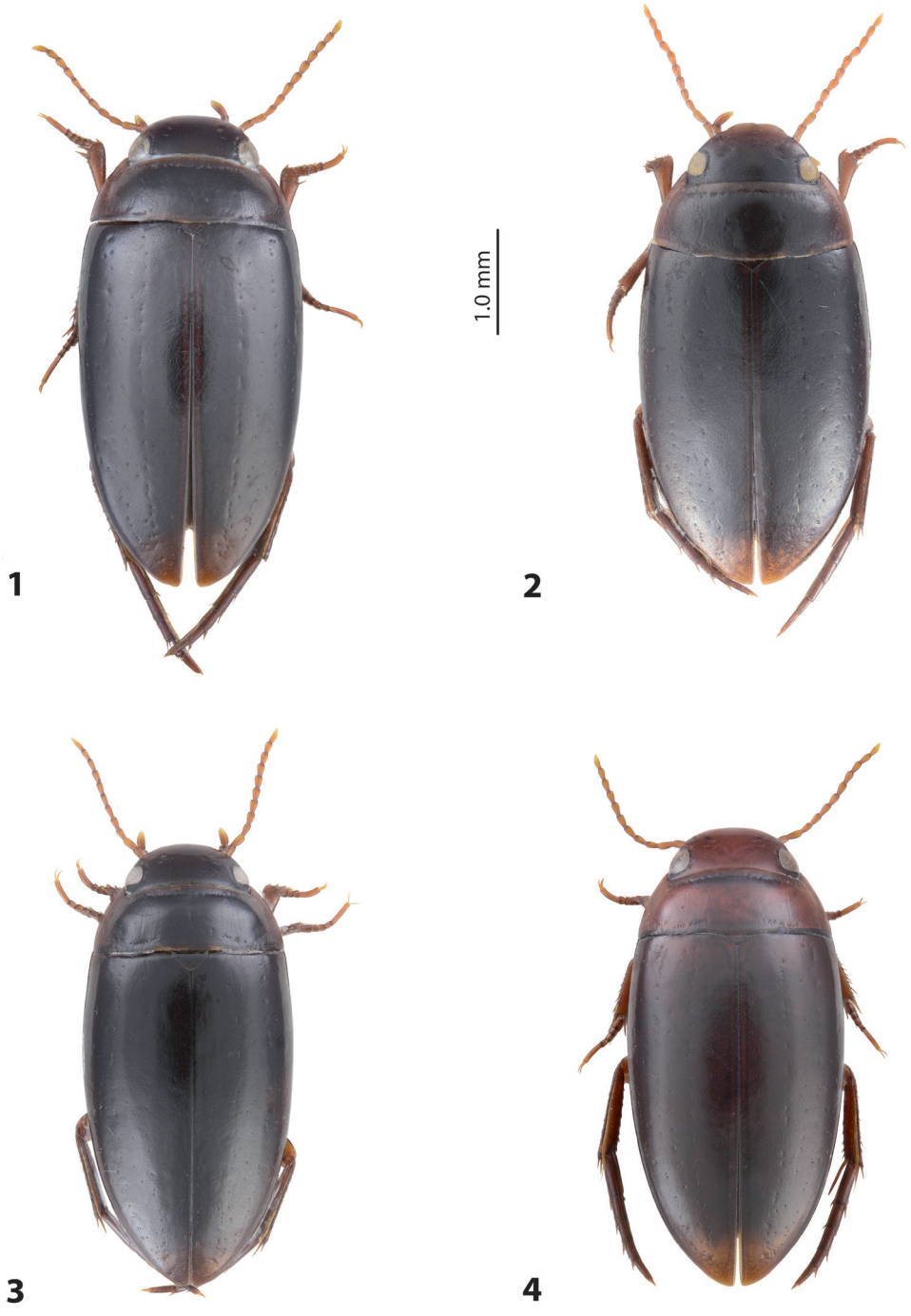
Copelatus (*Papuadytes*) *aipomek* Balke, 1998: 322; Nilsson 2001: 76 (catalogue).
Papuadytes aipomek (Balke, 1998): Nilsson and Fery 2006: 56 (comb. nov.).
Exocelina aipomek (Balke, 1998): Nilsson 2007: 33 (comb. nov.).
Exocelina aipomek MB3726: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.
Copelatus (*Papuadytes*) *santimontis* Balke, 1998: 335; Nilsson 2001: 77 (catalogue) syn. nov.
Papuadytes santimontis (Balke, 1998): Nilsson and Fery 2006: 56 (comb. nov.).
Exocelina santimontis (Balke, 1998): Nilsson 2007: 34 (comb. nov.).

Type locality. Indonesia: Papua Province: Pegunungan Bintang Regency, Aipomek, 04°27'S, 140°01'E, 1800 m a.s.l.

Type material studied. *Exocelina aipomek*: *Holotype*: male "IRIAN JAYA Aipomek Area 140°01'E 04°27'S", "Aipomek, 1800m 30./31.8.1992 leg.Balke (30)", "HOLOTYPUS" [red], "Copelatus aipomek Balke des. 1997" [red] (NHMW). *Paratypes*: 3 males, 1 female with the same label as the holotype and additionally with red labels "Paratypus Copelatus aipomek Balke des. 1997", one of the males with two additional labels "M.Balke 3272" [green] and "M.Balke 6403 DNA" [green text] (NHMW). ***Exocelina santimontis*:** *Holotype*: male "IRIAN JAYA: 1.10.1993 Eme Gebiet Okloma, 1500m", "ca. 139°55'E 04°14'S leg. M. Balke (28)", "HOLOTYPUS" [red], "Copelatus santimontis Balke des. 1997" [red] (NHMW). *Paratypes*: 8 males with the same label as the holotype and additionally with red labels "Paratypus Copelatus santimontis Balke des. 1997", one of the males with two additional labels "M.Balke 3289" [green] and "M.Balke 6412 DNA" [green text], another male with an additional green label "M.Balke 3288" (NHMW). 1 male "IRIAN JAVA: Borme Tarmlu 1500m 6.9.1993", "ca. 140°25'E 04°24'S leg. M. Balke (4–6)", "Paratypus Copelatus santimontis Balke des. 1997" (NHMW). 1 male "IRIAN JAYA: 22.9.1993 Bime – Calab Gebiet, Bime, 1400m", "ca. 140°12'E 04°20'S, leg. M. Balke (16)", "Paratypus Copelatus santimontis Balke des. 1997" [red] (NHMW)

Additional material. PNG: Sandaun: 2 males "Papua New Guinea: Sandaun, Ofektaman, 820m, 17.x.2008, 5.04.113S 141.35.841E, Ibalim (PNG 190)", one with an additional green label "M.Balke 3727" (ZSM).

Females of doubtful identity. IN: Papua: Pegunungan Bintang: 20 females "IRIAN JAYA: 22.9.1993 Bime – Calab Gebiet, Bime, 1400m", "ca. 140°12'E 04°20'S, leg. M. Balke (16)", "Paratypus Copelatus rivulus sp.n. Balke des. 1997" [red] (NHMW); these females are a mixture of two species: *E. damantiensis* (Balke, 1998)



Figures 1–4. Habitus and colouration **1** *Exocelina aipomek* (Balke, 1998) **2** *E. mekilensis* sp. nov. **3** *E. koroba* sp. nov. **4** *E. morobensis* sp. nov.

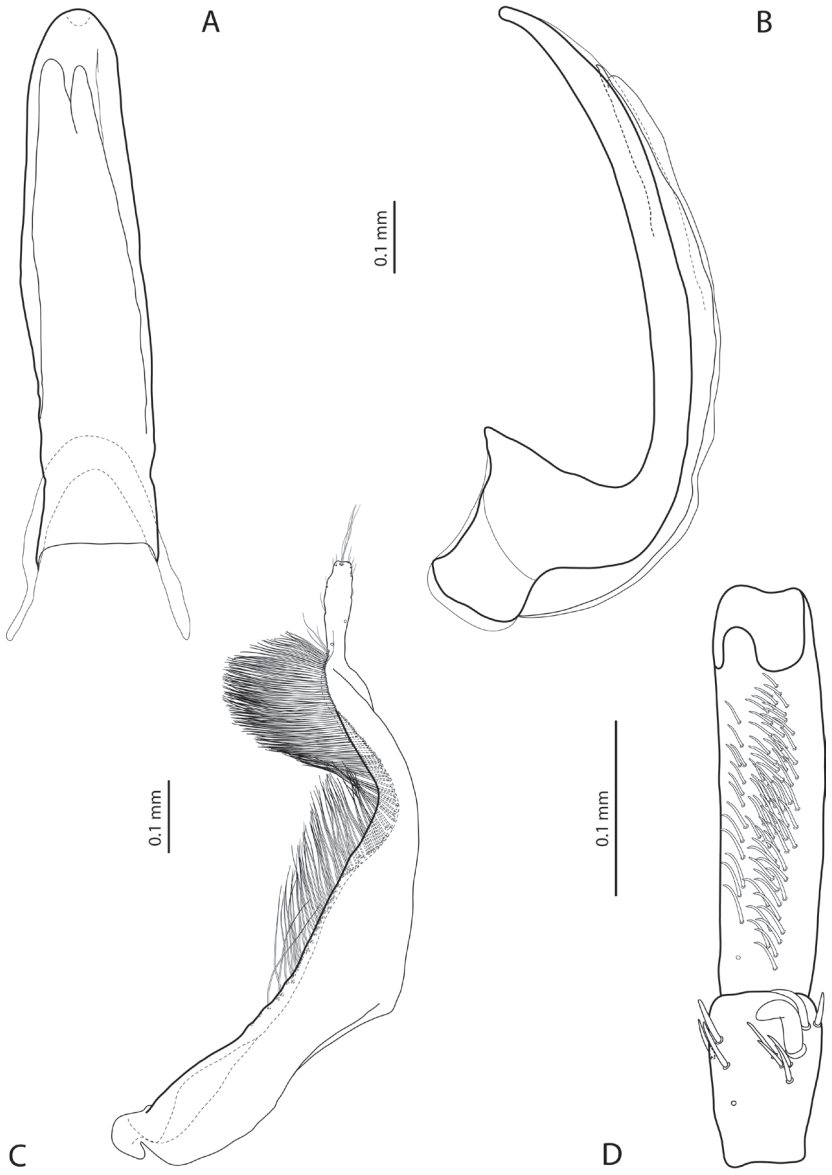
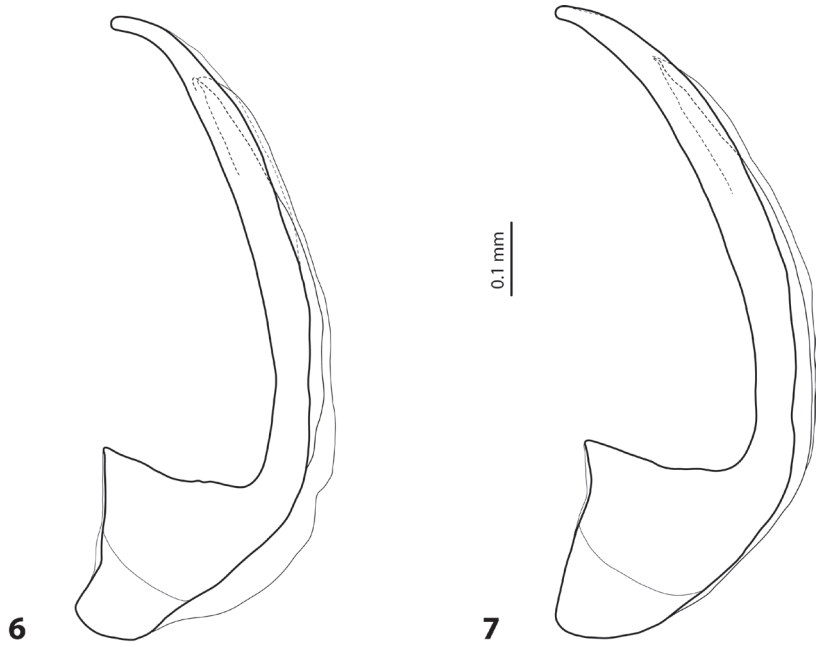


Figure 5. *Exocelina aipomek* (Balke, 1998), paratype **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

and *E. aipomek*. 13 females "IRIAN JAYA: 22.9.1993 Bime – Calab Gebiet, Bime, 1400m", "ca. 140°12'E 04°20'S, leg. M. Balke (16)" (NHMW); these females are a mixture of two species: *E. damantiensis* and *E. aipomek*. 1 female "IRIAN JAVA: Borme Tarmlu 1500m 6.9.1993", "ca. 140°25'E 04°24'S leg. M. Balke (4–6)" (NHMW). 3 females "IRIAN JAVA: Borme Tarmlu 1500m 6.9.1993", "ca. 140°25'E 04°24'S leg.



Figures 6, 7. *Exocelina aipomek* (Balke, 1998), median lobe in lateral view **6** specimen from Sandaun, Ofektaman **7** paratype of *E. sanctimontis* (Balke, 1998).

M. Balke (4)" (NHMW). 2 females "IRIAN JAVA: Borme Tarmlu 1500m 6.9.1993", "ca. 140°25'E 04°24'S leg. M. Balke (6)" (NHMW). These females are a mixture of four species: *E. damantiensis*, *E. ketembang* (Balke, 1998), *E. aipomek*, and *E. danae* (Balke, 1998). 1 male (no genitals), 27 females "IRIAN JAYA: 1.10.1993 Eme Gebiet Okloma, 1500m", "ca. 139°55'E 04°14'S, leg. M. Balke (28)" (NHMW); these specimens are a mixture of three species: *E. damantiensis*, *E. ketembang*, and *E. aipomek*. 13 females "IRIAN JAYA: 22.9.1993 Bime – Calab Gebiet, Bime, 1400m", "ca. 140°12'E 04°20'S, leg. M. Balke (16)" (NHMW). 2 females "IRIAN JAYA, 24.–26.9.1993 Eipomek [sic!] Gebiet Eipomek [sic!] - Diruemna", "ca. 140°01'E 04°27'S 1800–2600m, leg. M. Balke (21–22)" (NHMW). These females are a mixture of two species: *E. damantiensis* and *E. aipomek*. **PNG: Sandaun:** 7 females "Papua New Guinea: Sandaun, Ofektaman, 820m, 17.x.2008, 5.04.113S 141.35.841E, Ibalim (PNG 190)" (ZSM); these females might belong to three species: *E. sandaunensis* Shaverdo & Balke, 2014, *E. aipomek*, and *E. ketembang* (Balke, 1998).

Diagnosis. For complete description, see Balke (1998: 322). Beetle medium-sized (TL-H 4.0–4.35 mm), oblong-oval; piceous, sometimes with paler pronotal sides; dorsally shiny, with extremely fine, inconspicuous punctation and weakly impressed microreticulation; pronotum with distinct lateral bead (Fig. 1); male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; male protarsomere 5 ventrally with anterior band of more than 60 and posterior row of 14 relatively long setae (Fig. 5D); median lobe simple, in lateral view, evenly tapering to broadly pointed, somehow elongate and gently curved downwards apex, in ventral view, apex more or

less rounded; paramere with distinct dorsal notch and large, long subdistal part, dorsal setae numerous and strong, subdistal slightly denser and longer than proximal ones, the latter more or less distinct (Fig. 5A–C).

Variability. The species shows variability within and between populations in shape of the apex of the median lobe, which can be shorter or more elongate (Figs 6, 7).

Affinities. In the area of its distribution, *E. aipomek* co-occurs with numerous species: *E. ascendens* (Balke, 1998), *E. fume* (Balke, 1998), *E. takime*, species of the *E. bacchusi*, *E. ekari*, *E. danae*, *E. broschii*, *E. okbapensis*, and *E. aipo* groups. The species can be distinguished from them by its body size, form and colouration, inconspicuous dorsal punctation, and weakly impressed microreticulation, presence of the pronotal bead, shape and setation of its median lobe, paramere, and male protarsomere 4.

Distribution. Indonesia: Papua Province: Pegunungan Bintang Regency and Papua New Guinea: Sandaun Province (Fig. 11).

Exocelina koroba group

This group is characterised by relatively dense and coarse dorsal punctation; pronotum with distinct lateral bead; median lobe of aedeagus without setation, with apex thick, short, pointed and strongly curved downwards in lateral view; apexes of ventral sclerites of median lobe almost equal; paramere with distinct notch on dorsal side, subdistal part relatively large, rounded, with dense and strong setae, proximal setae inconspicuous.

2. *Exocelina koroba* Shaverdo & Balke, sp. nov.

http://zoobank.org/B6A930A9-0B56-48D9-8C04-4BD72F56A750
Figs 2, 8

Exocelina undescribed sp. MB1292: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Hela Province, Hedamali, ca. 05°41.85'S, 142°43.84'E, 1700–1900 m a.s.l.

Type material. *Holotype*: male "PAPUA N.G.: 6.–9.5.1998 Southern Highl. Prov. Tari-Koroba, Hedemari [Hedamali] 1700–1900 m, leg. Riedel" (NHMW). *Paratypes*: 1 male "Papua New Guinea: Southern Highlands, Koroba, 1600 m, 15.v.1994, 05.41.854S 142.43.836E, Balke (PNG 66)", "DNA M Balke 1292" (ZSM).

Description. *Body size and form*: Beetle medium-sized: TL-H 3.95–4.4 mm, TL 4.4–4.55 mm, MW 2.2–2.35 mm (holotype: TL-H 3.95 mm, TL 4.4 mm, MW 2.2 mm), with oblong-oval habitus.

Colouration: Piceous, with paler sides of pronotum. Head piceous, paler anteriorly; pronotum piceous, with brown sides; elytra piceous, with reddish sutural lines; head appendages and legs proximally reddish, legs distally darker, reddish brown (Fig. 2). Teneral specimen paler, brown.

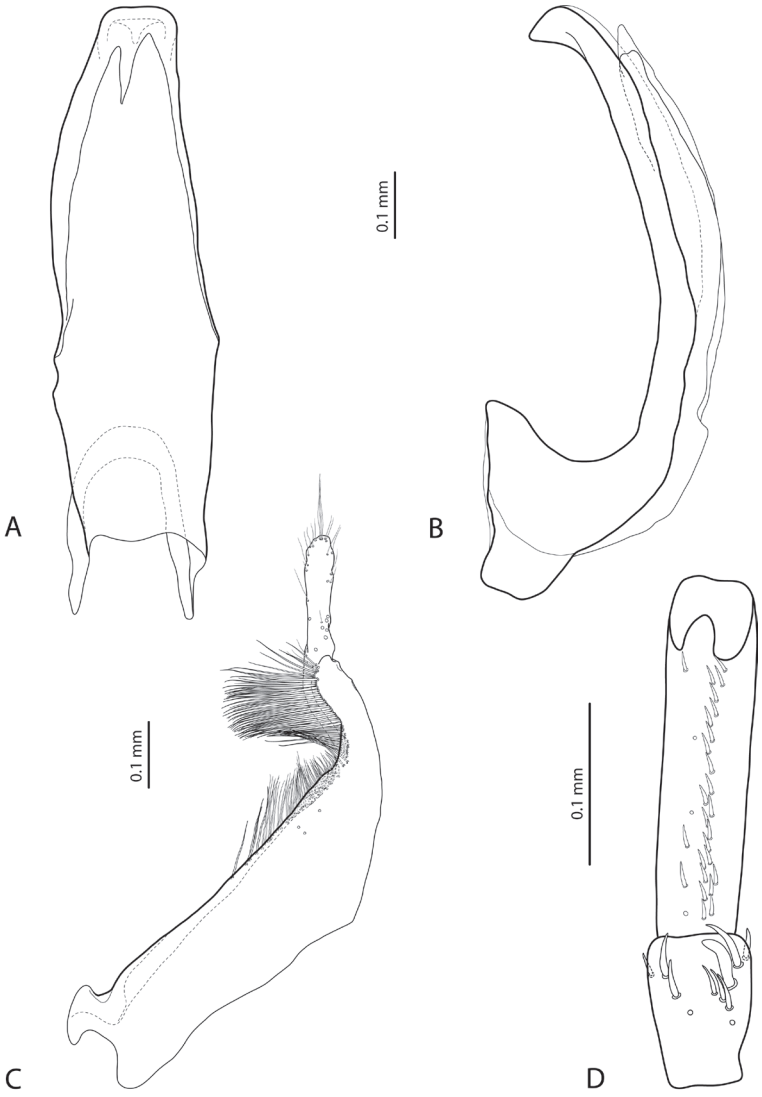


Figure 8. *Exocelina koroba* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

Surface sculpture: Submatt dorsally, with relatively dense and coarse punctation and evident microreticulation. Head with relatively dense and coarse punctation (spaces between punctures 1–2 times size of punctures); diameter of punctures almost equal to diameter of cells of microreticulation. Pronotum with finer, sparser punctation, and more evenly distributed punctation than on head. Elytra with coarser punctation than on pronotum. Pronotum and elytra with distinct microreticulation. Head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak trans-

verse wrinkles; abdominal ventrites with strioles. Venter with inconspicuous punctation, more evident on metacoxal plates and two last abdominal ventrites.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded and with few transverse strioles anteriorly, without anterolateral extensions. Blade of prosternal process lanceolate, relatively broad, convex, with distinct bead and few setae laterally. Abdominal ventrite 6 slightly truncate.

Male: Protarsomere 4 with rather small, slightly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior row of 23 short setae and posterior row of 6 setae (Fig. 8D). Abdominal ventrite 6 with 12–15 lateral striae on each side. Median lobe slightly curved, with apex thick, short, pointed and strongly curved downwards in lateral view (Fig. 8A–B). Paramere with distinct notch on dorsal side, subdistal part relatively large, rounded, with dense and strong setae, proximal setae thin and sparse, inconspicuous. (Fig. 8C).

Female: Unknown.

Affinities. The species can be distinguished from the species co-occurring in the same area (*E. pseudoedeltraudae* Shaverdo & Balke, 2014, *E. tariensis* Shaverdo & Balke, 2014, *E. marinae* (Shaverdo, Sagata & Balke, 2005), and *E. pseudomarinae* Shaverdo, Sagata & Balke, 2016) by size, relatively dense and coarse dorsal punctation, not modified male antennae, and the shape and setation of its median lobe and paramere.

Distribution. Papua New Guinea: Hela Province, Koroba area (Fig. 11).

Etymology. The species is named after Koroba Village. The name is a noun in the nominative singular standing in apposition.

***Exocelina mekilensis* group**

This group is characterised by fine and sparse dorsal punctation; pronotum without lateral bead; median lobe of aedeagus without setation, simple; in lateral view, apex thick, short and slightly curved downwards, its minuscule tip curved upwards; apexes of ventral sclerites of median lobe slightly unequal: left one slightly longer that right one; paramere without dorsal notch, evenly tapering to distal part, with numerous small spines and without long setae.

3. *Exocelina mekilensis* Shaverdo & Balke, sp. nov.

http://zoobank.org/4833A1FB-F7A6-4ED8-ACA2-442719E2A641
Figs 3, 9

Exocelina undescribed sp. MB0686: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Sandaun Province, Ofektaman, 05°04.11'S, 141°35.84'E, 820 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea: Sandaun, Ofektaman, 820m, 17.x.2008, 5.04.113S 141.35.841E, Ibalim (PNG 190)", "DNA M.Balke 3723" (ZSM). *Paratypes*: 1 male with the same label as the holotype (NHMW). 1 male "Papua New Guinea: Sandaun, Sokamin4, 1200m, 19.x.2003, 4 50.845S 141 37.865E, K. Sagata (WB102)", "DNA M. Balke 665" [green text] (ZSM). 1 male, 4 females "Papua New Guinea: Sandaun, MekilW100, 1718m, 14.x.2003, 4 48.637S 141 38.994E, K. Sagata (WB19)" (NHMW, ZSM). 1 male "DNA M. Balke 686" [green text], "Papua New Guinea: Sandaun, Mekil (WB19), 13.x.2003, K. Sagata, DNA M Balke: MB 686" (ZSM).

Description. *Body size and form*: Beetle medium-sized: TL-H 3.85–4.4 mm, TL 3.45–3.95 mm, MW 1.8–2.05 mm (holotype: TL-H 3.8 mm, TL 4.2 mm, MW 2.0 mm), with oblong-oval habitus.

Colouration: Dark brown, with paler sides of pronotum and head anteriorly. Head dark brown, piceous posteriorly; pronotum dark brown, with brown sides; elytra uniformly dark brown; head appendages and legs proximally reddish, legs distally darker, reddish brown (Fig. 3). Teneral specimen paler, brown to reddish brown with yellowish pronotal sides.

Surface sculpture: Shiny dorsally, with fine, sparse punctation and weakly impressed microreticulation. Head with relatively fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures almost equal to or smaller than diameter of cells of microreticulation. Pronotum and elytra with much finer and sparser punctation than on head, inconspicuous. Pronotum and elytra with weakly impressed microreticulation. Head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Venter with extremely inconspicuous punctation, more evident on metacoxal plates and two last abdominal ventrites.

Structures: Pronotum without lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 slightly truncate.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of ca. 60 and posterior row of ten relatively long setae (Fig. 9D). Abdominal ventrite 6 with 6–10 lateral striae on each side. Median lobe simple, slightly curved, in lateral view, apex thick, short and slightly curved downwards, its minuscule tip curved upwards (Fig. 9A, B). Paramere without notch on dorsal side, evenly tapering to distal part, with numerous small spines and without long setae (Fig. 9C).

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Affinities. From most species co-occurring in the same area (*E. sandaunensis*, *E. tabubilensis* Shaverdo & Balke, 2014, *E. damantiensis*, *E. okbapensis* Shaverdo & Balke, 2017, and *E. may* Shaverdo & Balke, 2017), *E. mekilensis* sp. nov. can be distinguished by its smaller size and absence of the pronotal bead, and simple male antennae. From the

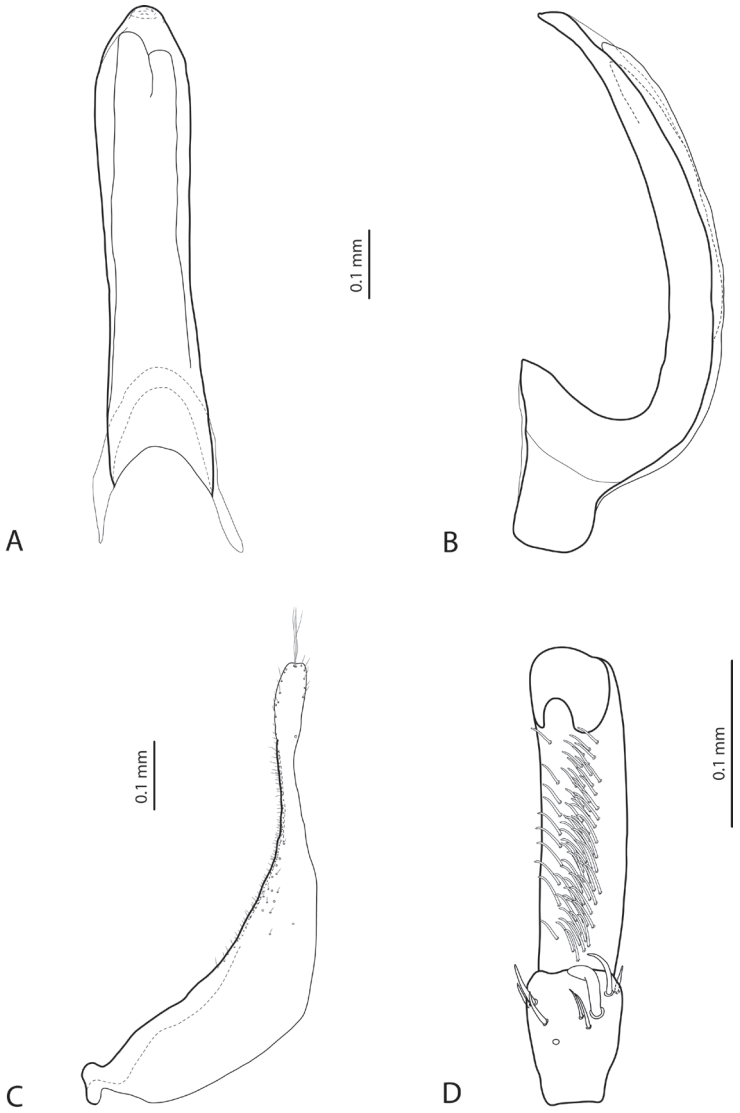


Figure 9. *Exocelina mekilensis* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

species without pronotal bead (*E. pseudobifidae* Shaverdo & Balke, 2014, *E. pseudoeme* Shaverdo & Balke, 2014, and *E. ibalimi* Shaverdo & Balke, 2018), it can be differentiated by the shape and setation of its median lobe and paramere, which are very characteristic and resemble those of the *E. ullrichi* group (Shaverdo and Balke 2014).

Distribution. Papua New Guinea: Sandaun Province (Fig. 11).

Etymology. The species is named after Mekil Village where most specimens of the species were found. The name is an adjective in the nominative singular.

Exocelina morobensis group

This group is characterised by fine and sparse dorsal punctation; pronotum with narrow lateral bead; median lobe of aedeagus without setation, evenly curved, rather thin, lateral margins thickened proximally; in lateral view, its apex elongate, slightly thickened and rounded, in ventral view, median lobe broad proximally and distinctly narrowed in distal half, its apex bluntly pointed; apexes of ventral sclerites of median lobe almost equal; paramere slightly concave on dorsal side, its subdistal part with dense, strong setae, proximal setae weaker, less distinct.

4. *Exocelina morobensis* Shaverdo & Balke, sp. nov.

http://zoobank.org/3DA0BA42-2D2B-4B41-A31C-92C74250DDD9
Figs 4, 10

Exocelina undescribed sp. MB1313: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.
Exocelina undescribed sp. MB3840: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Morobe Province, Garaina, 07°51'03"S, 147°07'01"E, 720 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea Garaina, 720m, vi.2008, 07.51.032S 147.07.007E Ibalim & Sosanika PNG216" (ZSM). *Paratypes*: **Morobe:** 72 males, 83 females with the same label as the holotype (NHMW, ZSM). 64 males, 69 females "Papua New Guinea: Morobe, Garaina, 800m, vi.2008, 07.53.091S 147.07.915E Ibalim & Sosanika PNG217" (NHMW, ZSM). 2 males, 4 females "Papua New Guinea Garaina, 800m, vi.2008, 07.53.091S 147.07.915E Ibalim & Sosanika PNG217" (ZSM). 27 males, 18 females "Papua New Guinea: Morobe, Garaina, 770m, vi.2008, 07 52.516S 147.10.427E Ibalim & Sosanika (PNG219)" (NHMW, ZSM). 26 males, 25 females "Papua New Guinea Morobe, Garaina, 800m, 27.vi.2009, (PNG220) 7.52.669S 147.07.196E Ibalim & Sosanika" (NHMW, ZSM). 11 males, 11 females "Papua New Guinea: Morobe, Garaina, 770m, 25.vi.2008, 07 50.859S 147.08.614E Ibalim & Sosanika (PNG222)" (NHMW, ZSM). 2 males, 1 female "Papua New Guinea Morobe, Garaina, 670m, 23vi2008 (PNG223) 7.52.431S 147.10.267E Ibalim & Sosanika (PNG223)" (ZSM). 9 males, 6 females "Papua New Guinea: Morobe, Garaina, 820m, 24.vi.2008, 07.52.287S 147.06.297E Ibalim & Sosanika, (PNG224)" (ZSM). 15 males, 14 females "Papua New Guinea: Morobe, Huon Pen., rd to Kwapsanek, 250m, 31.iii.2006, 06.30.270S (PNG 24) 146.59.581E, Balke & Sagata" (NHMW, ZSM). 4 males, 5 female "Papua New Guinea: Morobe, Huon Pen., rd to Kwapsanek, 250m, 31.iii.2006, 06.30.270S 146.59.581E, Balke & Sagata (PNG 24A)" (ZSM). 2 males, 1 female "Papua New Guinea: Morobe, Huon Pen., rd to Kwapsanek, 460m, 31.iii.2006, 06.32.736S 146.59.616E, Balke & Sagata

(PNG 26)", one male with an additional label "DNA M.Balke 1313" (ZSM). 73 males, 56 females "Papua New Guinea: Morobe, Herzog Mts., Bundun, 700–800m, 2.iv.1994, 06.51.598S 146.37.07E, Balke & Sagata (PNG 27)", one male with an additional green label "DNA M.Balke 1312" (NHMW, ZSM). 1 male "NEW GUINEA: Morobe Dist., Lae-Bulobo Rd., 28.xii.1964.", "Stn. No. 123.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 1 male, 2 females "Papua New Guinea: Morobe, Sattelberg, Zige River, 970m, 20.x.2009, 6 29.233S 147 46.482E, Inaho (11) (PNG211)", the male with an additional green label "DNA M.Balke 3828" (ZSM). 2 males, 1 female "Papua New Guinea: Morobe, Sattelberg, Zige River, ca 700m, x.2009, 6 29.233S 147 46.482E, Inaho (12a) (PNG212)", one of the males with an additional green label "DNA M.Balke 3823" (ZSM).

Description. *Body size and form*: Beetle medium-sized, rarely small: TL-H 3.3–4.1 mm, TL 3.6–4.5 mm, MW 1.75–2.1 mm (holotype: TL-H 3.9 mm, TL 4.35 mm, MW 2.05 mm), with oblong-oval habitus.

Colouration: Brown to dark brown, usually with reddish pronotum and head. Head reddish to brown, sometimes darker posterior eyes; pronotum reddish to brown, often broader or narrower darker area on disc; elytra brown to dark brown, sometimes with reddish sutural lines; head appendages and legs proximally reddish, legs distally darker, reddish brown to brown (Fig. 4). Teneral specimen paler.

Surface sculpture: Shiny dorsally, with fine, sparse punctation and weakly impressed microreticulation. Head with relatively fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures almost equal to or smaller than diameter of cells of microreticulation. Pronotum and elytra with much finer and sparser punctation than on head, often inconspicuous on elytra. Pronotum and elytra with weakly impressed microreticulation. Head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Venter with extremely inconspicuous punctation, more evident on metacoxal plates and two last abdominal ventrites.

Structures: Pronotum with narrow lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 very slightly truncate.

Male: Protarsomere 4 with with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of ca. 50 and posterior row of seven relatively long setae (Fig. 10D). Abdominal ventrite 6 with 5–7 lateral striae on each side. Median lobe evenly curved, rather thin, lateral margins thickened proximally; in lateral view, apex elongate, slightly thickened and rounded; in ventral view, median lobe broad proximally and distinctly narrowed in distal half, apex bluntly pointed (Fig. 10A, B). Paramere slightly concave on dorsal side, its subdistal part with dense, strong setae, proximal setae weaker, less distinct (Fig. 10C).

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

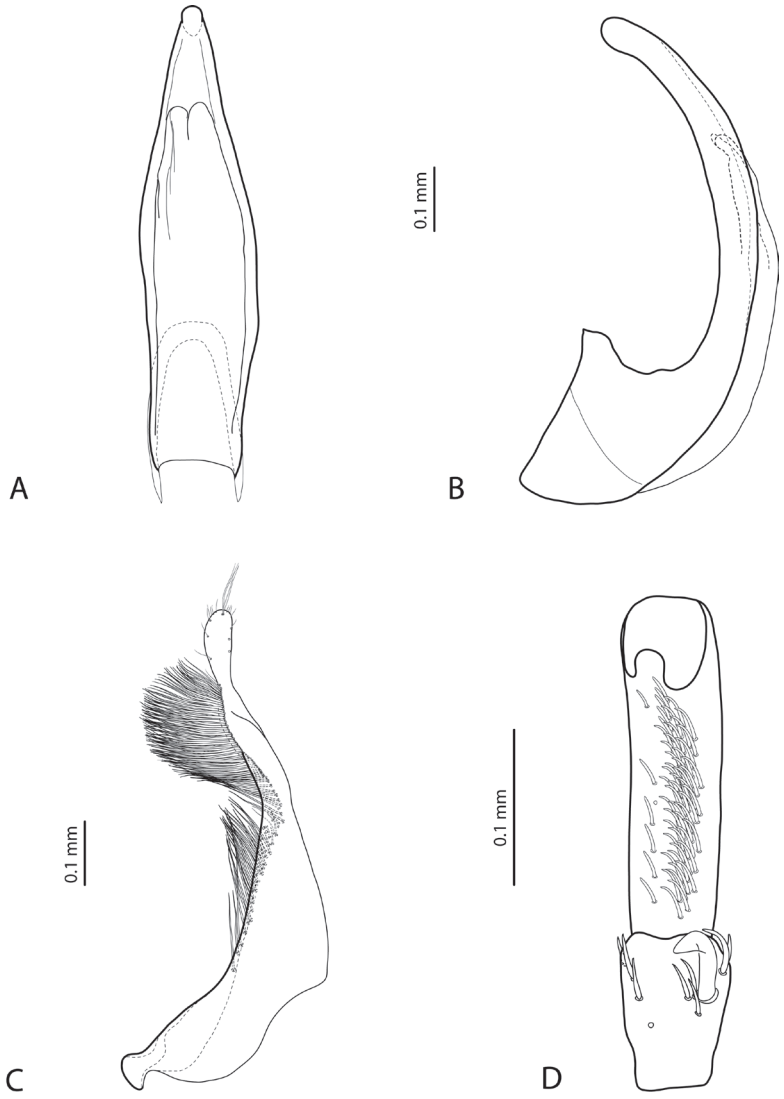


Figure 10. *Exocelina morobensis* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

Affinities. From the species co-occurring in the same area (*E. brahminensis* Shaverdo, Hendrich & Balke, 2012, *E. damantiensis*, and *E. garaina* Shaverdo & Balke, 2016), *E. morobensis* sp. nov. can be distinguished by its size, colouration, narrow pronotal bead, and shape and setation of the median lobe and paramere.

Distribution. Papua New Guinea: Morobe Province (Fig. 11).

Etymology. The species is named after Morobe Province, the only province of PNG where the species has been found. The name is an adjective in the nominative singular.

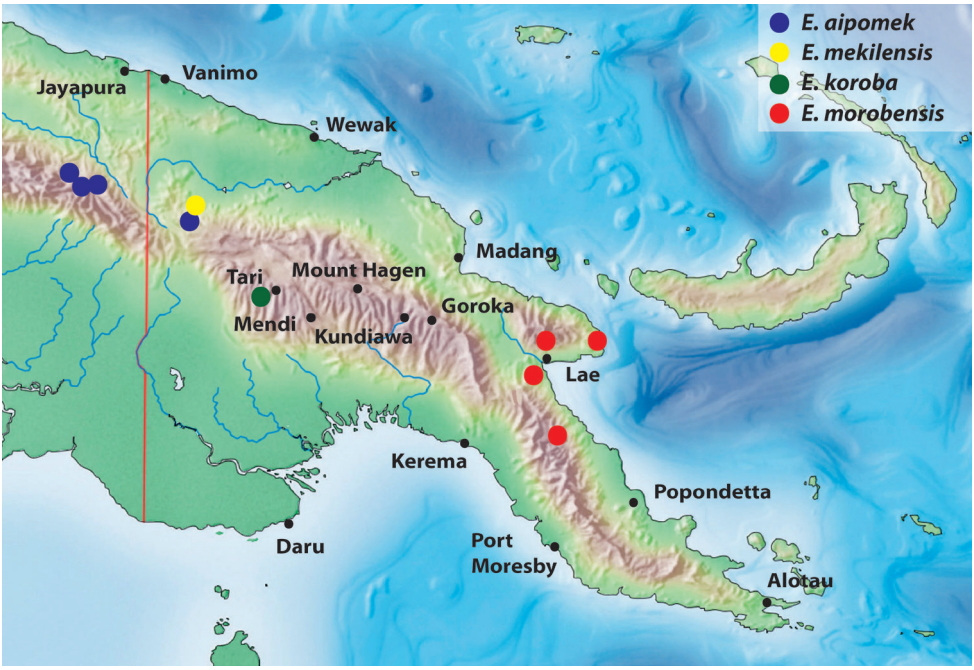


Figure 11. Map of the eastern part of New Guinea showing distribution of the species of the monotypic groups.

Other groups
Exocelina bacchusi group

The representatives of this group are characterised by fine to coarse dorsal punctation; pronotum with distinct lateral bead; median lobe of aedeagus without setation, simple, broadly pointed; apexes of ventral sclerites of median lobe almost equal; paramere evenly tapering to apex, proximal setae often longer and more distinct that subdistal.

5. *Exocelina akameku* Shaverdo & Balke, sp. nov.

http://zoobank.org/76FBDA94-6B7D-4CCB-8549-88841C285583
Figs 13, 19

Type locality. Papua New Guinea: Madang Province, Akameku - Brahmin, Bismarck Range, 05°49.89'S, 145°24.49'E, 750 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, 05.49.892S 145.24.491E, Balke & Kinibel (PNG 113)" (ZSM).

Description. *Body size and form*: Beetle small: TL-H 3.35 mm, TL 3.8 mm, MW 1.8 mm, with oblong-oval habitus.

Colouration: Dark brown, with reddish pronotal sides and head anteriorly. Head reddish brown, paler anteriorly; pronotum dark brown on disc, with reddish sides; elytra dark brown, with weakly indicated reddish sutural lines; head appendages and legs proximally yellowish, legs distally darker, reddish brown (Fig. 13).

Surface sculpture: Shiny dorsally, with weak and sparse punctation and weakly impressed microreticulation. Head with fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures equal to or smaller than diameter of cells of microreticulation. Pronotum with much finer and sparser punctation than on head, very inconspicuous. Punctation on elytra invisible. Pronotum and elytra with weakly impressed microreticulation; head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter invisible; inconspicuous on two last abdominal ventrites.

Structures: Pronotum with narrow lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, very slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 slightly truncate.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of more than 30 and posterior row of 7 relatively long setae (Fig. 19D). Abdominal ventrite 6 with 7–8 lateral striae on each side. Median lobe short, robust, evenly tapering to slightly pointed apex in lateral and ventral views; apex slightly sinuate in lateral view (Fig. 19A, B). Paramere as in Fig. 19C.

Female: Unknown.

Affinities. From the species co-occurring in the same area (from *E. danae*, *E. ekari*, *E. broschii*, and *E. ullrichi* groups), *E. akameku* sp. nov. can be distinguished by its size, dorsal punctation, and shape and setation of its median lobe and paramere. For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Madang Province, Bismarck Range (Fig. 25).

Etymology. The species is named after Akameku Village. The name is a noun in the nominative singular standing in apposition.

6. *Exocelina bacchusi* (Balke, 1998)

Figs 16, 22, 24

Copelatus (*Papuadytes*) *bacchusi* Balke, 1998: 326; Nilsson 2001: 76 (catalogue).
Papuadytes bacchusi (Balke, 1998): Nilsson and Fery 2006: 56 (comb. nov.).
Exocelina bacchusi (Balke, 1998): Nilsson 2007: 33 (comb. nov.).
Exocelina bacchusi MB1521: Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.
Exocelina undescribed sp. MB0257: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Madang Province, Finisterre Range, Damanti, 05°53'26.5"S, 145°57'50.6"E, 1180 m a.s.l.

Type material studied. *Holotype*: male "Stn. No. 39", "NEW GUINEA: Madang Dist., Finisterre Mts. Damanti 3,550 ft. 2–11.x.1964.", "M.E. Bacchus. B.M. 1965-120", "HOLOTYPUS" [red], "Copelatus bacchusi Balke des. 1997" [red] (BMNH). *Paratypes*: 1 male with the same label as the holotype and additionally with red label "Paratypus Copelatus bacchusi Balke des. 1997" (BMNH). 2 males "Stn. No. 49", "NEW GUINEA: Madang Dist., Finisterre Mts. Budemu c. 4000 ft. 15–24.x.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH, NHMW). 4 females "Stn. No. 74", "NEW GUINEA: Madang Dist., Finisterre Mts. Budemu c. 4000 ft. 15–24.x.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH, NHMW). Note: in the original description (Balke, 1998: 326), the paratypes with the same label as the holotype and from locality "Stn. No. 49" were erroneously indicated as females.

Additional material. Madang: 2 males "Papua New Guinea: Madang, Simbai area, 1200m, 11.iii.2007, 05.13.333S 144.37.611E, Kinibel (PNG 153) (ZSM). 15 males, 6 females "Papua New Guinea: Madang, Simbai-Mombeen, 1100m, 11. iii.2007, 05.12.876S 144.41.759E, Kinibel (PNG 154), one male with an additional green label "DNA M.Balke 3318" (NHMW, ZSM). 1 male, 14 females "Papua New Guinea: Madang, Keki-Sewan, Adalbert [sic!] Mts., 700m, 30.xi.2006, nr 04.41.802S 145.25.460E, Binatang Boys (PNG 120)" (ZSM). 4 males, 4 females "Papua New Guinea: Madang, Adalbert [sic!] Mts., creek nr Keki, 790m, 28.xi.1994, 04.42.300S 145.25.089E, Binatang Boys leg. (PNG 53a)" (NHMW, ZSM). 2 males, 5 females "Papua New Guinea: Madang, Adalbert [sic!] Mts., Keki, 850m, 4.v.2006, nr 04.42.300S 145.25.089E, Manaono leg. (PNG 52)" (ZSM). 83 males, 84 females "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 1200m, 24.xi.2006, nr 05.52.754S 145.23.209E, Balke & Kinibel (PNG 110)", one of them with an additional green label "DNA M.Balke 1521" (NHMW, ZSM). 7 males, 3 femlaes "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 1500m, 24.xi.2006, 05.51.964S 145.23.604E, Balke & Kinibel (PNG 111)" (ZSM). 3 females "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 800m, 24.xi.2006, 05.50.021S 145.24.664E, Balke & Kinibel (PNG 112)" (ZSM). 1 male, 1 female "Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, 05.49.892S 145.24.491E, Balke & Kinibel (PNG 113)" (ZSM). 1 male "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-P-1/8-d02 / Plot 16 / P1608 Vial 18767" (ZSM). 1 male "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-T-1/8-d02 / Plot 20 / P1640 Vial 18781" (ZSM). 3 females "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-P-1/8-d02 / Plot 16 / P1608 Vial 18767" (ZSM). 1 female "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-O-1/8-d02 / Plot 15 / P1600 Vial 18763" (ZSM). 1 female "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-K-1/8-d02 / Plot 11

/ P1568 Vial 17122" (ZSM). 1 female "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-A-2/8-d03 / Plot 1 / P1489 Vial 17237" (ZSM). 1 female "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-C-2/8-d03 / Plot 3 / P1505 Vial 17179" (ZSM). 6 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1529 Vial 16853" (ZSM). 1 male, 4 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1553 Vial 09007" (ZSM). 1 male, 4 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1545 Vial 16863" (ZSM). 1 male, 7 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1561 Vial 16873" (ZSM). 1 male "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-A-2/8-d03 / Plot 1 / P1489 Vial 17237" (ZSM). 7 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-E-2/8-d03 / Plot 5 / P1521 Vial 17210" (ZSM). 1 female "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1569 Vial 17302" (ZSM). 3 females "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1601 Vial 17313" (ZSM). 11 females "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1595 Vial 18799" (ZSM). 1 female "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1593 Vial 17462" (ZSM). 2 males "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1577 Vial 18802" (ZSM). 1 male "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1625 Vial 18821" (ZSM). 1 female "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1633 Vial 18848" (ZSM). 1 female "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1617 Vial 18813" (ZSM). 1 female "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1601 Vial 17313" (ZSM). 2 females "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1585 Vial 18825" (ZSM). 1 male, 13 females "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1609 Vial 18855" (ZSM). 1 female "Ibisca Niugini, PNG 29–31.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-D-3/8-d05 / Plot 4 / P1514 Vial 16946" (ZSM). 1 female "Ibisca Niugini, PNG 29–31.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-F-3/8-d05 / Plot 6 / P1530 Vial 16936" (ZSM). 1 female "Ibisca Niugini, PNG 29–31.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-A-3/8-d05 / Plot 1 / P1490 Vial 16931" (ZSM). 2 females "Ibisca Niugini, PNG 29–31.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-H-3/8-d05 / Plot 8 / P1546 Vial 17249" (ZSM). 1 female "Ibisca Niugini, PNG 29–31.x.2012 Mount

Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-C-3/8-d05 / Plot 3 / P1506 Vial 17235" (ZSM). 1 female "Ibisca Niugini, PNG 29–31.x.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-J-3/8-d05 / Plot 10 / P1562 Vial 16881" (ZSM). 2 females "Ibisca Niugini, PNG 30.x.–1.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1578 Vial 17625" (ZSM). 4 females "Ibisca Niugini, PNG 30.x.–1.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1570 Vial 17585" (ZSM). 1 female "Ibisca Niugini, PNG 30.x.–1.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1634 Vial 17605" (ZSM). 1 female "Ibisca Niugini, PNG 31.x.–2.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1547 Vial 17303" (ZSM). 1 female "Ibisca Niugini, PNG 31.x.–2.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1515 Vial 17326" (ZSM). 1 female "Ibisca Niugini, PNG 31.x.–2.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1491 Vial 17331" (ZSM). 1 female "Ibisca Niugini, PNG 31.x.–2.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1531 Vial 17347" (ZSM). 1 female "Ibisca Niugini, PNG 31.x.–2.xi.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-E-4/8-d07 / Plot 5 / P1523 Vial 17348" (ZSM). 2 females "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1579 Vial 18787" (ZSM). 8 females "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1643 Vial 18794" (ZSM). 1 female "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1595 Vial 18799" (ZSM). 3 females "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1571 Vial 16947" (ZSM). 1 female "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1635 Vial 16968" (ZSM). 1 female "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-S-4/8-d08 / Plot 19 / P1635 Vial 16968-CODYTI" (ZSM). 1 male, 10 females "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1611 Vial 16950" (ZSM). 2 females "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1611 Vial 16950" (ZSM). 2 females "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1635 Vial 16968" (ZSM). 1 female "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1516 Vial 17287" (ZSM). 2 females "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1548 Vial 17297" (ZSM). 2 females "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1532 Vial 17314" (ZSM). 1 female "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1492 Vial 17355" (ZSM). 1 male, 2 females "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1564 Vial 16857" (ZSM). 1 female "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m", "-5,72090292 145,2714691 FIT-MW1200-

C-5/8-d09 / Plot 3 / P1508 Vial 14052-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m", "-5,72090292 145,2714691 FIT-MW1200-I-5/8-d09 / Plot 9 / P1556 Vial 17374" (ZSM). 1 female "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702", "FIT-MW1200-E-5/8-d09 / Plot 5 / P1524 Vial 16861-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1636 Vial 17324" (ZSM). 2 males "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1612 Vial 17292" (ZSM). 1 male "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1572 Vial 18837" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-O-5/8-d10 / Plot 15 / P1604 Vial 17325" (ZSM). 1 male "Ibisca Niugini, PNG 4–6.xi.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-F-6/8-d11 / Plot 6 / P1533 Vial 17257" (ZSM). 1 male "Ibisca Niugini, PNG 5–7.xi.2012 Mount Wilhelm 1200m", "-5,720873833 145,2694702 FIT-MW1200-K-6/8-d12 / Plot 11 / P1573 Vial 17082" (ZSM). 1 female "Ibisca Niugini, PNG 8–10.xi.2012 Mount Wilhelm 1200m -5,721022129 145,2703094 MW1200 / P1503 Vial 16995" (ZSM). 1 female "Ibisca Niugini, PNG 8–10.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1527 Vial 16879" (ZSM). 1 female "Ibisca Niugini, PNG 8–10.xi.2012 Mount Wilhelm 1200m -5,720873833 145,2694702 MW1200 / P1503 Vial 16995" (ZSM). 1 male, 1 female "Ibisca Niugini, PNG 9–11.xi.2012 Mount Wilhelm 1200m," "-5,720873833 145,2694702 FIT-MW1200-T-8/8-d16 / Plot 20 / P1647 Vial 17039-CODYTI" (ZSM). 4 females "Ibisca Niugini, PNG 9–11.xi.2012 Mount Wilhelm 1200m," "-5,720873833 145,2694702 FIT-MW1200-P-8/8-d16 / Plot 16 / P1615 Vial 17012-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 9–11.xi.2012 Mount Wilhelm 1200m," "-5,720873833 145,2694702 FIT-MW1200-M-8/8-d16 / Plot 13 / P1591 Vial 17035-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 1700m -5,79269238 145,235611 MW1700 / P1961 Vial 06629" (ZSM). **Eastern Highlands:** 3 male, 3 females "Papua New Guinea: Eastern Highlands, Bena Bridge, 1400m, 8.xii.2007, 06.10.781S 145.26.034E, Balke & Sagata (PNG 164)" (ZSM). **Simbu/Eastern Highlands:** 2 males "Papua New Guinea: Simbu/EHPr. Crater Mountain, Sera - Herowana, Wara Pima, 900 m, 15IX2002, Balke & Sagata (PNG 011)" (ZSM). 16 males "Papua New Guinea: Crater Mountain, Sera - Herowana, upper Oh River, 1200 m, 15IX2002, Balke & Sagata (PNG 012)" (NHMW, ZSM). 2 males, 4 females "Papua New Guinea: Crater Mountain, Sera - Herowana, Jau river, 1100m, 15IX2002, Balke & Sagata (PNG 013)" (ZSM). 12 males "Papua New Guinea: Simbu/EHPr. Crater Mountain, Sera - Herowana, Jau river, 1000 m, 15IX2002, Balke & Sagata (PNG 015)" (NHMW, ZSM). 1 male, 3 females "Papua New Guinea: Simbu / EHP, Crater Mountain, Sera - Herowana, Sima river, 1250m, 15IX2002, Balke & Sagata (PNG 016)" (ZSM). **Simbu:** 5 males "Papua New Guinea: Supa Haia, 1023m, 10.ix.2002, K.Sagata (WB1)" (NHMW, ZSM). 1 male "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 600m,

12IX2002, Balke & Sagata, (PNG 003)" (ZSM). 3 males "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 005)" (ZSM). 1 male "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 006)" (ZSM). 11 males, 14 females "Papua New Guinea: Simbu/EHPr. Crater Mountain, Wara Sera Station, 800 m, 14IX2002, Balke & Sagata (PNG 009)" (NHMW, ZSM). 12 males, 7 females "Papua New Guinea: Simbu/EHPr. Crater Mountain, Wara Sera Station, 800 m, 14IX2002, Balke & Sagata (PNG 10)", one male with additional labels "257 DNA M Balke" [green], "sp.17 SEM 19" (ZSM). 27 males, 31 females "Papua New Guinea: Crater Mountain, Wara Sera Station, 800 m, 14IX2002, Balke & Sagata (PNG 010)" (NHMW, ZSM). **Morobe:** 62 males, 27 females "PAPUA N.G.: Morobe Prov. E Pindiu, Kobau 24.4.1998, 1400 m, leg. A. Riedel" (NHMW, ZSM). 1 male "Papua New Guinea: Morobe, Pindiu, Sulemana, 850 m, 15.x.2009, 06.25.169S 147.32.11E, Inaho (08) (PNG 208)", "DNA M.Balke 3825" [green] (ZSM). 2 males "PNG: Huon Peninsula, Morobe Prov., Yus conservation area [5°53'54"S, 146°48'15"E], 1398m, 24.viii.2010, Bega", "DNA M. Balke 6531" [green text], "DNA M. Balke 6532" [green text] (ZSM). 6 females "PNG: Huon Peninsula, Morobe Prov., Yus conservation area (Y7), 1398m, 24.viii.2010, Huon, Bega" (ZSM). **Gulf:** 9 males, 8 females "Papua New Guinea: Gulf, Marawaka, nr Ande, 1000m, 10.xi.2006, 07.03.598S 145.44.375E, Balke & Kinibel (PNG 89)" (NHMW, ZSM).

Females of doubtful identity. Simbu: 27 females "Papua New Guinea: Supa Haia, 1023m, 10.ix.2002, K.Sagata (WB1)" (ZSM); these females are a mixture of three species: *E. bacchusi*, *E. warasera*, and *E. haia*. 5 females "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 600m, 12IX2002, Balke & Sagata, (PNG 003)" (ZSM); these females are a mixture of two species: *E. bacchusi* and *E. warasera*. 3 females "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 005)" (ZSM); these females are a mixture of three species: *E. bacchusi*, *E. warasera*, and *E. haia*. **Simbu/Eastern Highlands:** 3 females "Papua New Guinea: Simbu/EHPr. Crater Mountain, Sera – Herowana, Wara Pima, 900 m, 15IX2002, Balke & Sagata (PNG 011)" (ZSM). 20 females "Papua New Guinea: Crater Mountain, Sera - Herowana, upper Oh River, 1200 m, 15IX2002, Balke & Sagata (PNG 012)" (ZSM). 4 females "Papua New Guinea: Simbu/EHPr. Crater Mountain, Sera - Herowana, Jau river, 1000 m, 15IX2002, Balke & Sagata (PNG 015)" (ZSM). These females are a mixture of two species: *E. bacchusi* and *E. warasera*.

Diagnosis. For complete description, see Balke (1998: 326). Beetle small to medium-sized: TL-H 3.05–3.9 mm, oblong-oval; dorsally uniformly reddish to dark brown or with paler head and sides of pronotum; shiny, with very fine to distinct punctation and usually weakly impressed microreticulation; pronotum with distinct lateral bead (Fig. 16); male protarsomere 4 with anterolateral seta very long and thin, evenly curved, smaller than more laterally situated large seta; male protarsomere 5 ventrally with anterior band of more than 50 and posterior row of 8 relatively long setae (Fig. 22D); median lobe simple, evenly attenuated to broadly pointed apex in lateral and

ventral views; paramere very slightly concave on dorsal side and with long, dense, thin setae, situated along dorsal margin; proximal setae longer that subdistal, more distinct (Fig. 22A–C).

Variability. The species shows variability in size, colouration, how strongly impressed dorsal punctation and, more seldom, microreticulation, and slightly in shape of the apex of the median lobe (Fig. 24).

Affinities. From the species co-occurring in the same area (*E. craterensis* Shaverdo & Balke, 2014, *E. damantiensis* (Balke, 1998), *E. hintelmannae* (Shaverdo, Sagata & Balke, 2005), *E. sima*, *E. kobau* sp. nov. and two species of the *E. larsoni* group), *E. bacchusi* can be distinguished by its reddish dorsal colouration and shape and setation of the median lobe and paramere. The most similar (in body size and form and colouration) to *E. bacchusi* are *E. warasera* sp. nov. and *E. haia* sp. nov., which occur with it. Only males of these species can be clearly separated by shape and setation of the median lobe and paramere; and therefore, dorsal setae of the paramere are important: in *E. bacchusi*, proximal setae longer that subdistal, more distinct. For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Madang, Simbu, Eastern Highlands, Morobe and Gulf Provinces (Fig. 25). This is one of the most abundant species in the region.

6a. *Exocelina bacchusi herzogensis* Shaverdo & Balke, ssp. nov.

http://zoobank.org/7E252D3A-EF0B-4BDA-BC3E-C90D754BDB18
Figs 17, 23

Exocelina undescribed sp. MB1383: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Central Province, Woitape, 08°33.17'S, 147°15.48'E, 1500 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea: Central, Woitape, 1500m, i.2008, [08°] 33.178S 147 15.481E, Posman (PNG 167)", "DNA M.Balke 3401" [green] (ZSM). *Paratypes*: 1 male, 2 females with the same labels as the holotype (NHMW, ZSM). 1 male "Papua New Guinea: Morobe, Wagau, Herzog Mts., 1150m, 19.xi.2006, 06.51.067S 146.48.068E, Balke & Kinibel (PNG 102)", "DNA M.Balke 1383" [green] (ZSM).

Description. *Body size and form*: Beetle small: TL-H 3.4–3.6 mm, TL 3.8–4.0 mm, MW 1.85–2.0 mm (holotype: TL-H 3.6 mm, TL 4.0 mm, MW 2.0 mm), with oblong-oval habitus.

Colouration: Yellow reddish to brown. Head reddish brown to brown, dark brown posterior to eyes. Pronotum yellowish reddish, with small dark area on disc or brown, with paler sides. Elytra yellow reddish to brown. Head appendages and legs proximally yellowish, legs distally darker, reddish brown (Fig. 17). Teneral specimen yellowish.

Surface sculpture: Shiny dorsally, with very fine punctation and weakly impressed microreticulation. Elytral punctation and microreticulation finer then in nominotypical subspecies. Elytral punctation usually invisible.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 slightly truncate.

Male: Protarsomere 4 with anterolateral seta rather long and thing, evenly curved, smaller than more laterally situated large seta. Protarsomere 5 ventrally with anterior band of more than 60 and posterior row of ten relatively long setae (Fig. 23D). Abdominal ventrite 6 with 6–8 lateral striae on each side. Median lobe simple, evenly tapering towards apex in lateral and ventral views; in lateral view, apex elongate, thin, with slightly enlarged, rounded tip (Fig. 23A, B). Paramere as in Fig. 23C.

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Variability. Colouration of the specimens from Woitape distinctly paler, yellowish; the specimen form Wagau much darker, brown.

Affinities. From the nominotypical subspecies, it can be distinguished by shinier dorsal surface, shorter setae of male protarsomere 4, and by apex of the median lone elongate, thinner, with slightly enlarged tip. The further study is necessary to confirm the status of this taxon, which seems to replace the nominotypical subspecies in the Papuan Peninsula.

Distribution. Papua New Guinea: Morobe and Central Provinces (Fig. 25).

Etymology. The subspecies is named after Herzog Mts., where the subspecies was the first time discovered. The name is an adjective in the nominative singular.

7. *Exocelina erteldi* (Balke, 1998)

Figs 14, 20

Copelatus (*Papuadytes*) *erteldi* Balke, 1998: 330; Nilsson 2001: 76 (catalogue).
Papuadytes erteldi (Balke, 1998): Nilsson and Fery 2006: 56 (comb. nov.).
Exocelina erteldi (Balke, 1998): Nilsson 2007: 33 (comb. nov.).

Type locality. Indonesia: Papua Province: Pegunungan Bintang Regency, Borme, ca. 04°24'S, 140°25'E, 1200 m a.s.l.

Type material studied. *Holotype*: male "IRIAN JAYA Zentralmassive 140°25'E 04°24'S", "14./17.8.1992 Borme, 1900m leg. Balke (11)", "Copelatus erteldi Balke des. 1997" [red], "HOLOTYPUS" [red] (NHMW). *Paratypes*: 1 female with the same label as the holotype and additionally with a red label "Paratypus Copelatus erteldi Balke des. 1997" (NHMW). 54 males, 35 females "IRIAN JAYA Zentralmassive 140°25'E 04°24'S", "Borme, 1800m 16.8.1992 leg. Balke (12, 12 A)", one of the males with two additional labels "M.Balke 3273" [green] and "M.Balke 6404 DNA" [green text], an-

other male with an additional green label "M.Balke 3273" (CGW, NHMW). Note: in the original description (Balke 1998), number of specimens of the locality (12, 12 A) is erroneously given as "43 males, 46 females". 1 female "12./18.8.1992 Borme, 100m leg. Balke (7)", "Paratypus Copelatus erteldi Balke des. 1997", this paratyte does not belong to species of *E. erteldi* but to *E. bifida* Shaverdo et al. 2012.

Additional material. 1 male "IRIAN JAYA Zentralmassive 140°25'E 04°24'S", "Borme, 1800m 16.8.1992 leg. Balke (12, 12 A)", "Paratypus Copelatus fume Balke des. 1997" [red] (NHMW).

Diagnosis. For complete description, see Balke (1998: 330). Beetle small (TL-H 3.45–3.75 mm), oblong-oval; brown to piceous, usually with paler pronotal sides; dorsally more or less shiny, with fine but conspicuous punctation and weakly impressed microreticulation; pronotum with distinct lateral bead (Fig. 14); male protarsomere 4 with anterolateral seta thin, weakly curved, smaller than more laterally situated large seta; male protarsomere 5 ventrally with anterior band of ca. 70 and posterior row of 6 relatively long setae (Fig. 20D); median lobe in lateral view evenly attenuated to elongate, thin apex, which slightly pointed in ventral view; paramere slightly concave on dorsal side and with distinct, long, dense, uniform setae, situated along dorsal margin (Fig. 20A–C).

Affinities. The species can be distinguished from the species co-occurring in the same area (*E. ascendens*, *E. aipomek*, *E. takime*, the *E. ekari* group: *E. eme* Shaverdo and *E. bifida*, the *E. danae* group: *E. damantiensis* and *E. danae*, the *E. okbapensis* group: *E. ketembang*, *E. talaki*, and *E. okbapensis*, and all species of the *E. aipo* group) by body size and colouration, presence of pronotal bead, fine but conspicuous dorsal punctation, and shape and setation of its median lobe, paramere, and male protarsomere 4. For the affinities within the group, see the "Key".

Distribution. Indonesia: Papua Province: Pegunungan Bintang Regency, Borme (Fig. 25). The species is known only from the type material.

8. *Exocelina oiwa* Shaverdo & Balke, sp. nov.

http://zoobank.org/DE65A0BD-5EAE-457F-99EA-1AA47E8B1916
Figs 12, 18

Type locality. Papua New Guinea: Morobe Province, Aseki, Oiwa (a village about 100 km to the west of Bulolo), 7°18'00.0"S, 146°14'00.0"E, 1600–1700 m a.s.l.

Type material. *Holotype*: male "PAPUA N. G.: Morobe Prov. Aseki, Oiwa, 1600–1700 m, 11.–12.3.1998 leg. A. Riedel" (NHMW). *Paratypes*: 4 males, 2 females with the same labels as the holotype, one male and one female additionally with labels "SEM 19" (NHMW, ZSM).

Description. *Body size and form*: Beetle small: TL-H 3.3–3.5 mm, TL 3.7–3.95 mm, MW 1.85–1.95 mm (holotype: TL-H 3.5 mm, TL 3.95 mm, MW 1.95 mm), with oblong-oval habitus.

Colouration: Fast uniformly reddish brown. Head reddish brown, darker posterior eyes. Pronotum reddish brown, slightly darker on disc. Elytra reddish brown, sometimes slightly darker than pronotum. Head appendages and legs proximally yellowish, legs distally darker, reddish (Fig. 12).

Surface sculpture: Submatt dorsally, with strong and dense punctation and strongly impressed microreticulation. Head with dense and coarse punctation (spaces between punctures 0–1 times size of punctures); diameter of punctures equal to or larger than diameter of cells of microreticulation. Pronotum and elytra with finer and sparser punctation than on head, very distinct, more even on elytra. Pronotum and elytra with strongly impressed microreticulation; head with microreticulation stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate, but shiny. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter weak; more distinct on two last abdominal ventrites.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 broadly rounded or slightly truncate.

Male: Protarsomere 4 with anterolateral seta rather long and thin, evenly curved, equal to laterally situated large seta. Protarsomere 5 ventrally with anterior band of ca. 60 and posterior row of five relatively long setae (Fig. 18D). Abdominal ventrite 6 with 8–9 lateral striae on each side. Median lobe short, evenly tapering to apex in lateral and ventral views, very tip of apex thickened dorsally (Fig. 18A, B). Paramere as in Fig. 18D.

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Affinities. From the species co-occurring in the same area (from *E. danae*, *E. ekari*, *E. broschii*, and *E. ullrichi* groups), *E. oiwa* sp. nov. can be distinguished by its size, dorsal punctation and colouration, shape and setation of its median lobe and paramere, and thin, evenly curved anterolateral seta of the protarsomere 4. The species is especially similar to *E. aseki* sp. nov., from which it can be distinguished by shape of its median lobe. For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Morobe Province (Fig. 25).

Etymology. The species is named after Oiwa Village. The name is a noun in the nominative singular standing in apposition.

9. *Exocelina oksibilensis* Shaverdo, Surbakti, Warikar & Balke, sp. nov.
http://zoobank.org/26C2CDCD-463E-4E23-9D11-225EE70A292C
Figs 15, 21

Type locality. Indonesia: Papua Province, Pegunungan Bintang Regency, south from Ok Sibil, tributary Digul River 05°03'25.9"S, 140°43'21.1"E, 359 m a.s.l.

Type material. *Holotype*: male "Indonesia: Papua, S Ok Sibil, tributary Digul Riv, 359m, 9.vi.2018, -5,05718389 140,722535848617, Sumoked (Pap051)" (MZB). *Paratypes*: 4 males, 13 females with the same label as the holotype, 2 males with additional labels "6996" [green text], "7001" [green text] (KSP, MZB, ZSM).

Description. *Body size and form*: Beetle small: TL-H 3.05–3.35 mm, TL 3.5–3.7 mm, MW 1.7–1.85 mm (holotype: TL-H 3.35 mm, TL 3.7 mm, MW 1.85 mm), usually with oval, egg-shaped habitus.

Colouration: Reddish brown to brown. Head reddish brown to dark brown, paler anteriorly. Pronotum dark brown on disc and narrower or broader reddish on sides. Elytra reddish brown to dark brown, with reddish sutural lines. Head appendages and legs proximally yellowish, legs distally darker, reddish brown (Fig. 15).

Surface sculpture: Shiny dorsally, with fine punctation and weakly impressed microreticulation. Head with fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures equal to or smaller than diameter of cells of microreticulation. Pronotum and elytra with much finer and sparser punctation than on head, sometimes inconspicuous. Pronotum and elytra with weakly impressed microreticulation; head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter invisible; inconspicuous on two last abdominal ventrites.

Structures: Pronotum with narrow lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 slightly truncate.

Male: Protarsomere 4 with anterolateral seta rather long and thing, evenly curved, smaller than more laterally situated large seta. Protarsomere 5 ventrally with anterior band of more than 60 and posterior row of 4 relatively long setae (Fig. 21D). Abdominal ventrite 6 with 3–6 lateral striae on each side. Median lobe simple, evenly tapering to broadly pointed apex in lateral and ventral views (Fig. 21A, B). Paramere as in Fig. 21C.

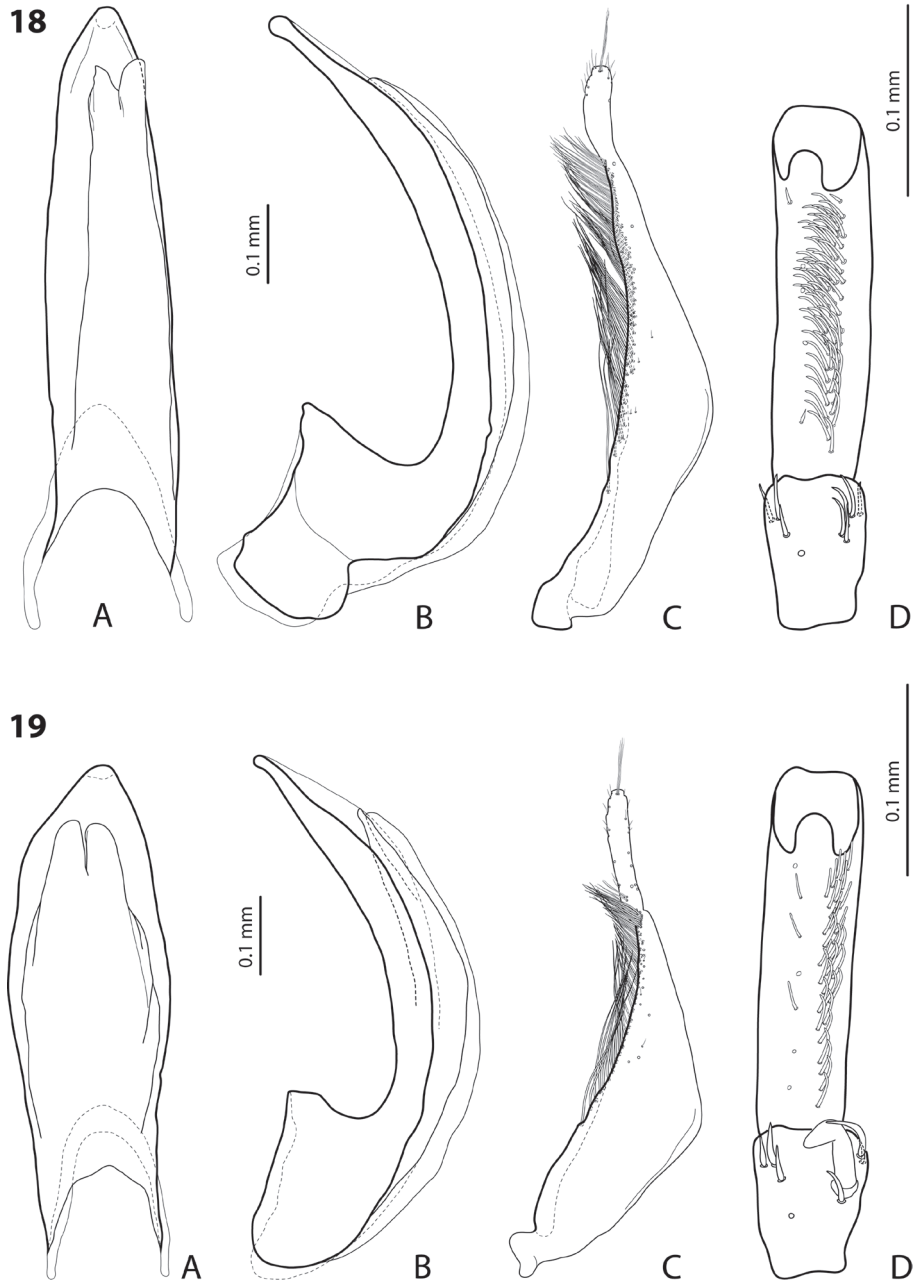
Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Affinities. The species is very similar to *E. bacchusi* in shape of the median lobe but can be distinguished from it by smaller size and egg-shaped habitus and shorter setae of male protarsomere 4. From the other species co-occurring in the same province (*E. ascendens*, *E. aipomek*, *E. takime*, the *E. ekari* group: *E. eme* Shaverdo and *E. bifida*, the *E. danae* group: *E. damantiensis* and *E. danae*, the *E. okbapensis* group: *E. ketembang*, *E. talaki* and *E. okbapensis*, and all species of the *E. aipo* group), it can be separated by body size and form, presence of pronotal bead, and the shape and setation of its median lobe, paramere, and male protarsomere 4. For the affinities within the group, see the "Key".

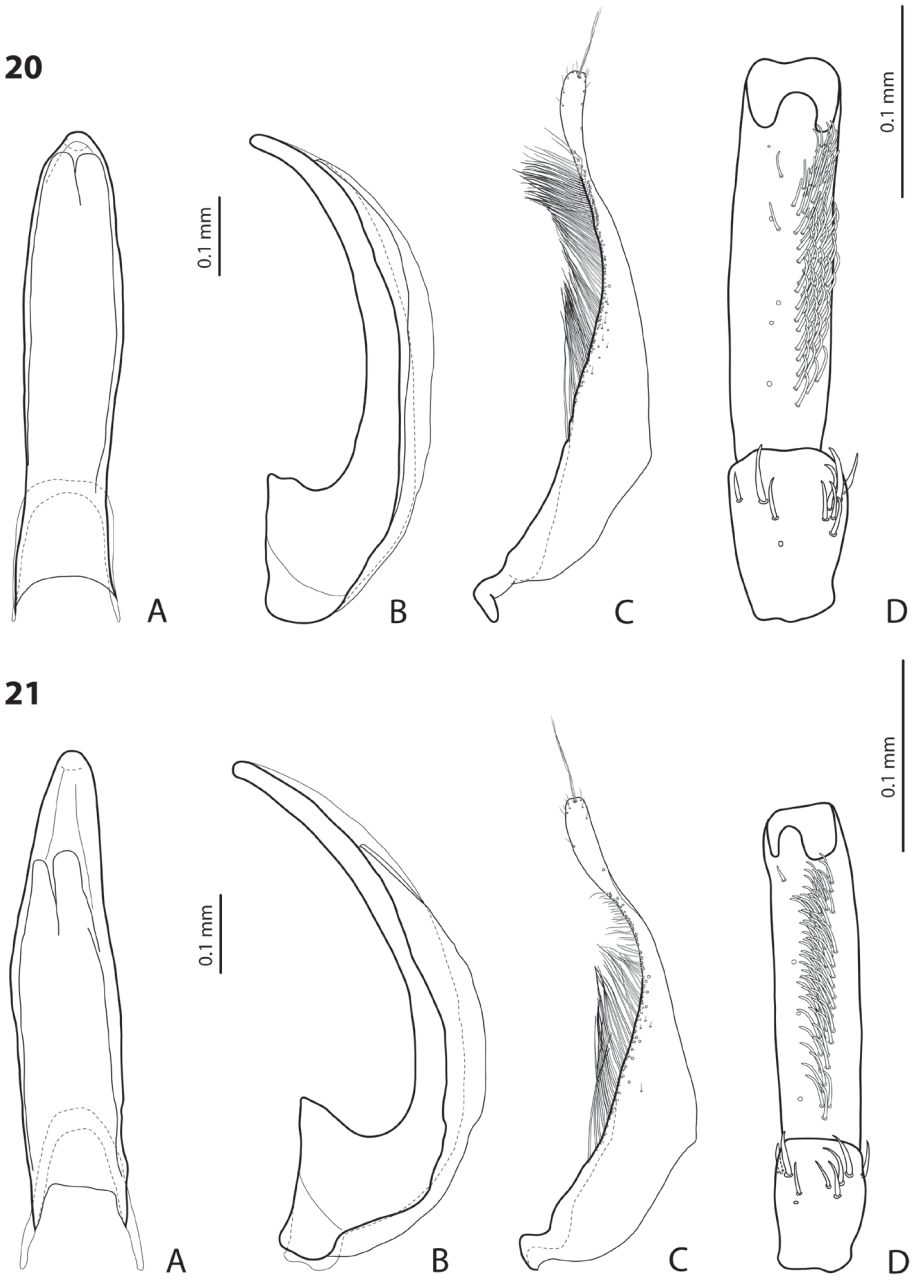
Distribution. Indonesia: Papua Province, Pegunungan Bintang Regency, Ok Sibil area (Fig. 25).

Etymology. The species is named after Ok Sibil River. The name is an adjective in the nominative singular.

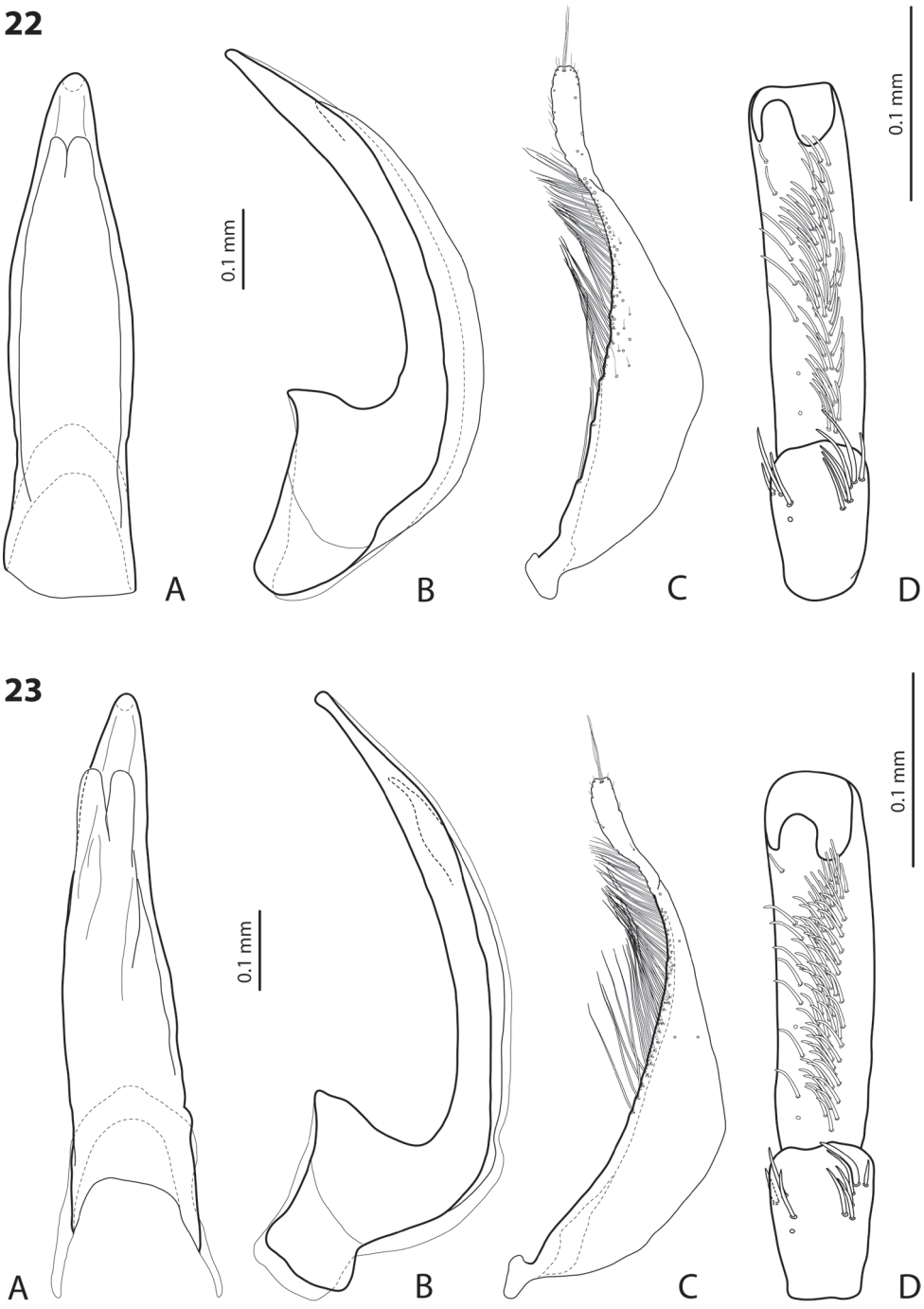
Figures 12–17. Habitus and colouration **12** *Exocelina oiwa* sp. nov. **13** *E. akameku* sp. nov. **14** *E. erteldi* (Balke, 1998) **15** *E. oksibilensis* sp. nov. **16** *E. bacchusi* (Balke, 1998) **17** *E. bacchusi herzogensis* sp. nov.



Figures 18, 19. 18 *Exocelina oiwa* sp. nov. **19** *E. akameku* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.



Figures 20, 21. 20 *Exocelina erteldi* (Balke, 1998) **21** *E. oksibilensis* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.



Figures 22, 23. 22 *Exocelina bacchusi* (Balke, 1998), paratype (Madang, Damanti) **23** *E. bacchusi herzogensis* ssp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

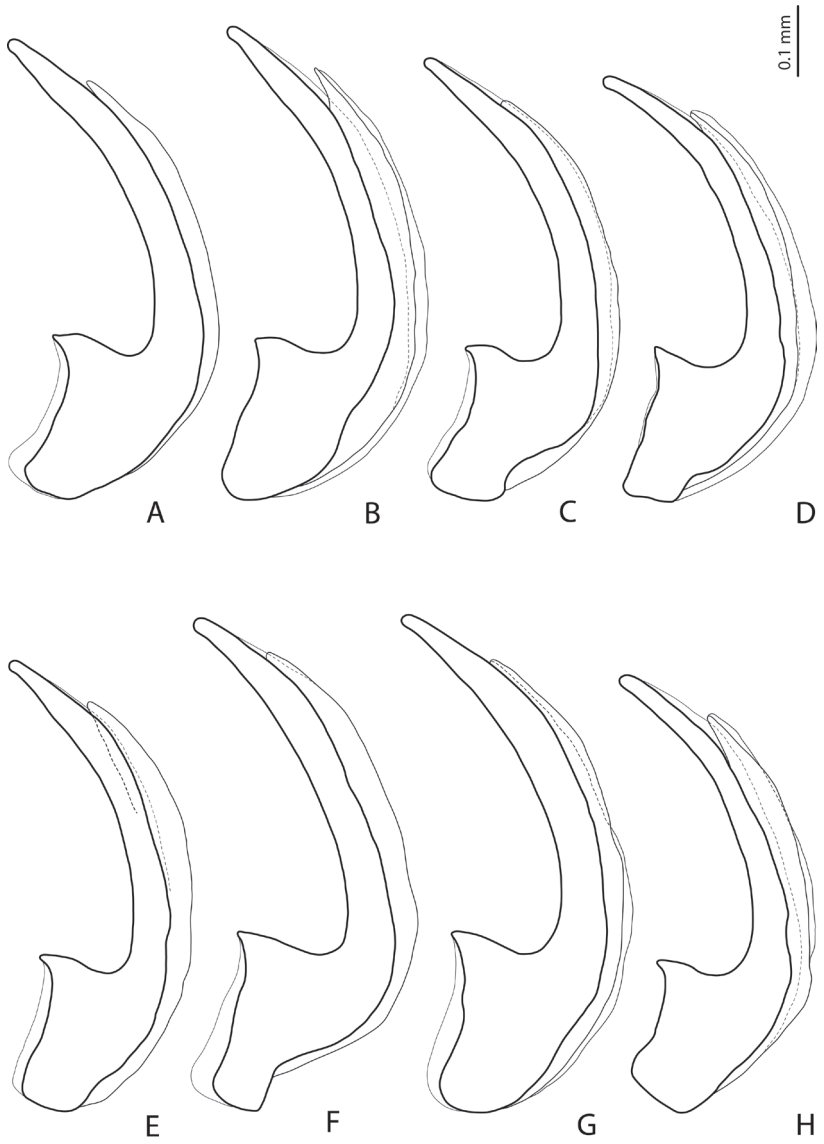


Figure 24. *Exocelina bacchusi* (Balke, 1998), median lobe in lateral view **A** Madang, Adelbet Mt **B** Madang, Bismarck Range **C** Madang, Wilhelm Mt **D** Simbu, Crater Mt **E** EHL, Bena **F** Morobe, Kobau **G** Morobe, Yus **H** Gulf, Marawaka.

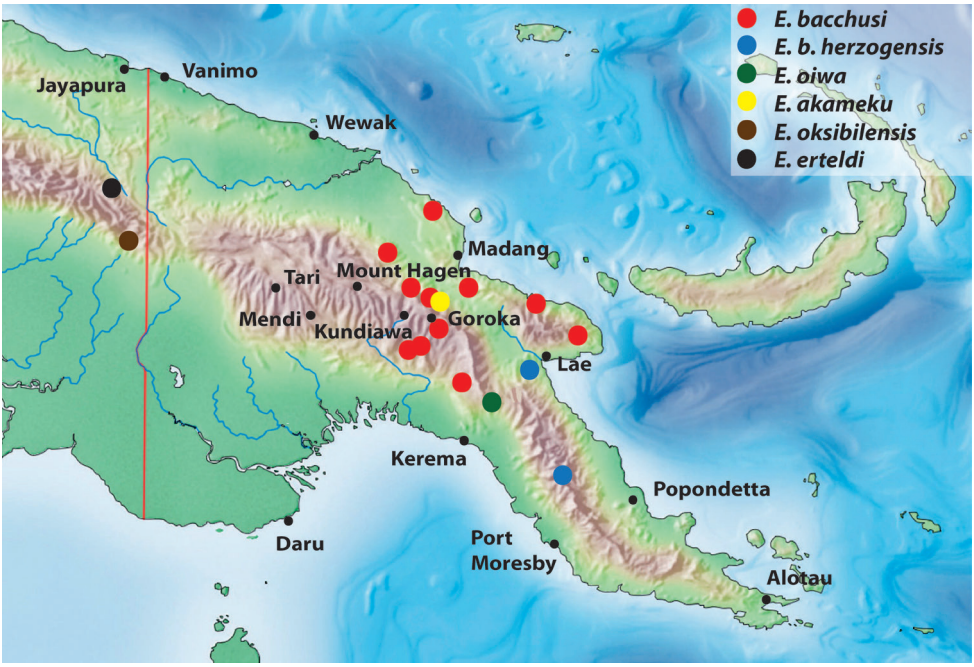


Figure 25. Map of the eastern part of New Guinea showing distribution of the species of the *E. bacchusi* group.

Key to the species of *Exocelina bacchusi* group

1 Beetle dorsally submatt, with strong and dense punctation and strongly impressed microreticulation (Fig. 12) ..... ***oiwa* sp. nov.**

– Beetle dorsally shiny, often with very weak punctation, invisible on elytra, and weakly impressed microreticulation **2**

2 Anterolateral seta of male protarsomere 4 hook-like, large, strongly curved (Fig. 19D) ..... ***akameku* sp. nov.**

– Anterolateral seta of male protarsomere 4 thin, long, slightly curved, equal to or smaller than more laterally situated large setae **3**

3 Median lobe with subparallel sides and short apex in ventral view; in lateral view, apex elongate. Setae of paramere uniform, distinct (Fig. 20) ..... ***erteldi* (Balke, 1998)**

– Median lobe more or less evenly tapering to apex in ventral and lateral views. Proximal setae of paramere usually longer, sometimes also much stronger, than subdistal **4**

4 Beetle usually smaller, TL-H 3.05–3.35 mm (Fig. 15), oval, egg-shaped. Anterolateral seta of male protarsomere 4 shorter and thicker (Fig. 21D). Median lobe and paramere as in Fig. 21A–C ..... ***oksibilensis* sp. nov.**

– Beetle usually larger, TL-H 3.05–3.9 mm (Figs 16, 17), elongate. Anterolateral seta of male protarsomere 4 very long and thing (Fig. 22D). Median lobe and paramere as in Fig. 22A–C **5**

5 Beetle with stronger elytral microreticulation and more distinct punctation, duller (Fig. 16). Apex of median lobe shorter, thicker (Fig. 22A, B) .... ***bacchusi* (Balke, 1998)**

– Beetle with weaker elytral microreticulation and usually invisible elytral punctation, shinier (Fig. 17). Apex of median lobe more elongate, thinner (Fig. 23A, B)..... ***bacchusi herzogensis* ssp. nov.**

Exocelina jaseminae group

This group is characterised by fine to coarse dorsal punctation; pronotum with distinct lateral bead; median lobe of aedeagus without setation; in ventral view, with distinctly concave apex forming two apical lobes; in lateral view, apex tip prolongated into characteristic "nose"; apexes of ventral sclerites of median lobe almost equal or slightly unequal; paramere without distinct notch but slightly concave on dorsal side, its subdistal part with dense, strong setae, proximal setae inconspicuous.

10. *Exocelina aseki* Shaverdo & Balke, sp. nov.

http://zoobank.org/6253C250-9E5C-454C-86FD-ED376372D449
Figs 21–23, 49

Type locality. Papua New Guinea: Morobe Province, Aseki, Oiwa, ca. 07°21'01.5"S, 146°11'38.4"E, 1600–1700 m a.s.l.

Type material. *Holotype*: male "PAPUA N. G.: Morobe Prov. Aseki, Oiwa, 1600–1700 m, 11.–12.3.1998 leg. A. Riedel", "SEM 19" (NHMW).

Description. *Body size and form*: Beetle small: TL-H 3.4 mm, TL 3.8 mm, MW 1.8 mm, with oblong-oval habitus.

Colouration: Reddish brown. Head reddish brown. Pronotum reddish brown, dark brown on disc and almost yellowish on lateral sides. Elytra brown, with reddish sutural lines. Head appendages and legs proximally yellowish, legs distally darker, reddish (Fig. 26).

Surface sculpture: Submatt dorsally, with strong and dense punctation and strongly impressed microreticulation. Head with dense and coarse punctation (spaces between punctures 0–1 times size of punctures); diameter of punctures equal to or larger than diameter of cells of microreticulation. Pronotum and elytra with finer and sparser punctation than on head, very distinct, more even on elytra. Pronotum and elytra with strongly impressed microreticulation; head with microreticulation stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate, but shiny. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter weak; more distinct on two last abdominal ventrites.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process

lanceolate, relatively broad, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 broadly rounded.

Male: Protarsomere 4 with anterolateral seta very long and thin, evenly curved, in size equal to more laterally situated large seta. Protarsomere 5 ventrally with anterior band of ca. 80 and posterior row of ca. 16 relatively long setae, which mixed up medially (Fig. 30D). Abdominal ventrite 6 with 4–6 lateral striae on each side. Median lobe in lateral view with apical lobes distinct but shallow, slightly rounded, "nose" elongate, large (Fig. 30A, B). Paramere as in Fig. 30C.

Female: Unknown.

Affinities. From the species co-occurring in the same area (from *E. danae*, *E. ekari*, *E. broschii*, and *E. ullrichi* groups), *E. aseki* sp. nov. can be distinguished by its size, dorsal punctation and colouration, shape and setation of its median lobe and paramere, and thin anterolateral seta of the male protarsomere 4. The species is especially similar to *E. oiwa* sp. nov., from which it can be distinguished by shape of its median lobe. For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Morobe Province (Fig. 34).

Etymology. The species is named after Aseki Village. The name is a noun in the nominative singular standing in apposition.

11. *Exocelina jaseminae* (Balke, 1998)

Figs 27, 31

Copelatus (*Papuadytes*) *jaseminae* Balke, 1998: 331; Nilsson 2001: 77 (catalogue).
Papuadytes jaseminae (Balke, 1998): Nilsson and Fery 2006: 56 (comb. nov.).
Exocelina jaseminae (Balke, 1998): Nilsson 2007: 33 (comb. nov.).
Exocelina jaseminae MB1382: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Morobe Province, Herzog Range, Wagau (Vagau), ca. 06°48'S, 146°48'E, ca. 1300 m a.s.l.

Type material studied. *Holotype*: male "Stn. No. 150", "NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4–17.i.1965", "M. E. Bacchus. B. M. 1965-120", "HOLOTYPUS" [red], "Copelatus jaseminae sp. nov. Balke des. 1997" [red] (BMNH). *Paratypes*: 2 males, 3 females with the same label as the holotype and additionally with a red label "Paratypus Copelatus jaseminae sp.n. Balke des. 1997", one of the males with an additional label "measured J. Parkin 85" (BMNH, NHMW). 1 male with the same label as the holotype, the red paratype label missing (BMNH).

Additional material. Morobe: 1 male "Stn. No. 149A", "NEW GUINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000ft. 4–17.i.1965", "M. E. Bacchus. B. M. 1965-120", "Paratypus Copelatus monae sp.n. Balke des. 1997" [red], "Exocelina jaseminae (Balke) det. H.Shaverdo 2014" (BMNH). 2 males "Papua New Guinea: Morobe, Wagau, Herzog Mts., 1150m, 19.xi.2006, 06.51.067S 146.48.068E, Balke & Kinibel (PNG 102)", one male with an additional green label "DNA M.Balke 1382" (ZSM). 1 male, 2 females

"Papua New Guinea: Morobe, Wagau, Herzog Mts., 1150m, 19.xi.2006, 06.51.067S 146.48.068E, Balke & Kinibel (PNG 103)" (ZSM). 2 males "Papua New Guinea: Gulf [sic!], Menyamya, Mt Inji 1700m, 14.xi.2006 nr 07.14.813S 146.01.330E Balke & Kinibel (PNG 96)" (ZSM). 9 males "PAPUA N. G.: Morobe Prov. Aseki, Oiwa, 1600–1700 m, 11.–12.3.1998 leg. A. Riedel" (NHMW). 6 males, 2 females "Papua New Guinea: Gulf [Morobe], Marawaka, Andakombe towards Morobe, 1100m, 12.xi.200, 07.09.766S, 145.46.333E, Balke & Kinibel (PNG 92)" (NHMW, ZSM). **Eastern Highlands:** 38 males, 38 females "Papua New Guinea: Eastern Highlands, Marawaka, Ande, 1700m, 8.xi.2005, 07.01.697S 145.49.807E, Balke & Kinibel (PNG 86)", one male with an additional green label "DNA M.Balke 1365" (NHMW, ZSM). 49 males, 40 females "Papua New Guinea: Eastern Highlands, Marawaka, Ande, 1700–1800m, 9.xi.2006, 07.01.697S 145.49.807E, Balke & Kinibel (PNG 87)" (NHMW, ZSM).

Diagnosis. For complete description, see Balke (1998: 331). Beetle medium-sized: TL-H 3.55–4.1 mm; oblong-oval; brown to dark brown, with reddish to reddish brown pronotal sides or pronotum and often head; shiny, with very fine, on elytra often almost invisible punctation and weakly impressed microreticulation; pronotum with lateral bead (Fig. 27); male protarsomere 4 with anterolateral seta thin, evenly curved, smaller than or equal to more laterally situated large seta; male protarsomere 5 ventrally with anterior band of more than 60 and posterior row of 13–15 relatively long setae (Fig. 31D); median lobe in lateral view with apical lobes distinctly developed and rounded, "nose" small but distinct; paramere slightly concave on dorsal side and with long, dense, thin setae, situated along dorsal margin distinctly divided to dense and strong subdistal setae and sparser proximal ones, setae in middle short and fine (Fig. 31A–C).

Affinities. In the area of its distribution, *E. jaseminae* co-occurs with numerous species of the *E. ekari*, *E. ullrichi*, *E. broschii*, and *E. danae* groups. From them, this species can be distinguished by its size, dorsal colouration, surface sculpture, simple male antennae, presence of pronotal bead, and mainly by the shape of its median lobe. In its external appearance, *E. jaseminae* is especially similar to *E. monae* (Balke, 1998), from which can be distinguished by the shape of its median lobe. For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Eastern Highlands and Morobe Provinces (Fig. 34).

12. *Exocelina kailaki* Shaverdo & Balke, sp. nov.

http://zoobank.org/1C4730A9-D83B-4A8F-B4AB-99591F7E99DD
Figs 28, 32

Exocelina undescribed sp. MB3409: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Central Province, Kailaki, 09°24.134'S, 147°33.521'E, 827 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea: Central, Moroka area, Kailaki, 827 m, 26.x.2009, 9.24.134S 147.33.521E, Sagata (PNG225)" (ZSM). *Paratypes*:

14 males, 27 females with the same label as the holotype (NHMW, ZSM). 3 males, 5 females "Papua New Guinea Central, Moroka, Kailaki Wareaga, 760m, 27x2009 9.25.424S 147.31.068E Sagata (PNG227)" (ZSM). 1 male "Stn. No. 200B", "PAPUA: Musgrave River, Sogeri Plateau, Nr. Pt. Moresby 16.iii.1965", "M.E. Bacchus. B.M. 1965-120" (BMNH). 15 males, 16 females "Papua New Guinea: Central, Myola, 1110m, i.2008, 09 12.630S 147 31.880E, Posman (PNG 177)", one male with an additional green label "DNA M.Balke 3409" (NHMW, ZSM). 7 males, 6 females "Papua New Guinea: Central, Kokoda Trek, 1390m, i.2008, [09°] 00.338S 147 44.252E, Posman (PNG 173)" (NHMW, ZSM). 1 male "Papua New Guinea: Central, 755m, 28.x.2009 S9 25 47 5 E147 32 59.1, Sagata (PNG229)" (ZSM).

Description. *Body size and form*: Beetle small: TL-H 3.1–3.85 mm, TL 3.45–4.35 mm, MW 1.7–2.05 mm (holotype: TL-H 3.4 mm, TL 3.75 mm, MW 1.85 mm), with oblong-oval habitus.

Colouration: Piceous, with paler sides of pronotum and head anteriorly. Head reddish brown to dark brown, paler anteriorly. Pronotum dark brown, to piceous on disc and to reddish on sides. Elytra uniformly dark brown to piceous. Head appendages and legs proximally yellowish to reddish, legs distally darker, reddish brown (Fig. 28). Teneral specimen paler, brown to reddish brown with to yellowish pronotum and head.

Surface sculpture: Shiny dorsally, with extremely fine, sparse punctation and weakly impressed microreticulation. Head with fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with much finer and sparser punctation than on head, very inconspicuous. Punctation on elytra invisible. Pronotum and elytra with weakly impressed microreticulation; head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles. Punctation on venter invisible; inconspicuous on two last abdominal ventrites.

Structures: Pronotum with narrow lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 truncate.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior narrow band of 26 setae and posterior row of six relatively long setae (Fig. 32D). Abdominal ventrites 1–3 with long strioles, abdominal ventrites 4–6 without strioles or with 1–2 small lateral strioles on each side. Median lobe with apical lobes weakly developed, not rounded, truncate in lateral view, "nose" usually indistinct (Fig. 32A, B). Paramere as in Fig. 32C.

Female: Without evident differences in external morphology from males, except for not modified protarsi. Abdominal ventrites 1–2 with strioles, abdominal ventrites 3–6 without strioles.

Variability. Shape of apex of the medial lobe varies. In some specimens, especially from Myola, it is not clearly truncate in lateral view but very slightly concave and, due to that, the "nose" is more distinct.

Affinities. *Exocellina kailaki* sp. nov. can be distinguished from the species of the *E. danae* group, *E. nomax* and *E. pulchella* sp. nov., co-occurring in the same area by its size, dorsal colouration and punctation, and shape and setation of its median lobe and paramere. For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Central Province (Fig. 34).

Etymology. The species is named after Kailaki Village. The name is a noun in the nominative singular standing in apposition.

13. *Exocelina pseudojaseminae* Shaverdo & Balke, sp. nov.

http://zoobank.org/EE9EC355-5082-49BA-9A0B-563702855B0F
Figs 29, 33

Type locality. Papua New Guinea: Central Province, Kokoda Track, 09°14.34'S, 147°40.54'E, 1400 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea: Central, Kokoda Trek, 1400m, i.2008, [09°] 14.339S 147 40.538E, Posman (PNG 171)" (ZSM). *Paratypes*: 3 males, 2 females with the same label as the holotype (NHMW, ZSM).

Description. *Body size and form*: Beetle medium-sized: TL-H 3.4–3.85 mm, TL 3.8–4.25 mm, MW 1.8–2.1 mm (holotype: TL-H 3.65 mm, TL 4.0 mm, MW 1.95 mm), with oblong-oval habitus.

Colouration: Brown to dark brown, with paler sides of pronotum and head. Head reddish brown, dark brown posterior to eyes. Pronotum reddish brown to brown, with reddish sides. Elytra brown to dark brown, sometimes with weak reddish sutural lines. Head appendages and legs proximally yellowish to reddish, legs distally darker, reddish brown (Fig. 29).

Surface sculpture: More or less shiny dorsally, with fine but distinct punctation and distinctly impressed microreticulation. Head with coarse and dense punctation (no spaces between punctures or spaces 1–2 times size of punctures); diameter of punctures equal to diameter of cells of microreticulation. Pronotum with much finer and sparser punctation than on head. Elytra with distinct punctation, slightly finer and sparser than on pronotum. Pronotum and elytra with weakly or more strongly impressed microreticulation; head with microreticulation stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles. Abdominal ventrites with strioles and very fine, sparse punctation.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 slightly truncate.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of more than 60 and posterior band of ca. 30 relatively long setae, which connected approximately in middle (Fig. 33D). Abdominal ventrite 6 with 1–4 lateral strioles on each side. Median lobe with apical lobes very strongly developed, rounded in lateral view, "nose" small but distinct (Fig. 33A, B). Paramere as in Fig. 33C.

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrites 5 and 6 without strioles.

Affinities. *Exocellina pseudojaseminae* sp. nov. can be distinguished by its size, dorsal colouration and punctation, shape and setation of its median lobe and paramere from the species of the *E. danae* group (*E. nomax* and *E. pulchella* sp. nov.) co-occurring in the same area. In its external appearance and shape of the median lobe, *E. pseudojaseminae* is very similar to *E. jaseminae* but it has more strongly developed apical lobes of the median lobe and much larger, hook-like anterolateral seta of the male protarsomere 4. For further affinities within the group, see the "Key".

Distribution. Papua New Guinea: Central Province (Fig. 34).

Etymology. The species was mistaken for *E. jaseminae* due to their similarity in general appearance and shape of the median lobe. The name is a noun in the nominative singular standing in apposition.

Key to the species of *Exocelina jaseminae* group

1 Beetle dorsally submatt, with strong and dense punctation and strongly impressed microreticulation (Fig. 26) ..... ***aseki* sp. nov.**

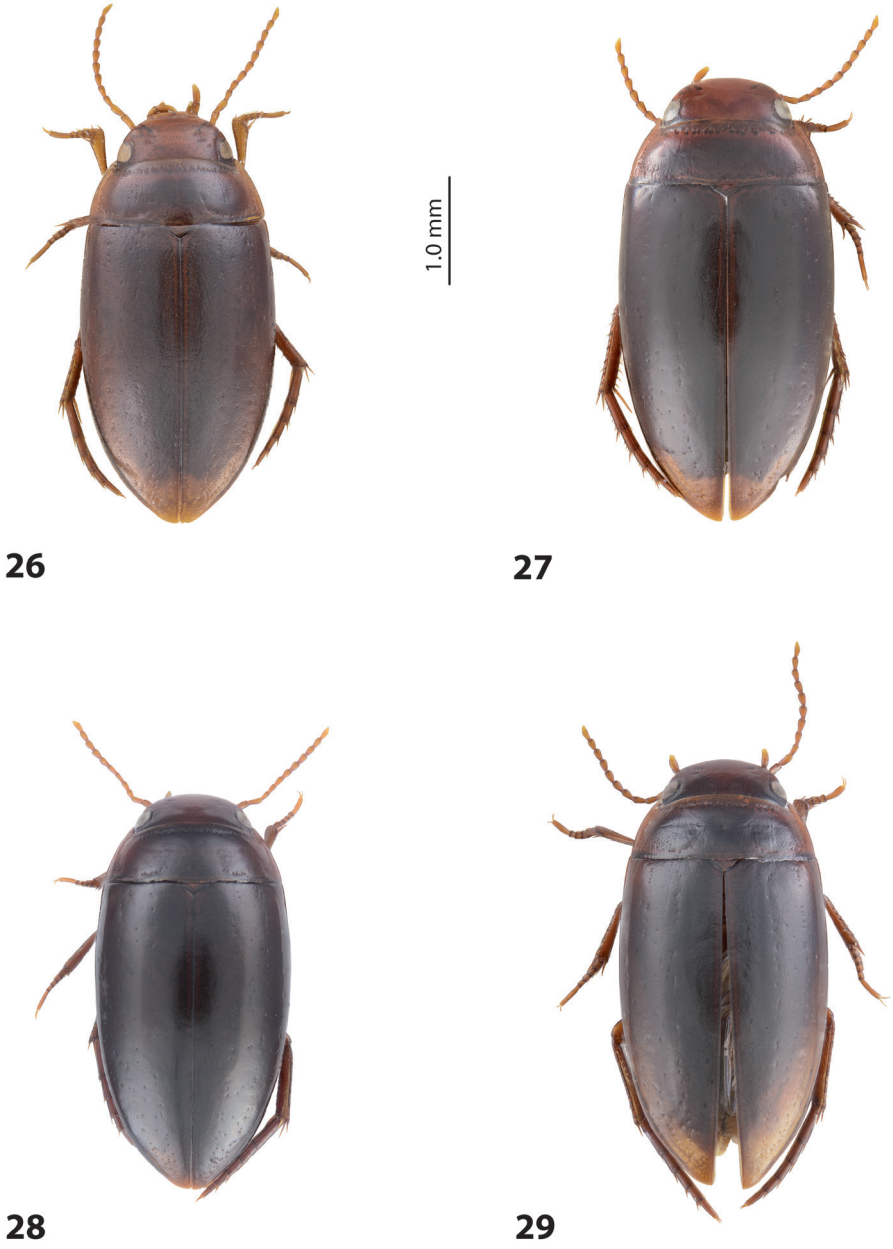
– Beetle dorsally shiny, with very weak punctation, often invisible on elytra, and weakly impressed microreticulation (e.g., Fig. 27) **2**

2 Anterolateral seta of male protarsomere 4 thin, slightly curved, equal to or smaller than more laterally situated large setae (Fig. 31D). Median lobe and paramere as in Fig. 31A, C..... ***jaseminae* (Balke, 1998)**

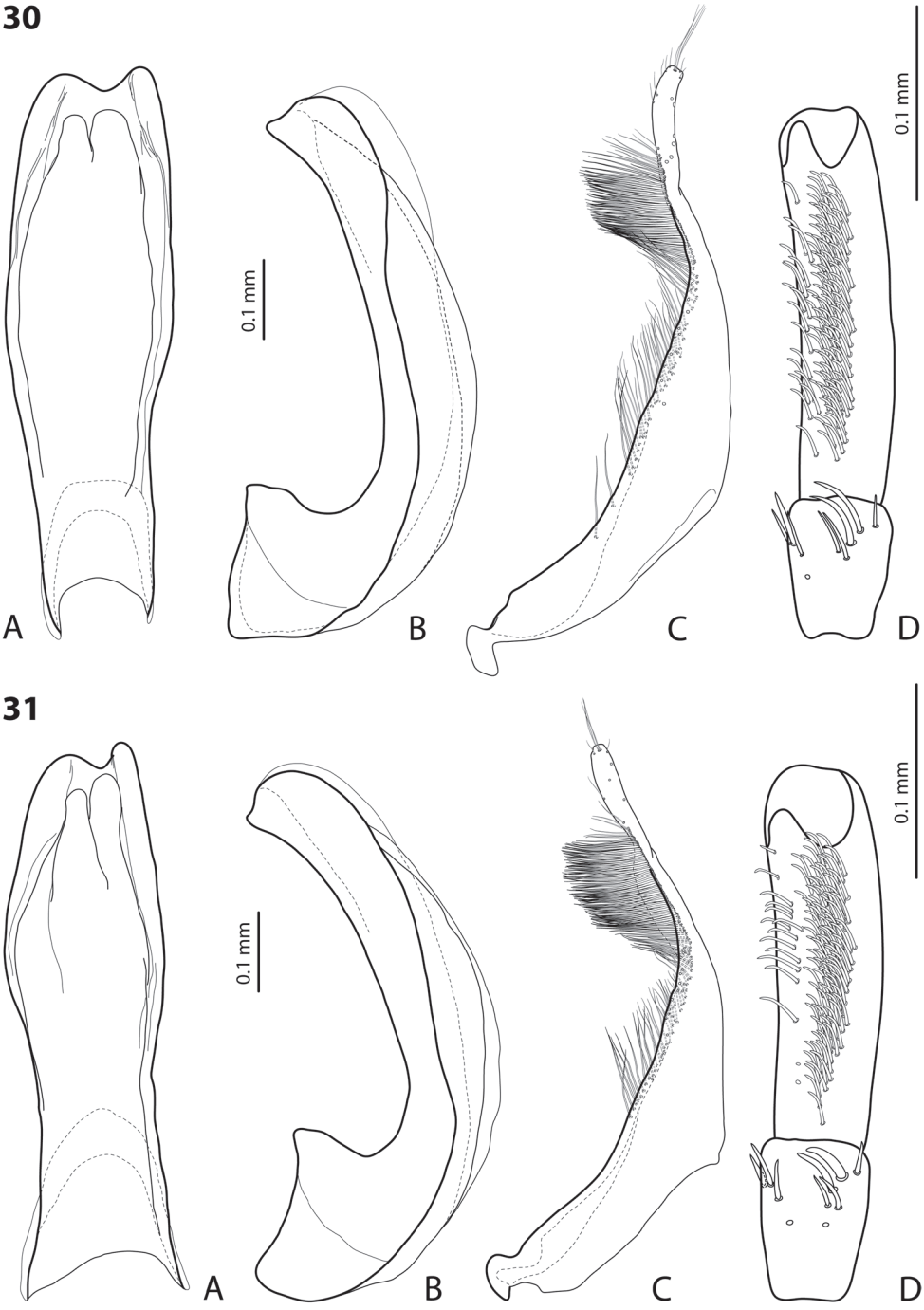
– Anterolateral seta of male protarsomere 4 hook-like, large, strongly curved **3**

3 Apical lobes of median lobe weak, truncate in lateral view, "nose" indistinct (Fig. 32B). Paramere as in Fig. 32C. Beetle smaller, TL-H 3.1–3.85 mm (Fig. 28)..... ***kailaki* sp. nov.**

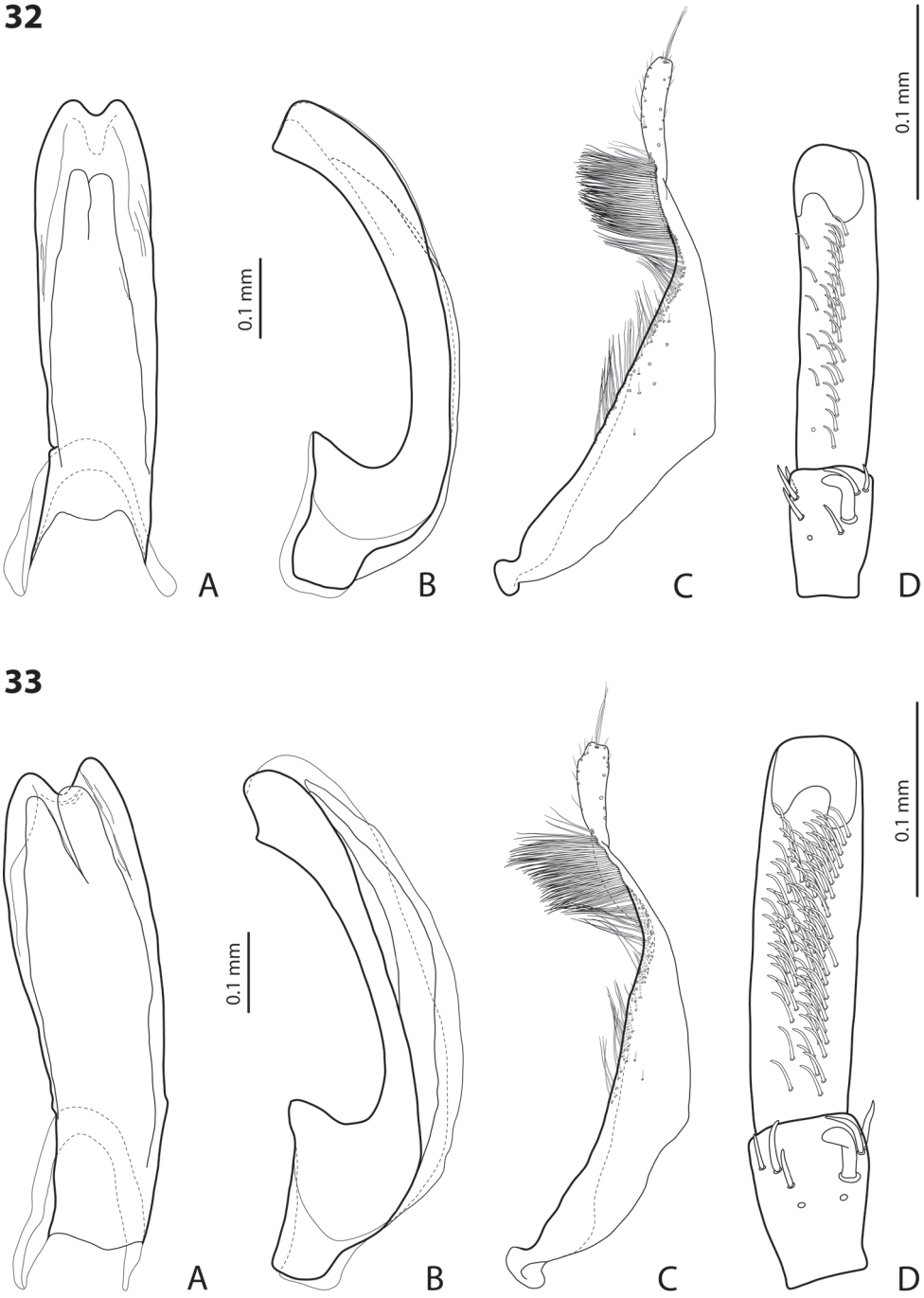
– Apical lobes of median lobe strong, rounded in lateral view, "nose" distinct (Fig. 33B). Paramere as in Fig. 33C. Beetle larger, TL-H 3.4–3.85 mm (Fig. 29)..... ***pseudojaseminae* sp. nov.**



Figures 26–29. Habitus and colouration **26** *Exocelina aseki* sp. nov. **27** *E. jaseminae* (Balke, 1998) **28** *E. kailaki* sp. nov. **29** *E. pseudojaseminae* sp. nov.



Figures 30, 31. 30 *Exocelina aseki* sp. nov. **31** *E. jaseminae* (Balke, 1998) **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.



Figures 32, 33. 32 *Exocelina kailaki* sp. nov. **33** *E. pseudojaseminae* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

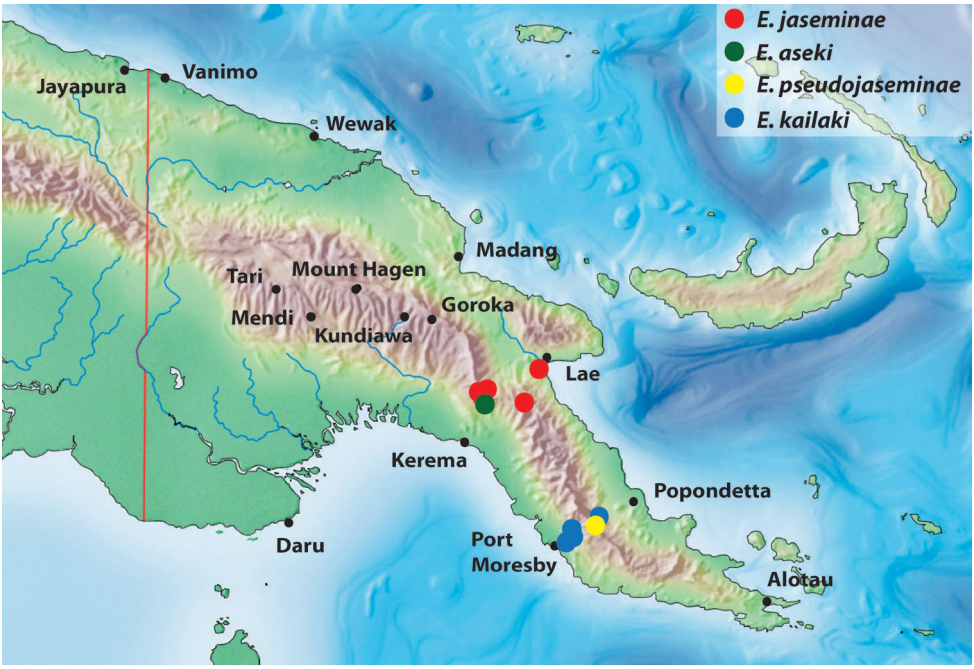


Figure 34. Map of the eastern part of New Guinea showing distribution of the species of the *E. jaseminae* group.

Exocelina larsoni group

This group is characterised by fine and sparse dorsal punctation; pronotum with very narrow lateral bead; median lobe of aedeagus with or without setation, very broad, robust, with sides strongly thickened; in ventral view, almost parallel-sided, with slight median constriction; apexes of ventral sclerites of median lobe very unequal: right one much longer than left one; paramere slightly concave on dorsal side and with long and dense subdistal and inconspicuous proximal setae.

14. *Exocelina larsoni* (Balke, 1998)

Figs 35, 40

Copelatus (*Papuadytes*) *larsoni* Balke, 1998: 332; Nilsson 2001: 77 (catalogue).
Papuadytes larsoni (Balke, 1998): Nilsson and Fery 2006: 56 (comb. nov.).
Exocelina larsoni (Balke, 1998): Nilsson 2007: 34 (comb. nov.).
Exocelina larsoni MB1299: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Madang Province, Baiteta, 05°01'00"S, 145°45'00"E, ca. 700 m a.s.l.

Type material studied. *Paratypes*: 2 males "PAPUA NEW GUINEA Baiteta March 13, 1991 D. J. Larson" (NHMW). Note: According to the original description (Balke 1998), the holotype is deposited in the collection of D. Larson and is in the Australian National Insect Collection now. The holotype was not studied since the species is very characteristic and two paratypes from the same locality were examined.

Additional material. Madang: 7 males, 2 females "Papua New Guinea: Madang Province, Wanang village, ca 110 m, 20.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-13)" (NHMW, ZSM). 4 males, 5 females "Papua New Guinea: Madang Province, Wanang village env., Wanang conservation area, 250 m, 21.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-20)" (NHMW, ZSM). 1 male "Papua New Guinea: Madang Province, Wanang village env., Wanang conservation area, 250 m, 22.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-24)" (NHMW). 1 female "Papua New Guinea: Madang Province, Wanang village env., Wanang conservation area, 250 m, 22.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-31)" (NHMW). 16 males, 4 females "Papua New Guinea: Madang Province, Wanang village env., Wanang conservation area, 250 m, 23.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-33)" (NHMW, ZSM). 8 males, 11 females "Papua New Guinea: Madang Province, Wanang village env., Wanang conservation area, 250 m, 23.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-37)" (NHMW, ZSM). 2 males, 1 female "Papua New Guinea: Madang Province, Wanang village env., Wanang conservation area, 250 m, 24.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-39)" (NHMW). 33 males, 3 females "Papua New Guinea: Madang Province, Wanang village env., Wanang conservation area, 250 m, 25.ix.2013, 05.15.458S 145.02.389E, David Boukal (PNG2013-44)" (NHMW, ZSM). 4 males, 1 female "V.Kolář Lgt. Papua New Guinea Wanang III 4–20.7.2013" (NHMW). 1 female "Ibisca Niugini, PNG 18–20.xi.2012 Wanang -5,227670193 145,0797424", "FIT-WAN-G-1/8-d01 / Plot 7 / P0596 Vial 22305-CODYTI" (ZSM). 1 male "Ibisca Niugini, PNG 20–22.xi.2012 Wanang -5,227670193 145,0797424", "FIT-WAN-P-2/8-d04 / Plot 16 / P0669 Vial 22273-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 24–26.xi.2012 Wanang -5,227670193 145,0797424", "FIT-WAN-H-4/8-d07 / Plot 8 / P0607 Vial 17640-CODYTI" (ZSM). 1 male "Ibisca Niugini, PNG 30.x.–2.xii.2012 Wanang -5,227670193 145,0797424", "FIT-WAN-L-7/8-d14 / Plot 12 / P0642 Vial 17744-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 2–4.xii.2012 Wanang FIT-WAN-D-8/8-d15 / Plot 4 / P0579 Vial 17568-CODYTI" (ZSM). 3 males "Papua New Guinea: Madang, below Bundi, 500 m, 26.IX.2002 Balke & Sagata (PNG 023)", one of them with an additional green label "269 DNA M Balke" and "sp 24 SEM 19" (ZSM). 5 males, 3 females "Papua New Guinea: Madang, Brahmin, 150 m, 26.IX.2002 Balke & Sagata (PNG 024)", two of males with additional green labels "274 DNA M Balke", "275 DNA M Balke" (NHMW, ZSM). 1 male "Papua New Guinea: Madang, Adalbert [sic!] Mts., Keki, 850m, 4.v.2006, nr 04.42.300S 145.25.089E, Manaono leg. (PNG 52)" (ZSM). 2 males, 5 females "Papua New Guinea: Madang, Adalbert [sic!] Mts., creek nr Keki, 790m, 28.xi.1994, 04.42.300S 145.25.089E, Binatang Boys leg. (PNG 53a)"

(ZSM). 1 male, 1 female "Papua New Guinea: Madang, Adalbert Mts., Keki to Sewan, 650m, 7.v.1994, 04.41.802S 145.25.460E, Balke (PNG 54)", male with an additional green label "DNA M.Balke 1299" (ZSM). 16 males, 8 females "Papua New Guinea: Madang, Usino, 260m, 15.iii.2007, 05.31.125S 145.25.316E, Kinibel (PNG 158)", one male with an additional green label "DNA M. Balke 3307" (NHMW, ZSM). 1 male, 1 female "Papua New Guinea: Madang, Mt. Tapo, 180 m, ii.2008 5 24.11.00 S 145 36 17 16 E, BRC leg. (PNG 178)" (ZSM). 4 males, 8 females "Papua New Guinea: Madang, Wannang, 270m 31.x.2008, 05.15.458S 145.02.389E, Posman, (PNG187)" (ZSM). 17 males, 25 females "Papua New Guinea: Madang, Wannang, 230m 3.x.2008, 05.17.235S 145.06.160E, Posman (PNG188)", three males additionally with green labels "DNA M.Balke 3763", "DNA M.Balke 3767", "DNA M.Balke 3768" (NHMW, ZSM). 2 males "Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 250–500m, 25.xi.2006, nr 05.47.026S 145.24.131E, Balke & Kinibel (PNG 115)", one of them with an additional green abel "DNA M.Balke 1363" (ZSM). 13 males, 22 females "Papua New Guinea: Madang, Keki, Adalbert Mts., 500m, 29.xi.1994, 04.43.058S 145.24.437E, Balke & Kinibel (PNG 118)" (NHMW, ZSM). 38 males, 56 females "Papua New Guinea: Madang, Keki, Adalbert Mts., 400m, 29.xi.1994, 04.43.058S 145.24.437E, Binatang Boys, (PNG 119)" (NHMW, ZSM). 60 males, 97 females "Papua New Guinea: Madang, Keki-Sewan, Adalbert Mts., 700m, 30.xi.1994 nr 04.41.802S 145.25.460E Binatang Boys (PNG 120)" (NHMW, ZSM). 7 males, 8 females "Papua New Guinea: Madang, Keki-Sewan, Adalbert Mts., 300m 30.xi.1994, 04.40.558S 145.27.187E, Binatang Boys, (PNG 121)" (ZSM). 1 female "Ibisca Niugini, PNG 25–27.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-C-1/8-d01 / Plot 3 / P1114 Vial 16039-CODYTI" (ZSM). 1 male "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 700m FIT-MW700-O-1/8-d02 / Plot 1 / P1210 Vial 16172-CODYTI" (ZSM). 4 females "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1210 Vial 16172" (ZSM). 1 male, 1 female "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-S-1/8-d02 / Plot 19 / P1242 Vial 16118-CODYTI" (ZSM). 2 males, 3 females "Ibisca Niugini, PNG 26–28.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1234 Vial 16270" (ZSM). 1 female "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-A-2/8-d03 / Plot 1 / P1099 Vial 15960-CODYTI" (ZSM). 2 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-C-2/8-d03 / Plot 3 / P1115 Vial 15923-CODYTI" (ZSM). 1 male, 2 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-A-2/8-d03 / Plot 1 / P1099 Vial 15958-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-G-2/8-d03 / Plot 7 / P1147 Vial 16042-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 27–29.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-H-2/8-d03 / Plot 8 / P1155 Vial 15976-CODYTI" (ZSM). 2 females "Ibisca Niugini, PNG 27–29.x.2012 Mount Wil-

helm 700m -5,731960773 145,2521667", "FIT-MW700-E-2/8-d03 / Plot 5 / P1131 Vial 15937-CODYTI" (ZSM). 2 females "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1243 Vial 16156" (ZSM). 2 males, 5 females "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW700 / P1235 Vial 16164" (ZSM). 3 males, 5 females "Ibisca Niugini, PNG 28–30.x.2012 Mount Wilhelm 700m FIT-MW700-O-2/8-d0 / Plot 15 / P1211 Vial 16189-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 30.x.–1.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1252 Vial 15993" (ZSM). 1 female "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1213 Vial 16236" (ZSM). 1 female "Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 700m FIT-MW700-M-4/8-d08 / Plot 13 / P1197 Vial 15762-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-A-5/8-d09 / Plot 1 / P1102 Vial 16027-CODYTI" (ZSM). 2 females "Ibisca Niugini, PNG 2–4.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-E-5/8-d09 / Plot 5 / P1134 Vial P1134-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1222 Vial 16098" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1254 Vial 16105" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 700m FIT-MW700-M-5/8-d10 / Plot 13 / P1198 Vial 16087-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 700m FIT-MW700-O-5/8-d10 / Plot 15 / P1214 Vial 16088-CODYTI" (ZSM). 1 male, 2 females "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-R-5/8-d10 / Plot 18 / P1238 Vial 15969-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-K-5/8-d10 / Plot 11 / P1182 Vial 16083-CODYTI" (ZSM). 4 females "Ibisca Niugini, PNG 4–6.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-E-6/8-d11 / Plot 5 / P1135 Vial 07232-CODYTI" (ZSM). 2 males, 1 female "Ibisca Niugini, PNG 4–6.xi.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-A-6/8-d11 / Plot 1 / P1103 Vial 07195-CODYTI" (ZSM). 4 females "Ibisca Niugini, PNG 4–6.xi.2012 Mount Wilhelm 700m", "-5,731960773 145,2521667 FIT-MW700-C-6/8-d11 / Plot 3 / P1119 Vial 07081-CODYTI" (ZSM). 1 female "Ibisca Niugini, PNG 4–6.xi.2012 Mount Wilhelm 700m FIT-MW700-D-6/8-d11 / Plot 4 / P1127 Vial 07061" (ZSM). 1 male, 1 female "Ibisca Niugini, PNG 5–7.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1239 Vial 16263" (ZSM). 1 male, 1 female "Ibisca Niugini, PNG 6–8.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667", "FIT-MW700-E-7/8-d13 / Plot 5 / P1136 Vial15886-CODYTI" (ZSM). 2 females "Ibisca Niugini, PNG 9–11.xi.2012 Mount Wilhelm 700m -5,731960773 145,2521667 MW0700 / P1217 Vial 16106" (ZSM). 1 male, 3 females "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 200m -5,739897251 145,329742 MW0200 / P0856 Vial 09605" (ZSM). 1 female "Ibisca Niugini, PNG 3–5.xi.2012 Mount Wilhelm 200m -5,739897251 145,329742 MW0200 / P0865 Vial 09576"

(ZSM). **Eastern Highlands:** 6 males, 7 females "Papua New Guinea: Eastern Highlands, Bena Bridge, 1400m, 8.xii.2007, 06.10.781S 145.26.034E, Balke & Sagata (PNG 164)" (NHMW, ZSM).

Diagnosis. For complete description, see Balke (1998: 332). Beetle small or medium-sized: TL-H 3.45–3.9 mm; oblong-oval, sometimes slightly more attenuated posteriorly; with characteristic dorsal colouration: dark (brown to piceous) elytra and pale (reddish to reddish brown pronotum, except for darker disc, and head; shiny, with very fine, on elytra often almost invisible punctation and weakly impressed microreticulation; pronotum with very narrow lateral bead (Fig. 35); male protarsomere 4 with medium-sized, thick, strongly curved anterolateral hook-like seta; male protarsomere 5 with anterior band of ca. 30 and posterior row of nine relatively long setae (Fig. 40D); median lobe robust, without lateral setae apically; in lateral view, with broadened, triangle apex; in ventral view, apex deeply concave; paramere very slightly concave on dorsal side and with long and dense subdistal and inconspicuous proximal setae (Fig. 40A–C).

Affinities. In the area of its distribution, *E. larsoni* co-occurs with numerous species of the *E. ekari*, *E. ullrichi*, *E. broschii*, and *E. danae* groups. From all them, this characteristic species can be easily distinguished by its size, colouration, fine surface sculpture, simple male antennae, and mainly by the shape of the median lobe. Even females of the species differ from more similar in body form *E. brahminensis* Shaverdo et al., 2012 and *E. broschii* (Balke, 1998) in colouration (more uniform in two latter species) and narrow pronotal bead (absent *E. brahminensis* in and distinct in *E. broschii*). For affinities within the group, see the "Key".

Distribution. Papua New Guinea: Madang and Eastern Highlands Provinces. The species is known from numerous specimens from the central and wertern part of Madang and from northern part of Eastern Highlands (Fig. 45).

15. *Exocelina nomax* (J. Balfour-Browne, 1939)

Figs 36, 41

Copelatus nomax J. Balfour-Browne, 1939: 65–66; Guignot 1956: 55 (catalogue); Guéorguiev 1968: 34 (catalogue).

Copelatus nomax J. Balfour-Browne, 1939 sensu Guéorguiev 1978: 268–269 (key); Guéorguiev and Rocchi 1993: 148.

Copelatus (*Papuadytes*) *nomax* J. Balfour-Browne, 1939: Balke 1998: 334 (notes, diagnosis); Nilsson 2001: 77 (catalogue).

Papuadytes nomax (J. Balfour-Browne, 1939): Nilsson and Fery 2006: 56 (comb. nov.).

Exocelina nomax (J. Balfour-Browne, 1939): Nilsson 2007: 34 (comb. nov.).

Exocelina undescribed sp. MB3405: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Central Province, Mafulu, ca. 08°30'S, 147°00'E, ca. 1219 m a.s.l.

Type material. *Holotype*: female "Type" [round, with red bead], "PAPUA: Mafulu. 4,000ft. i.1934. L.E.Cheesman. B.M.1934-321.", "Copelatus nomax, ♀ Type nov.sp." [hw, the word "type" with red ink], "Holotype" [red] (BMNH).

Additional material. Central: 23 males, 32 females "Papua New Guinea: Central, Kokoda Trek, 320m, i.2008 [09°] 19.236S 147 31.791E, Posman (PNG 168)", one male with an additional green label "DNA M.Balke 3405" (NHMW, ZSM). 4 males "Papua New Guinea: Central, Kokoda Trek, 980m, i.2008, [09°] 15.933S 147 36.590E, Posman (PNG 169)", one of them with an additional green label "DNA M.Balke 3411" (ZSM). 1 female "Papua New Guinea: Central, Kokoda Trek, 980m, i.2008, [09°] 15.933S 147 36.590E, Posman (PNG 169)", "DNA M.Balke 4117" [green] (ZSM). 10 males, 2 females "Papua New Guinea: Central, Kokoda Trek, 590m, i.2008, [09°] 14.339S 147 36.920E, Posman (PNG 170)" (NHMW, ZSM). 19 males, 31 females "Papua New Guinea: Central, Tapini, 1200m, 31.x.2007, 08.21.557S 146.58.712E, Kinibel (PNG 162)", one of the males with an additional green label "DNA M.Balke 3306" (NHMW, ZSM). 2 males, 3 females "Papua New Guinea: Central, Moreguina [10°'57"S, 148°28'27"E], 16.viii.2008, Posman (PNG 183)", males and one female with additional green labels "DNA M.Balke 3745", "DNA M.Balke 3816", "DNA M.Balke 3746" respectively (ZSM). 5 males, 9 females "Papua New Guinea: Central, Moroka area, Kailaki, 827 m, 26.x.2009, 9.24.134S 147.33.521E, Sagata (PNG225)" (NHMW, ZSM). 14 males, 8 females "Papua New Guinea: Central, Moroka, Kailaki, 827 m, 26.x.2009, 9.24.113S 147.33.524E, Sagata (PNG226)" (NHMW, ZSM). 1 female "Papua New Guinea Central, Moroka, Kailaki Wareaga, 760m, 27x2009 9.25.424S 147.31.068E Sagata (PNG227)" (ZSM). 27 males, 39 females "Papua New Guinea: Central, 755m, 28.x.2009 S9 25 47 5 E147 32 59.1, Sagata (PNG229)" (NHMW, ZSM). **National Capital District:** 2 males, 3 females "Papua New Guinea: National Capital District, Varirata NP, 600m, 16.xii.2007, 09.26.13S 147.22.09E, Balke & Sagata (PNG 159)", males with additional green labels "DNA M.Balke 3304" and "DNA M.Balke 3305" (ZSM).

Redescription. *Body size and form*: Beetle small: TL-H 3.0–3.8 mm, TL 3.45–4.2 mm, MW 1.7–2.15 mm (holotype: TL-H 3.5 mm, TL 3.95 mm, MW 1.95 mm), with oblong-oval habitus.

Colouration: Dark brown, with paler sides of pronotum and head. Head reddish to reddish brown, darker posterior to eyes. Pronotum brown to dark brown on disc and reddish to reddish brown on sides. Elytra uniformly dark brown. Head appendages and legs proximally yellowish, legs distally darker, reddish brown (Fig. 36). Teneral specimen paler.

Surface sculpture: Shiny dorsally, with inconspicuous punctation and weakly impressed microreticulation. Head with fine and sparse punctation (spaces between punctures 1–3 times size of punctures); diameter of punctures smaller than or equal to diameter of cells of microreticulation. Pronotum with finer and sparser punctation than on head. Punctation on elytra finer and sparser than on pronotum, inconspicuous, in some specimens invisible. Disc of pronotum and elytra with weakly impressed microreticulation; head and lateral sides of pronotum with microreticulation stronger.

Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter inconspicuous, slightly stronger on two last abdominal ventrites.

Structures: Pronotum with narrow lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, rounded anteriorly. Blade of prosternal process lanceolate, narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 truncate.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of ca. 30 and posterior row of nine relatively long setae (Fig. 41D). Abdominal ventrite 6 with 7–11 lateral striae on each side. Median lobe slender, without lateral setae apically; in lateral view, evenly curved to broadly pointed, elongate apex; in ventral view, apex slightly truncate, asymmetrical (Fig. 41A, B). Paramere very slightly concave on dorsal side, with long and dense subdistal and inconspicuous proximal setae (Fig. 41C).

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Notes on identity of the additional material with the holotype, affinities. Balke (1998: 334) indicates *Exocelina nomax* as species minus cognitus. However, our study of the material collected from Tapini, village ca. 20 km north to Mafulu, allows us to consider with certain confidence that it belongs to *E. nomax*. It is the only *Exocelina* species collected from this area, and it was collected in abundant number (50 specimens) in Tapini. We assume this locality as the most northern distribution border of the species, which is very numerous in Kokoda and Kailaki areas. Morphologically, the specimens from Tapini, Kokoda, Kailaki and Varirata are identical to the holotype (Fig. 36A, B). Only three species occur close to Tapini-Mafulu area: *E. garaina*, *E. posmani* Shaverdo & Balke, 2016, and *E. woitapensis* Shaverdo & Balke, 2016 (the *E. danae* group). But they are larger (TL-H 3.6–4.5 mm), and the smallest of them, *E. woitapensis*, is matt dorsally. Moreover, *E. nomax* can be differentiated from them by its narrow pronotal bead, a very characteristic feature. Smaller size and narrow bead of the pronotum can be used to distinguish it from E. *jaseminae*, a species very similar to it in colour and surface structures. From the other species co-occurring in the Central and National Capital District Provinces (*E. bacchusi*, *E. pulchella* sp. nov., and species of the *E. danae* and *E. jaseminae* groups), *E. nomax* can be distinguished by its body size and colouration, dorsal punctation and microreticulation, narrow pronotal bead, and shape and setation of its median lobe and paramere. See also under *E. warahulenensis* sp. nov. and "Key".

The specimen from Telefomin (Sandaun Province), 1 male "PAPUA, Selminumtem [Selminum Tem, 45 km SWS Telefomin, ca. 5°S; 141°15'E], W.Sepik d. P.Beron leg.", "Copelatus nomax J.B.Br. det.V. Guéorguiev 1917" [partly hw] (NHMW), which was identified by Guéorguiev & Rocchi (1993: 148) as *E. nomax* and indicated by Balke (1998: 334, 338) as "sp. 4" has been recently described under the name *E. okbapensis* Shaverdo & Balke, 2017 (Shaverdo et al. 2017).

Distribution. Papua New Guinea: Central and National Capital District Provinces (Fig. 45). The species is known from numerous specimens in the Central Province and a small population in the National Capital District.

16. *Exocelina warahulenensis* Shaverdo & Balke, sp. nov.

http://zoobank.org/C9CEE1CF-A8D3-4D90-967A-65BD803519F7
Figs 37, 42

Exocelina undescribed sp. MB0265: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Simbu Province, Crater Mountain, Haia, ca. 06°39'39.9"S, 145°00'28.4"E, 700 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea: Crater Mountain, Haia, 700m, 11IX2002, Balke & Sagata, (PNG 001)" (ZSM). *Paratypes*: **Simbu:** 12 males, 7 females with the same label as the holotype (NHMW, ZSM). 2 males "PAPUA NEW GUINEA: Simbu / EHPr. Crater Mountain, Haia, 700m, 11IX2002, Balke & Sagata, (PNG 1)", "258 DNA M Balke" [green], "259 DNA M Balke" [green] (ZSM). 2 males, 4 females "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 004)" (ZSM). 5 males, 3 females "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 005)" (NHMW, ZSM). **Simbu/Eastern Highlands:** 1 male "265 DNA M Balke" [green], "PNG Simbu / EHPr. Crater Mountain, Sera - Herowana, Wara Hulene, 1000 m, 16IX2002, Balke & Sagata (PNG 17)" (ZSM).

Description. *Body size and form*: Beetle small to medium-sized: TL-H 3.4–3.9 mm, TL 3.7–4.3 mm, MW 1.8–2.2 mm (holotype: TL-H 3.9 mm, TL 4.3 mm, MW 2.1 mm), with oblong-oval habitus.

Colouration: Piceous, with reddish sides of pronotum and head. Head reddish to reddish brown, darker posterior to eyes. Pronotum brown to piceous on disc and reddish to reddish brown on sides. Elytra dark brown to piceous. Head appendages and legs proximally yellowish, legs distally darker, reddish brown (Fig. 37). Teneral specimen paler.

Surface sculpture: Shiny dorsally, with inconspicuous punctation and weakly impressed microreticulation. As in *E. nomax*.

Structures: Pronotum with narrow lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 truncate or slightly concave.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior row of 20 and posterior row of seven relatively long setae (Fig. 42D). Abdominal ventrite 6 with 9–12 lateral striae on each side.

Median lobe slender, with lateral setae apically; in lateral view, evenly curved to broadly pointed, short apex; in ventral view, apex slightly concave (Fig. 42A, B). Paramere very slightly concave on dorsal side, with long and dense subdistal and inconspicuous proximal setae (Fig. 42C).

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Affinities. *Exocellina warahulenensis* sp. nov. can be distinguished by body size, form, colouration, inconspicuous dorsal punctation, simple male antenna, and shape and setation of its median lobe and paramere from the species co-occurring in the same area (*E. damantiensis*, *E. hintelmannae*, and *E. ullrichi* (Balke, 1998)). In the dorsal colouration and surface sculpture, the new species is similar to *E. larsoni* but differs from it in shape and presence of setation of the median lobe. *Exocelina warahulenensis* sp. nov. is also very similar to *E. nomax* but is slightly larger and has darker colouration and longer median lobe, with lateral setae apically and shorter, broader apex in lateral view.

Distribution. Papua New Guinea: Simbu and Eastern Highlands Provinces (Fig. 45). The species is known only from Crater Mountain area.

Etymology. The species is named after Wara Hulene Village where one of the paratype was collected. The name is an adjective in the nominative singular.

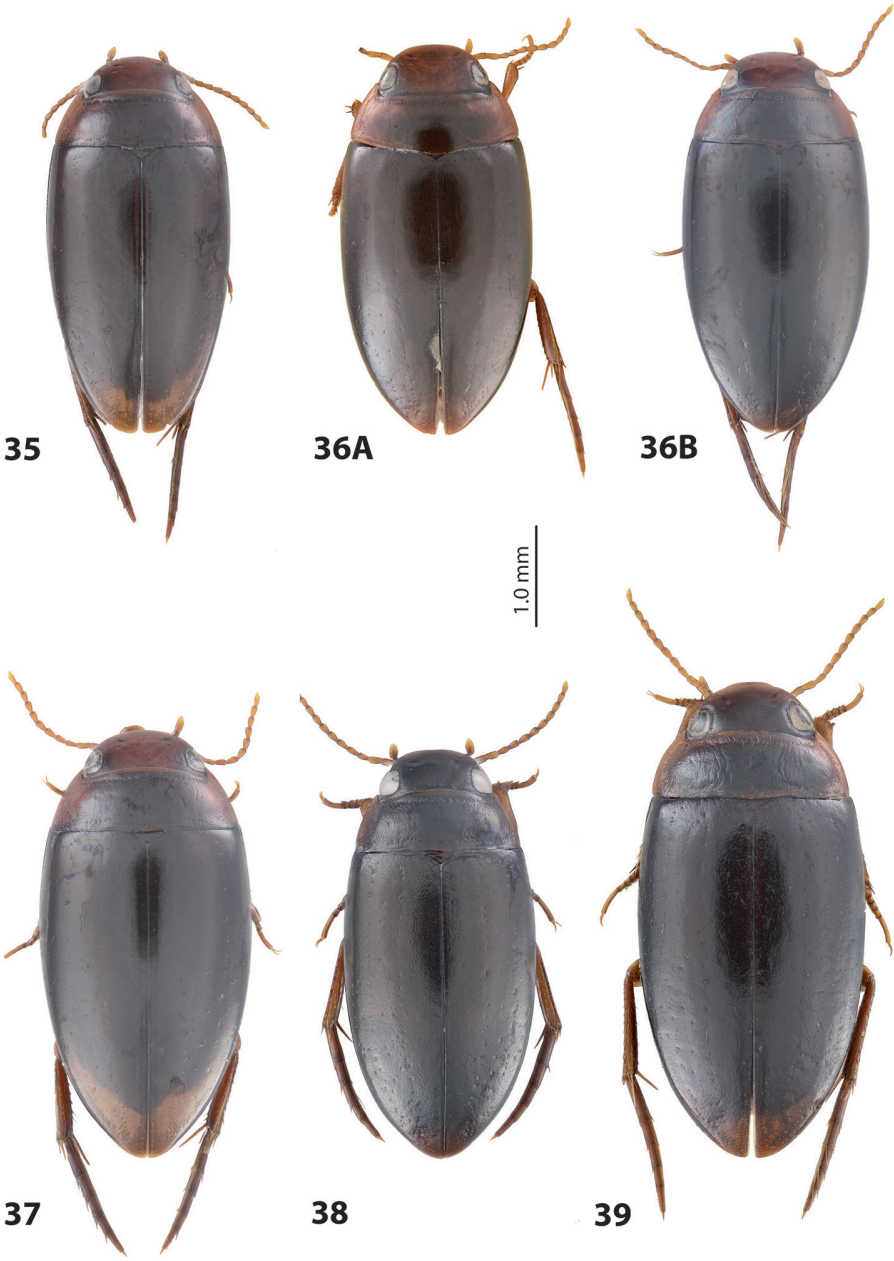
Key to the species of *Exocelina larsoni* group

1 Median lobe robust, lateral sides strongly thickened and apex much broader in lateral view and deeply concave in ventral view (Fig. 40A). Paramere as in Fig. 40C ..... ***larsoni* (Balke, 1998)**

– Median lobe slender, lateral sides more weakly thickened and apex thinner in lateral view and slightly concave in ventral view (e.g., Fig. 41). Paramere as in e.g., Fig. 41C **2**

2 Beetle brownish, usually smaller, TL-H 3.0–3.8 mm (Fig. 36). Apex of median lobe elongate and thinner in lateral view, without lateral setae (Fig. 41A). Paramere as in Fig. 41C ..... ***nomax* (J. Balfour-Browne, 1939)**

– Beetle piceous, usually larger, TL-H 3.4–3.9 mm (Fig. 37). Apex of median lobe shorter and broader in lateral view, with lateral setae (Fig. 42A). Paramere as in Fig. 42C..... ***warahulenensis* sp. nov.**



Figures 35–39. Habitus and colouration **35** *Exocelina larsoni* (Balke, 1998) **36** *E. nomax* (J. Balfour-Browne, 1939) **A** holotype **B** specimen from Tapini **37** *E. warahulenensis* sp. nov. **38** *E. mianminensis* sp. nov. **39** *E. takime* (Balke, 1998).

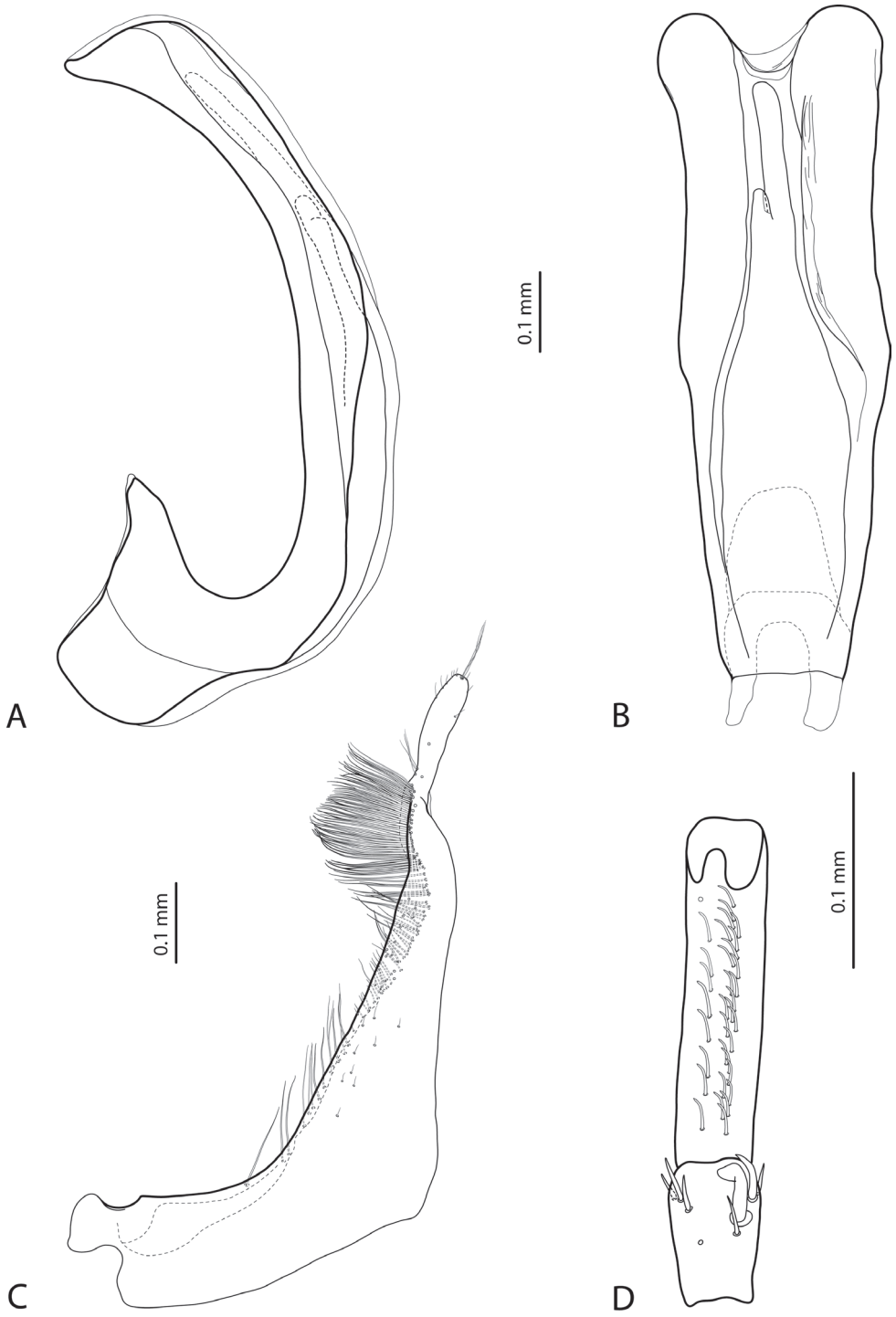
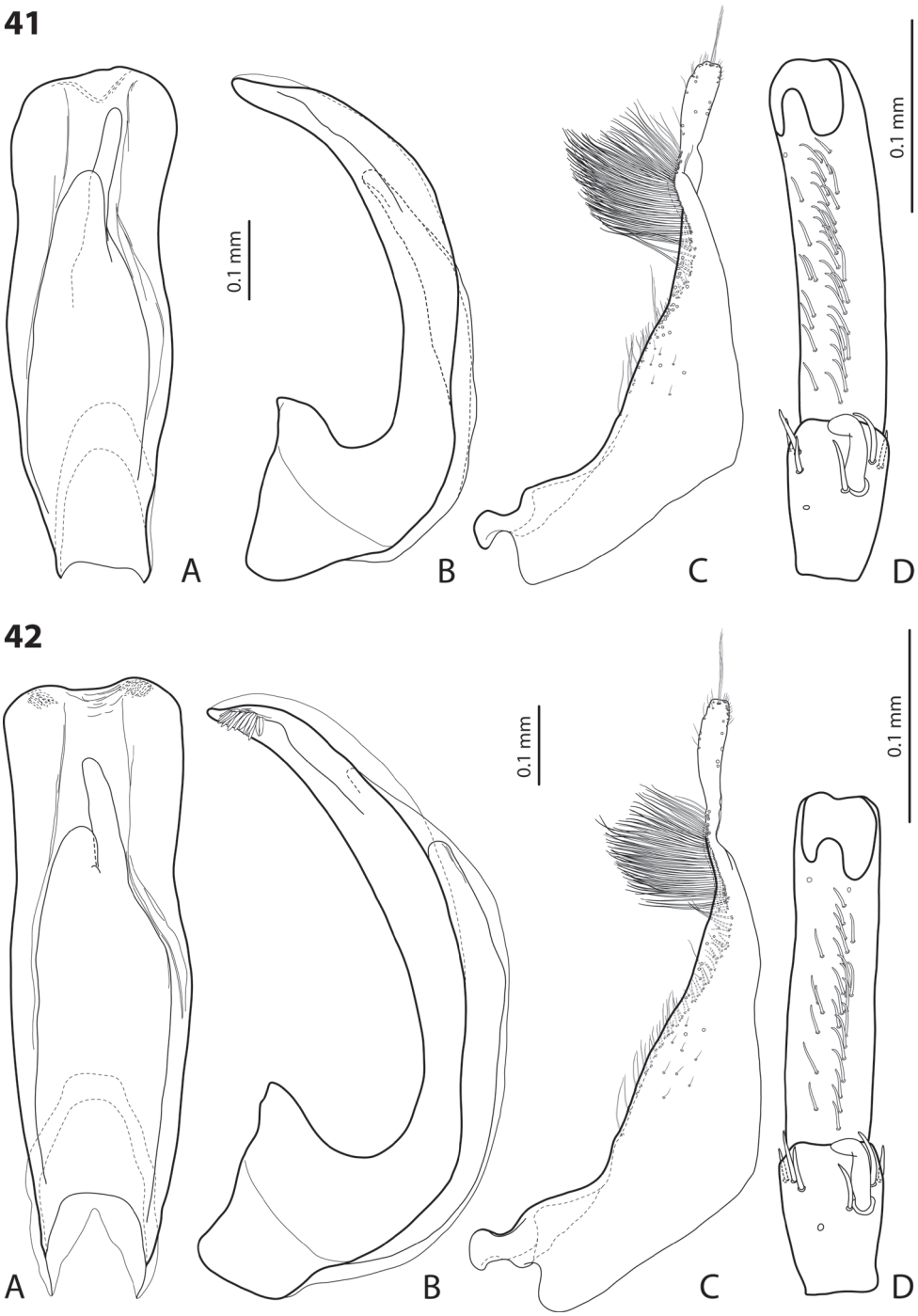


Figure 40. *Exocelina larsoni* (Balke, 1998) **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.



Figures 41, 42. 41 *Exocelina nomax* (J. Balfour-Browne, 1939) **42** *E. warahulenensis* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

Exocelina takime group

This group is characterised by more or less coarse and dense dorsal punctation; pronotum with narrow lateral bead; median lobe of aedeagus without setation, broad, robust, sides slightly thickened; in ventral view, it broadened medially or subdistally; apexes of ventral sclerites of median lobe almost equal; paramere with distinct dorsal notch and subdistal part well developed, with long and dense subdistal and inconspicuous proximal setae.

17. *Exocelina mianminensis* Shaverdo & Balke, sp. nov.

http://zoobank.org/10F38B28-E1B6-46F2-B443-7C19A4A36D18
Figs 38, 43

Exocelina undescribed sp. MB0688: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Sandaun Province, Mianmin, 04°52.86'S, 141°31.71'E, 700 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea: Sandaun, Mianmin (pool), 700m, 21.x.2008, 04.52.858S 141.31.706E, Ibalim (PNG 198), "DNA M.Balke 3749" [green] (ZSM). *Paratypes*: 16 males, 8 females with the same label as the holotype, one male with an additional green label "DNA M.Balke 3758" (NHMW, ZSM). 2 males, 3 females "Papua New Guinea: Sandaun, Mianmin (pool), 700m, 21.x.2008, 04.52.858S 141.31.706E, Ibalim (PNG 197) (ZSM). 1 male "Papua New Guinea: Sandaun, Mianmin (pool), 990m, 23.x.2008, 4.54.570S 141.35.490E, Ibalim (PNG 193) (ZSM). 4 males "Papua New Guinea: Sandaun, May River, 970m, 19.x.2003, 4 49.779S 141 38.174E, K. Sagata (WB43)", one of them with an additional green label "DNA MB688" (ZSM).

Description. *Body size and form*: Beetle medium-sized: TL-H 3.75–4.25 mm, TL 4.15–4.6 mm, MW 1.95–2.3 mm (holotype: TL-H 3.75 mm, TL 4.15 mm, MW 1.95 mm), with oblong habitus.

Colouration: Piceuos. Head piceous, with reddish brown anterior margin. Pronotum dark brown to piceous, with reddish brown to brown sides. Elytra uniformly piceous. Head appendages and legs proximally yellowish, legs distally darker, reddish brown (Fig. 38). Teneral specimen paler.

Surface sculpture: Submatt dorsally, with dense and coarse punctation and weakly impressed microreticulation. Head with very dense and coarse punctation (no spaces between punctures or spaces 1–2 times size of punctures); diameter of punctures equal to diameter of cells of microreticulation. Pronotum with distinct punctation, finer than on head. Punctation on elytra distinct, finer and sparser than on head. Elytra with weakly impressed microreticulation; head and pronotum with microreticulation stronger than on elytra. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites 2–4 with few strioles, two last one without strioles but with very weak wrinkles. Punctation on venter fine but distinct.

Structures: Pronotum with narrow lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, rounded anteriorly. Blade of prosternal process lanceolate, narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 truncate or very slightly concave.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of ca. 60 and posterior row of 17 relatively long setae (Fig. 43D). Abdominal ventrite 6 without lateral striae on each side, except one with setae. Median lobe slender, lateral sides slightly thickened; in lateral view, apex short, pointed, and curved downwards; in ventral view, lateral sides evenly expanded subdistally and apex slightly concave (Fig. 43A, B). Paramere with distinct dorsal notch and subdistal part well developed, with long and dense subdistal and inconspicuous proximal setae (Fig. 43C).

Female: Without evident differences in external morphology from males, except for not modified protarsi.

Affinities. In the area of its distribution, *E. mianminensis* co-occurs with species of the *E. ekari*, *E. okbapensis*, *E. broschii*, *E. casuarina* and *E. danae* groups. From species of the *E. ekari* group, the species differs in larger size, presence of the pronotal bead, evidently stronger dorsal punctation, and the shape of the median lobe. From the other species, *E. mianminensis* sp. nov. can be distinguished by body size, form, and colouration, dorsal punctation, simple male antenna, and shape and setation of its median lobe and paramere. In the general appearance, the new species is more similar to *E. ibalimi* Shaverdo et al., 2018, but can be easily distinguished from it in presence of the pronotal bead. Male abdominal ventrite 6 without lateral striae was so far known only for *E. sima* Shaverdo et al., 2018 among New Guinea *Exocelina*. For affinities within the group, see the "Key".

Distribution. Papua New Guinea: Sandaun Province (Fig. 45).

Etymology. The species is named after Mianmin Village. The name is an adjective in the nominative singular.

18. *Exocelina takime* (Balke, 1998)

Figs 39, 44

Copelatus (*Papuadytes*) *takime* Balke, 1998: 336; Nilsson 2001: 77 (catalogue).
Papuadytes takime (Balke, 1998): Nilsson and Fery 2006: 56 (comb. nov.).
Exocelina takime (Balke, 1998): Nilsson 2007: 34 (comb. nov.).

Type locality. Indonesia: Papua Province: Pegunungan Bintang Regency, Bime, ca. 04°20'S, 140°12'E, 1400 m a.s.l.

Type material studied. *Holotype*: male "IRIAN JAYA: 11.9.1993 Bime – Calab Gebiet, Bime, 1400m", "leg. M. Balke (12) ca. 140°12'E 04°20'S", "HOLOTYPUS" [red], "Copelatus takime Balke des. 1997" [red] (NHMW). *Paratypes*: 10 males, 14 females with the same label as the holotype, one female with an additional green label "DNA M.Balke 3291" (NHMW). 11 males, 2 females "IRIAN JAYA: 22.9.1993 Bime – Calab Gebiet, Bime, 1400m", "ca. 140°12'E 04°20'S, leg. Balke (16)", one of the

males with an additional green label "DNA M.Balke 3290" (NHMW). 3 males, 1 female "IRIAN JAYA Zentralmassiv 140°25'E 04°24'S", "Kali Takime, 900m 18.8.1992 leg. Balke (17)" (NHMW). 7 males, 6 females "IRIAN JAYA: 29.9.1993 Eme Gebiet Emdoman, 800m", "ca. 139°55'E 04°14'S, leg. M. Balke (24)" (NHMW). All these specimens are with red paratype labels "PARATYPUS Copelatus takime Balke des. 1997" or "Paratypus Copelatus takime Balke des. 1997" [red]. Note: in the original description (Balke 1998), 8 males and 4 females are reported from the locality 16; there are 11 males, 2 females in the NHMW, therefore, some mistakes were made in presenting the type material in the original description or/and during labeling the material.

Additional material. 2 females "IRIAN JAYA: 11.9.1993 Bime – Calab Gebiet, Bime, 1400m", "leg. M. Balke (12) ca. 140°12'E 04°20'S" (NHMW).

Diagnosis. For complete description, see Balke (1998: 336). Beetle medium-sized: TL-H 4.1–4.5 mm; oblong-oval; dark brown to piceous, with brownish pronotal sides and head anteriorly; shiny, but with distinct dorsal punctation and weakly impressed microreticulation; pronotum with narrow lateral bead (Fig. 39); male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; male protarsomere 5 with anterior band of ca. 40 and posterior row of eight relatively long setae (Fig. 44D); median lobe robust, in lateral view, evenly curved to narrowly rounded, not curved downwards apex; in ventral view, with more strongly thickened lateral sides, distinctly expanded in middle and narrowing to broadly pointed apex; paramere with distinct dorsal notch and subdistal part well developed, with long and dense subdistal and inconspicuous proximal setae (Fig. 44A–C).

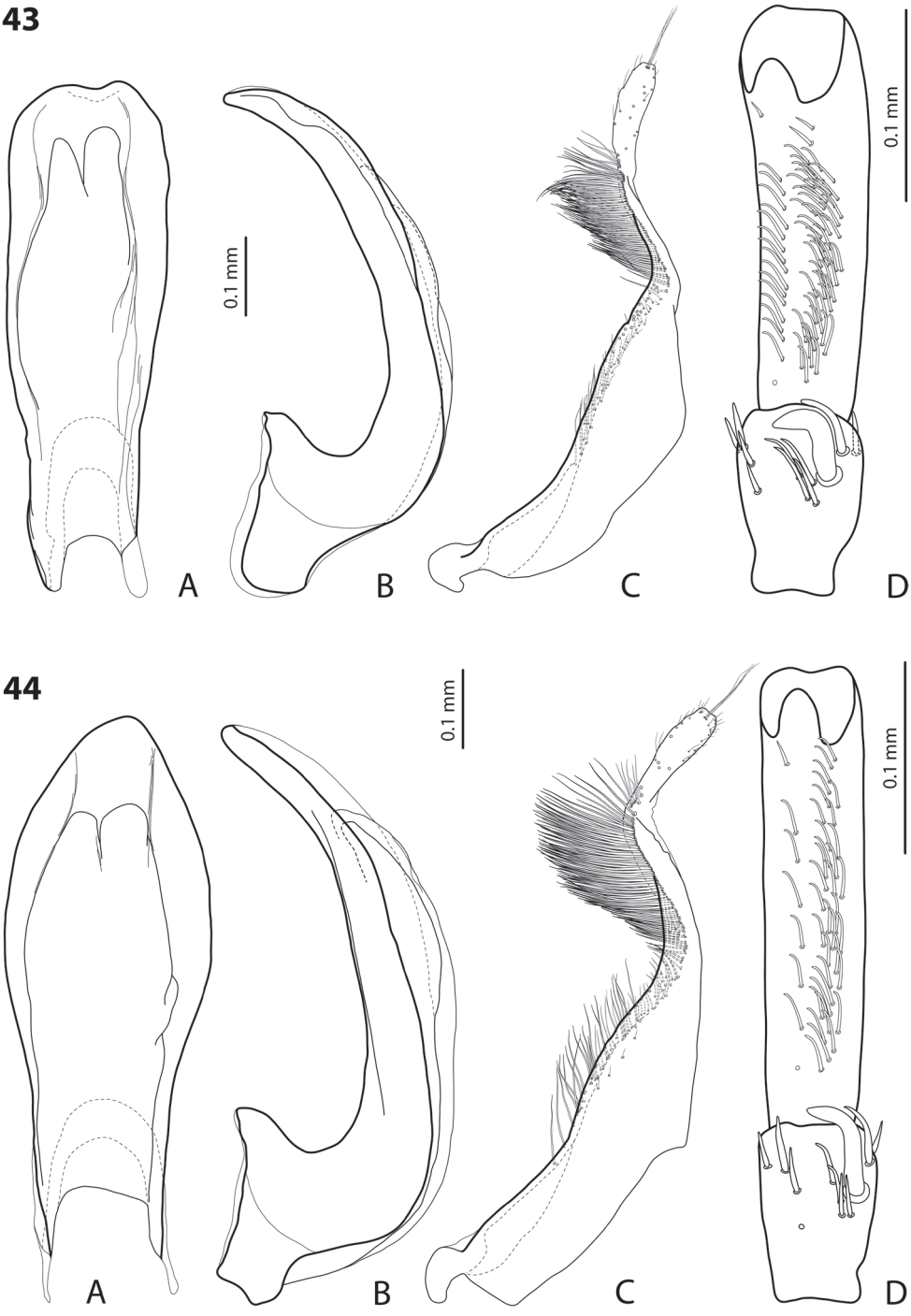
Affinities. In the area of its distribution, *E. takime* co-occurs with *E. aipomek*, *E. ascendens* and species of the *E. bacchusi*, *E. ekari*, *E. aipo*, *E. okbapensis*, *E. casuarina*, and *E. danae* groups. From species of the *E. ekari* group, the species differs in larger size, evidently stronger dorsal punctation, and the shape of the median lobe. In the latter character, *E. takime* differs also from the species of the remaining groups. For separating it from some of these species, also presence of the pronotal bead and simple male antennae, and shape and setation of the paramere can be used. For affinities within the group, see the "Key".

Distribution. Indonesia: Papua Province: Pegunungan Bintang Regency. The species is known only from the type material, i.e., Borme – Bime – Emdoman area (Fig. 45).

Key to the species of *Exocelina takime* group

1 Beetle smaller, TL-H 3.75–4.25 mm. Dorsal punctation coarser (Fig. 38). Median lobe slender, with lateral sides slightly thickened; in ventral view, evenly expanded subdistally, apex slightly concave; in lateral view, apex short, pointed, and curved downwards (Fig. 43). Paramere as in Fig. 43C ..... ***mianminensis* sp. nov.**

– Beetle larger, TL-H 4.1–4.5 mm. Dorsal punctation finer (Fig. 39). Median lobe with strongly thickened lateral sides; in ventral view, distinctly expanded in middle and narrowing to broadly pointed apex; in lateral view, evenly curved to narrowly rounded, not curved downwards apex (Fig. 44). Paramere as in Fig. 44C ..... ***takime* (Balke, 1998)**



Figures 43, 44. 43 *Exocelina mianminensis* sp. nov. **44** *E. takime* (Balke, 1998) **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

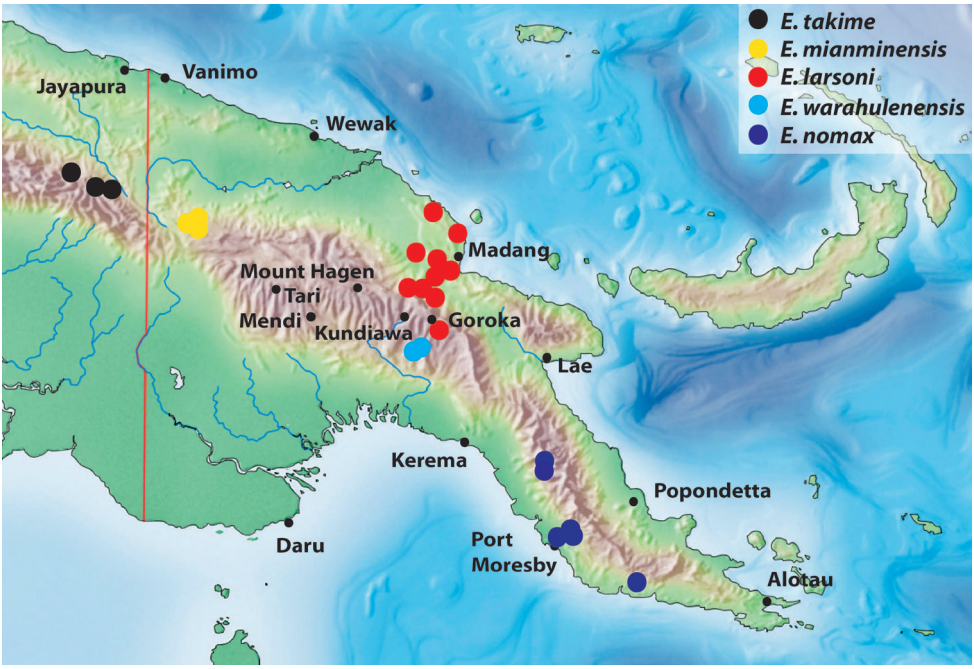


Figure 45. Map of the eastern part of New Guinea showing distribution of the species of the *E. larsoni* and *takime* groups.

Exocelina warasera group

This group is characterised by extremely fine and sparse dorsal punctation; pronotum with distinct lateral bead; median lobe of aedeagus simple; in lateral view, slightly or more strongly curved, apex slightly curved downwards and bluntly pointed; in ventral view, apex bluntly pointed and often twisted sidewards; apexes of ventral sclerites of median lobe almost equal; paramere slightly concave on dorsal side, subdistal setae strong and dense, proximal setae usually inconspicuous.

19. *Exocelina haia* Shaverdo & Balke, sp. nov.

http://zoobank.org/D1562E8F-F21A-4588-9F23-23E6142A5272
Figs 49, 53

Type locality. Papua New Guinea: Simbu Province, between Supa and Haia Villages (Airstrips), ca. 6°39'39.9"S, 145°00'28.4"E, 1032 m.

Type material. *Holotype*: male "Papua New Guinea: Supa Haia, 1023m, 10.ix.2002, K. Sagata (WB1)" (ZSM). *Paratypes*: 2 males with the same label as the holotype (NHMW, ZSM). 1 male "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 005)" (ZSM).

Females of doubtful identity. See under *E. bacchusi*.

Description. *Body size and form*: Beetle small: TL-H 3.4–3.45 mm, TL 3.7–3.75 mm, MW 1.8 mm (holotype: TL-H 3.4 mm, TL 3.7 mm, MW 1.8 mm), with oblong-oval habitus.

Colouration: Dark brown, with paler sides of pronotum and head anteriorly. As in *E. warasera* sp. nov. (Fig. 49).

Surface sculpture: Shiny dorsally, with extremely fine and sparse punctation and weakly impressed microreticulation. As in *E. warasera* sp. nov.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 very slightly concave.

Male: Protarsomere 4 with anterolateral seta thin and evenly curved, smaller than more laterally situated large seta. Protarsomere 5 ventrally with anterior band of ca. 80 and posterior row of two relatively long setae (Fig. 53D). Abdominal ventrite 6 with 6–8 lateral striae on each side. Median lobe short, curved, with broadly pointed apex in lateral view, and evenly tapering to pointed apex in ventral view (Fig. 53A, B). Paramere concave on dorsal side, with dorsal setae distinct: subdistal setae only slightly stronger and denser than proximal (Fig. 53C).

Female: Unknown.

Affinities. *Exocellina haia* sp. nov. can be distinguished by the shape and setation of its median lobe and paramere and/or by its size and colouration from the species co-occurring in the same area (*E. bacchusi*, *E. craterensis* Shaverdo & Balke, 2014, *E. damantiensis*, *E. hintelmannae* (Shaverdo, Sagata & Balke, 2005), *E. warasera* sp. nov.). For affinities within the group, see the "Key".

Distribution. Papua New Guinea: Simbu Province, Crater Mountain area (Fig. 54). The species is named after Haia Village. The name is a noun in the nominative singular standing in apposition.

20. *Exocelina kobau* Shaverdo & Balke, sp. nov.

http://zoobank.org/6773EB08-F9C3-4CD8-A4C6-25B49D19AD5C
Figs 46, 50

Type locality. Papua New Guinea: Morobe Province, E Pindiu, Kobau, ca. 6°25'10.1"S, 147°32'06.6"E, 1400 m a.s.l.

Type material. *Holotype*: male "PAPUA N.G.: Morobe Prov. E Pindiu, Kobau 24.4.1998, 1400 m, leg. A. Riedel", "SEM 13" (NHMW).

Description. *Body size and form*: Beetle medium-sized: TL-H 4.25 mm, TL 4.75 mm, MW 2.2 mm, with oblong-oval habitus.

Colouration: Piceous, with paler sides of pronotum and head anteriorly. Head dark brown, paler anteriorly. Pronotum dark brown, with brown sides. Elytra piceous, with weakly indicated reddish sutural lines. Head appendages and legs proximally reddish, legs distally darker, reddish brown (Fig. 46).

Surface sculpture: Shiny dorsally, with extremely fine and sparse punctation and weakly impressed microreticulation. Head with fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures equal to or smaller than diameter of cells of microreticulation. Pronotum with much finer and sparser punctation than on head, very inconspicuous. Punctation on elytra invisible. Pronotum and elytra with weakly impressed microreticulation; head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter invisible; inconspicuous on two last abdominal ventrites.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 truncate.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of 25 and posterior row of five relatively long setae (Fig. 50D). Abdominal ventrite 6 with 3–4 lateral striae on each side. Median lobe short, robust, evenly tapering to broadly pointed apex in lateral and ventral views (Fig. 50A, B). Paramere slightly concave on dorsal side, subdistal setae strong and dense, proximal setae inconspicuous (Fig. 50C).

Female: Unknown.

Affinities. *Exocellina kobau* sp. nov. can be distinguished by its size, dorsal punctation, shape and setation of its median lobe and paramere, and large anterolateral hook-like seta of the male protarsomere 4 from the species co-occurring in the same area (*E. damantiensis*, *E. kabwumensis* Shaverdo & Balke, 2016, and *E. bacchusi*). For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Morobe Province (Fig. 54).

Etymology. The species is named after Kobau Village. The name is a noun in the nominative singular standing in apposition.

21. *Exocelina pulchella* Shaverdo & Balke, sp. nov.

http://zoobank.org/48FF81EF-7022-493E-9B4E-719933174A43
Figs 47, 51

Exocelina undescribed sp. MB3408: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Central Province, Moroka, Kailaki, Wareaga, 09°25.42'S, 147°31.07'E, 760 m a.s.l.

Type material. *Holotype*: male "Papua New Guinea Central, Moroka, Kailaki Wareaga, 760m, 27x2009 9.25.424S 147.31.068E Sagata (PNG227)" (ZSM). *Paratypes*: 24 males, 43 females with the same label as the holotype, one male with an

additional green label "DNA M.Balke 3832" (NHMW, ZSM). 1 male "Papua New Guinea: Central, Moroka area, Kailaki, 827 m, 26.x.2009, 9.24.134S 147.33.521E, Sagata (PNG225)" (ZSM). 5 males, 9 females "Papua New Guinea: Central, 755m, 28.x.2009 S9 25 47 5 E147 32 59.1, Sagata (PNG229)", one male with an additional green label "DNA M.Balke 3831" (NHMW, ZSM). 2 males, 1 female "Papua New Guinea: Central, Kokoda Trek, 320m, i.2008 09 19.236S 147 31.791E, Posman (PNG 168)", one male with a green label "DNA M.Balke 3403" (ZSM). 2 males, 2 females "Papua New Guinea: Central, Kokoda Trek, 980m, i.2008, 09 15.933S 147 36.590E, Posman (PNG 169)" (NHMW, ZSM). 1 female "Papua New Guinea: Central, Kokoda Trek, 590m, i.2008, 09 14.339S 147 36.920E, Posman (PNG 170)" (ZSM). 3 males "Papua New Guinea: Central, Myola, 1110m, i.2008, 09 12.630S 147 31.880E, Posman (PNG 177)", one of them with an additional green label "DNA M.Balke 3408" (ZSM).

Description. *Body size and form*: Beetle small: TL-H 2.85–3.3 mm, TL 3.15–3.7 mm, MW 1.6–1.8 mm (holotype: TL-H 3.05 mm, TL 3.4 mm, MW 1.75 mm), with oblong-oval habitus.

Colouration: Reddish head and bicoloured elytra: yellowish at shoulders and brownish distally. Head reddish, reddish brown posterior eyes. Pronotum reddish brown to brown on disc (broader or narrower) and yellowish to yellowish reddish on sides. Elytra bicoloured: yellowish in proximal 1/4 to 1/3 (rarely to 1/2) and yellowish brown to brown distally, proximal yellowish colouration sometimes more distinctly boarded as shoulder spots slightly elongated along sutural lines, but mostly fuzzy, not boarded. Head appendages and legs proximally yellowish, legs distally darker, reddish to reddish brown (Fig. 47). Teneral specimens paler.

Surface sculpture: Shiny dorsally, with extremely fine and sparse punctation and weakly impressed microreticulation. Head with fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with much finer and sparser punctation than on head, very inconspicuous. Punctation on elytra invisible. Pronotum and elytra with weakly impressed microreticulation; head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter invisible; inconspicuous on two last abdominal ventrites.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 broadly rounded or slightly truncate.

Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band ca. 60 and posterior row of eight relatively long setae (Fig. 51D). Abdominal ventrite 6 with 4–7 lateral striae on each side. Median lobe simple, short, slightly curved, with broadly pointed apex in lateral view, and evenly tapering to broadly pointed apex in ventral view (Fig. 51A, B). Paramere slightly concave on dorsal side, with strong, long, dense subdistal setae, proximal setae inconspicuous (Fig. 51C).

Female: Without evident differences in external morphology from males, except for not modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Affinities. From species of the *E. danae*, *E. bacchusi* and *E. jaseminae* groups (Shaverdo et al. 2016d) known from Central Province, *E. pulchella* sp. nov. can be easily distinguished by its small size, characteristic colouration, extremely fine dorsal punctation, and shape of the median lobe. For the affinities within the group, see the "Key".

Distribution. Papua New Guinea: Central Province (Fig. 54).

Etymology. The species name derives from Latin *pulchellus*, a diminutive of *pulcher* (beautiful), to express the small size and nice colouration of the beetles; this species is the most colourful of all known New Guinea *Exocelina*. The species name is an adjective in the nominative singular.

22. *Exocelina warasera* Shaverdo & Balke, sp. nov.

http://zoobank.org/DC3A4143-1103-4192-8401-C40780202ED8
Figs 48, 52

Exocelina undescribed sp. MB0261: Toussaint et al. 2014: supplementary figs 1–4, tab. 2; Toussaint et al. 2015: supplementary figs S1, S2, tab. S3, and information S5, S6.

Type locality. Papua New Guinea: Simbu Province, between Supa and Haia Villages (Airstrips), ca. 6°39'39.9"S, 145°00'28.4"E, 1032 m.

Type material. *Holotype*: male "Papua New Guinea: Supa Haia, 1023m, 10.ix.2002, K.Sagata (WB1)" (ZSM). *Paratypes*: **Simbu:** 5 males with the same label as the holotype (NHMW, ZSM). 3 males, 3 females "Papua New Guinea: Simbu/EHPr. Crater Mountain, trek Haia - Wara Sera, 750 m, 12IX2002, Balke & Sagata, (PNG 2)" (NHMW, ZSM). 4 males "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 600m, 12IX2002, Balke & Sagata, (PNG 003)" (NHMW, ZSM). 2 males, 1 female "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 004)" (ZSM). 2 males "Papua New Guinea: Crater Mountain, trek Haia - Wara Sera, 500m, 12IX2002, Balke & Sagata, (PNG 005)" (ZSM). 1 male, 3 females "Papua New Guinea Simbu/EHPr. Crater Mountain, WaraSera Station, 820 m, 14IX2002, Balke & Sagata (PNG 8)" (ZSM). **Simbu/Eastern Highlands:** 4 males "Papua New Guinea: Simbu/EHPr. Crater Mountain, Sera - Herowana, Wara Pima, 900 m, 15IX2002, Balke & Sagata (PNG 011)" (NHMW, ZSM). 1 male "261 DNA M Balke" [green], "PNG Simbu/EHP, Crater Mountain, Sera - Herowana, upper Oh River, 1200 m, 15IX2002, Balke & Sagata (PNG 012)", "sp.21 SEM 19" (ZSM). 1 male "Papua New Guinea: Crater Mountain, Sera - Herowana, upper Oh River, 1200 m, 15IX2002, Balke & Sagata (PNG 012)" (ZSM). 3 males "Papua New Guinea: Simbu/EHPr. Crater Mountain, Sera - Herowana, Jau river, 1000 m, 15IX2002, Balke & Sagata (PNG 015)" (NHMW, ZSM). 1 female "266 DNA M Balke" [green], "PNG Simbu / EHPr. Crater Mountain, Sera - Herowana, Wara Hulene, 1000 m, 16IX2002, Balke & Sagata (PNG 17)" (ZSM). 2 females "Papua New Guinea: Simbu / EHPr.

Crater Mountain, Sera - Herowana, Hulene river, 1000m, 16IX2002, Balke & Sagata (PNG 017)" (ZSM).

Females of doubtful identity. See for *E. bacchusi*.

Description. *Body size and form*: Beetle small: TL-H 3.15–3.8 mm, TL 3.5–4.15 mm, MW 1.65–2.05 mm (holotype: TL-H 3.4 mm, TL 3.8 mm, MW 1.8 mm), with oblong-oval habitus.

Colouration: Dark brown, with paler sides of pronotum and head anteriorly. Head dark brown, paler anteriorly. Pronotum dark brown, with brown sides. Elytra uniformly dark brown. Head appendages and legs proximally reddish, legs distally darker, reddish brown (Fig. 48). Teneral specimen paler, brown to reddish brown with yellowish pronotal sides and head anteriorly.

Surface sculpture: Shiny dorsally, with extremely fine and sparse punctation and weakly impressed microreticulation. Head with fine and sparse punctation (spaces between punctures 2–3 times size of punctures); diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with much finer and sparser punctation than on head, very inconspicuous. Punctation on elytra invisible. Pronotum and elytra with weakly impressed microreticulation; head with microreticulation slightly stronger. Metaventrite, metacoxae, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal strioles and weak transverse wrinkles; abdominal ventrites with strioles. Punctation on venter invisible; inconspicuous on two last abdominal ventrites.

Structures: Pronotum with lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct bead and few setae laterally. Abdominal ventrite 6 truncate or very slightly concave.

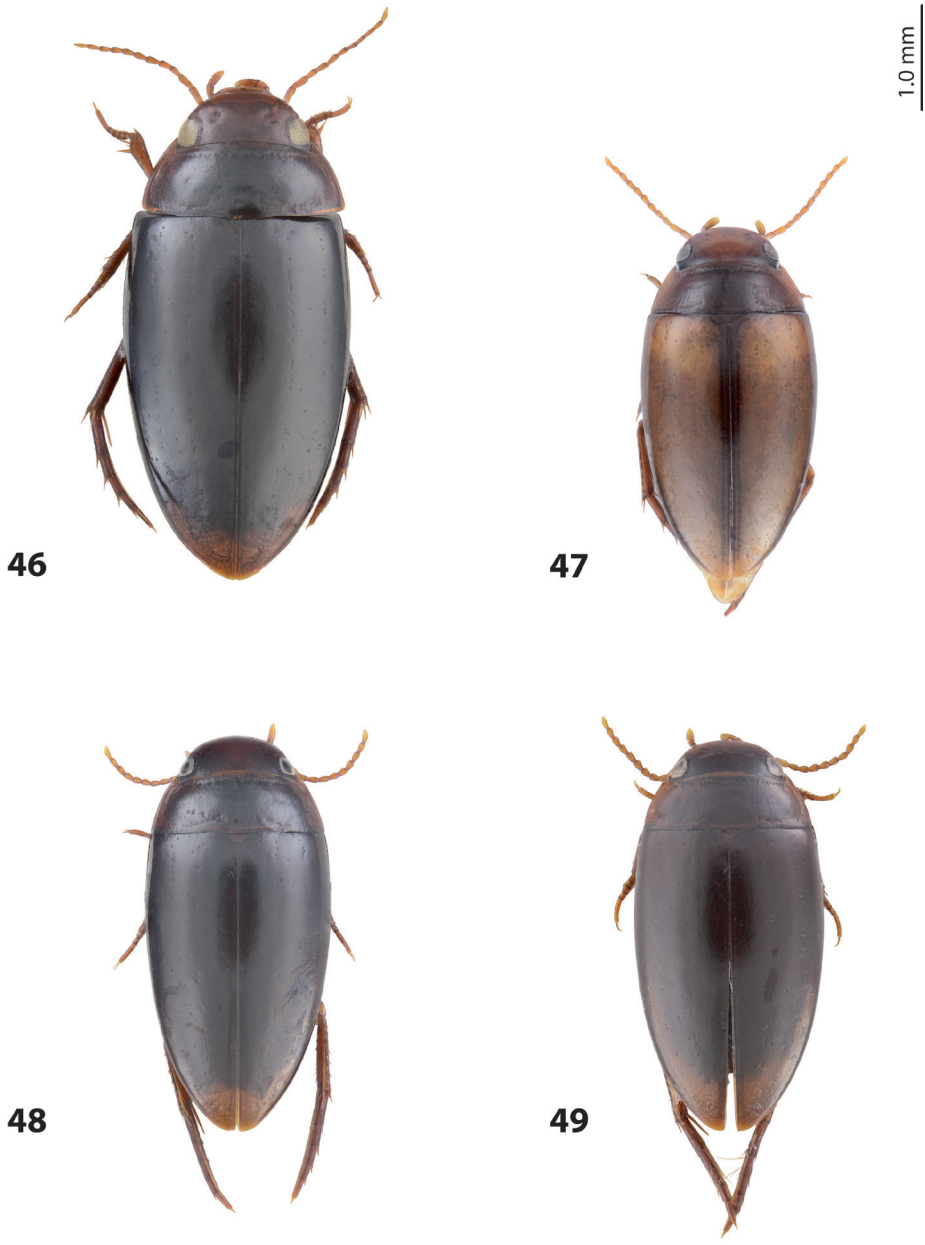
Male: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of ca. 50 and posterior row of eight relatively long setae (Fig. 52D). Abdominal ventrite 6 with 2–4 lateral striae on each side. Median lobe short, curved, with broadly pointed apex in lateral view, and evenly tapering to pointed apex in ventral view; its right lateral margin slightly concave at apex (Fig. 52A, B). Paramere slightly concave on dorsal side, its subdistal part with numerous, dense, very strong setae, proximal setae long, but weaker, less distinct (Fig. 52C).

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

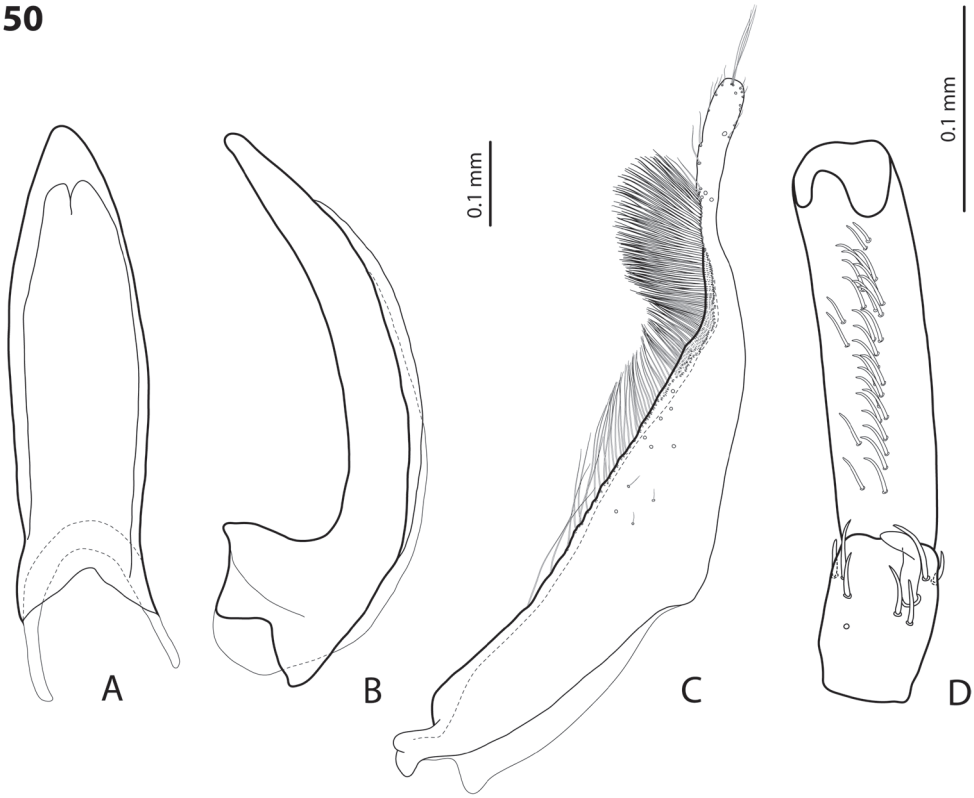
Affinities. From the species co-occurring in the same area (*E. bacchusi*, *E. craterensis*, *E. damantiensis*, *E. hintelmannae*, and *E. haia* sp. nov.), *E. warasera* sp. nov. can be distinguished by the shape and setation of its median lobe and paramere and/or by its size and colouration. For the affinities within the group, see the "Key".

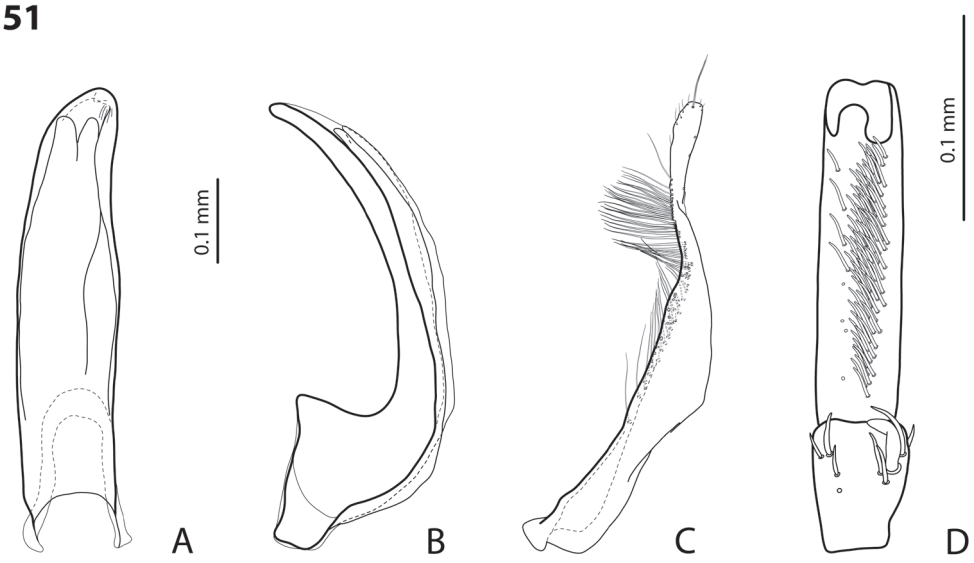
Distribution. Papua New Guinea: Simbu and Eastern Highlands Provinces, Crater Mountain area (Fig. 54).

Etymology. The species is named after Haia Village. The name is a noun in the nominative singular standing in apposition.

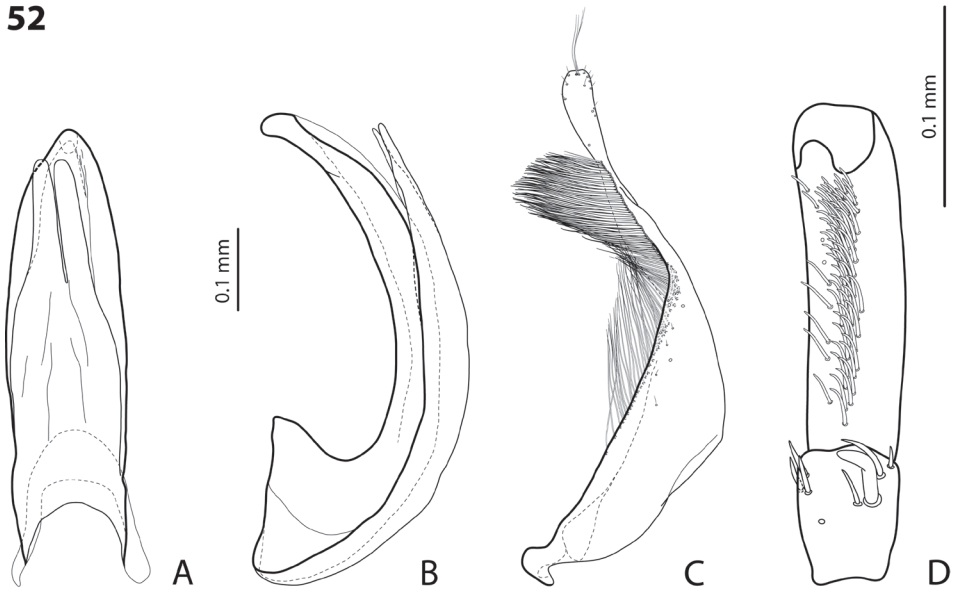


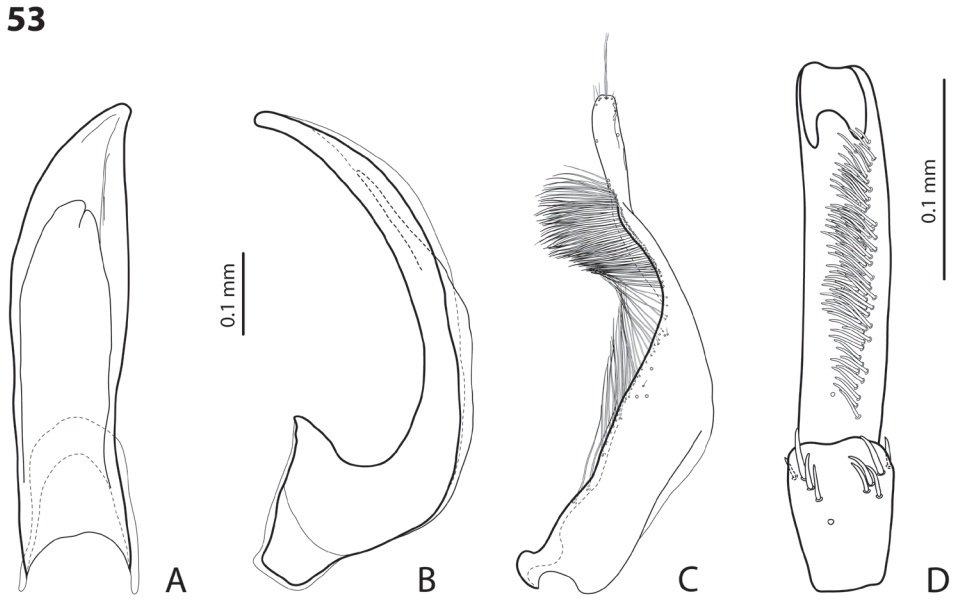
Figures 46–49. Habitus and colouration **46** *Exocelina kobau* sp. nov. **47** *E. pulchella* sp. nov. **48** *E. warasera* sp. nov. **49** *E. haia* sp. nov.





Figures 50, 51. 50 *Exocelina kobau* sp. nov. **51** *E. pulchella* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.





Figures 52, 53. 52 *Exocelina warasera* sp. nov. **53** *E. haia* sp. nov. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

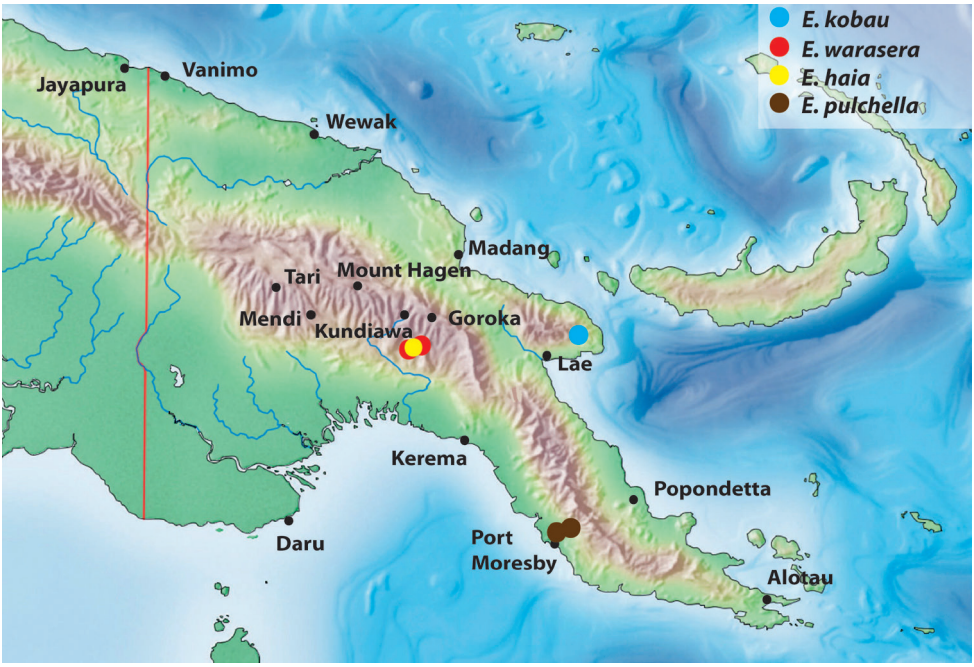


Figure 54. Map of the eastern part of New Guinea showing distribution of the species of the *E. warasera* group.

Key to species of *Exocelina warasera* group

1 Beetle larger, TL-H 4.25 mm (Fig. 46) ..... ***kobau* sp. nov.**
– Beetle smaller, TL-H 2.85–3.8 mm (e.g., Fig. 47)..... **2**
2 Beetle colourful, with reddish head and bicoloured elytra: yellowish at shoulders and brownish distally; smaller, TL-H 2.85–3.3 mm (Fig. 47) .... ***pulchella* sp. nov.**
– Beetle dark brown, with paler sides of pronotum and head anteriorly; larger, TL-H 3.15–3.8 mm (Figs 48, 49)..... **3**
3 Apex of median lobe shorter and thicker, with right lateral margin slightly concave (Fig. 52) ..... ***warasera* sp. nov.**
– Apex of median lobe longer and thinner, its lateral margins straight (Fig. 53)... ..... ***haia* sp. nov.**

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RESEARCH ARTICLE

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First record of the genus *Schistomitra* Butler, 1881 (Lepidoptera, Epicopeiidae) from China, with the description of a new species

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Abstract

The epicopeiid moth genus *Schistomitra* Butler, 1881 is reported outside Japan for the first time, with a new species, *Schistomitra joelmineti* Huang & Wang, **sp. nov.**, described from the southern part of Shaanxi and Gansu Province in China. Photographs of adults and genitalia are provided, and the distribution pattern of the genus is discussed.

Keywords

East Asia, Geometroidea, host plant, oriental swallowtail moth, *Stewartia,* taxonomy

Introduction

Epicopeiidae Swinhoe, 1892, commonly known as oriental swallowtail moths, belongs to the superfamily Geometroidea within Macroheterocera *sensu* Mitter et al. (2017). Hitherto this small family is comprised of 10 genera and less than 30 species restricted in the Asian Palaearctic and Oriental regions. The family can be distinguished by having a head without ocelli, forewing without an areole and in the forewing venation – vein R_5 usually stalked with vein M_1 (Minet 2003). Members of the family nearly all come out at day with few exceptions, and are usually mimickers of some diurnal lepidopterous families such as Papilionidae, Pieridae, Riodinidae and Zygaenidae. Immature stages are only known in the genera *Epicopeia* Westwood, 1841, *Psychostrophia*

Butler, 1877 and *Schistomitra* Butler, 1881, and their larva and pupa are covered by a waxy substance on the surface (Janet and Wytsman 1903, Sugi 1972, Nakamura 2006).

The genus *Schistomitra* was erected by Butler in 1881 based on its type species, *S. funeralis* Butler, 1881. It is characterized by the following two characters: labial palpi entirely blackish brown and gnathos represented by a pair of short and sclerotized arms which are dentate dorsally (Minet 2003). Externally *Schistomitra* is unique within Epicopeiidae by imagoes having an extensive pale yellowish ground color which is divided into patches of different sizes and shapes by blackish patterns on the upper sides of wings. Adults of *S. funeralis* are diurnal, occurring from late spring to early summer, with numbers usually peaking between mid-May and mid-June. They can be found sucking nectar from flowers and water on damp ground. The larva, covered externally by waxy matter commonly found in other Epicopeiidae larvae, feeds on *Stewartia pseudocamellia* (Korean stewartia, Japanese stewartia, or deciduous camellia). It overwinters as a pupa (Sugi 1972).

Inoue (1982) established Schistomitrinae based on the genus *Schistomitra*, which contained two genera from Japan, viz. *Schistomitra* Butler, 1881 and *Psychostrophia* Butler, 1877, as a new subfamily under Epiplemidae (now the Epipleminae under Uraniidae). Minet (2003) synonymized Schistomitrinae with Epicopeiidae because in the analysis based on morphological characters proposed in the same paper, *Schistomitra* was found to be the sister group of the clade (*Nossa* Kirby, 1892 + *Epicopeia* Westwood, 1841); thus, there was no need to maintain this subfamily. In the molecular phylogenetic tree proposed in Wei and Yen (2017), *Schistomitra* was found to be the sister group of either the clade (*Chatamla* Moore, 1881 + *Mimaporia* Wei & Yen, 2017) or the clade (*Chatamla* Moore, 1881 + *Mimaporia* Wei & Yen, 2017 + *Parabraxas* Leech, 1897). Hence, the precise relationships between these genera is still unclear and needs further investigation.

For a long time, *Schistomitra* was regarded as an endemic Japanese genus only found in Honshu, Shikoku, and Kyushu (Sugi 1972, Owada 2011, Association of Aso area world agriculture inheritance promotion 2014). Unexpectedly, recently we received some interesting epicopeiid moth material which was collected from southern Shaanxi and Gansu from 2007 to 2017, and they shared many external similarities with the genus *Schistomitra*. After examining the genitalia and comparing them with those of *Schistomitra funeralis*, all the results lead to a conclusion that these materials belong to an undescribed species of the genus *Schistomitra* and it is described here.

Materials and methods

Specimens examined in this study were all collected during the day with an insect net and are deposited in the collection of South China Agricultural University (**SCAU**), Guangzhou, PR China and the Bavarian State Collection of Zoology (Zoologische Staatssammlung München), Munich, Germany (**ZSM**). All adult photographs in the laboratory were taken with a Nikon CoolPix S7000 camera, the adults in wild and habitat photos were taken with a Canon EOS 80D camera by collector Mr Wenhao Sun. Abdomens were removed and macerated in 10% NaOH for examination of male and female genitalia. Photographs of genitalia were all taken under a Keyence

VHX-5000 digital microscope, and were all processed by Adobe Photoshop CS5 software. Terminology of adult morphology and genitalia follows Klots (1970), Kristensen (2003), Minet (2003), and Wei and Yen (2017).

Taxonomy

Genus *Schistomitra* Butler, 1881

Schistomitra Butler, 1881: 3.

Type species. *Schistomitra funeralis* Butler, 1881 [Type locality: Fusiyama, Nikko (Honshu, Japan)].

Schistomitra joelmineti Huang & Wang, sp. nov.

http://zoobank.org/8063CEFF-BE04-4007-A627-45C0EEEE187E
Figs 1–5, 9–14, 18–19, 21, 22

Type material. ***Holotype:*** male, altitude 800–1000 m, 22.IV.2017, Chengguan Town, Ningshan County, Shaanxi Province, PR China, leg. Di Lu & Wen-hao Sun (SCAU). ***Paratype:*** 1 female, same data as holotype; 1 female, 26.V.2007, Houzhenzi Town, Zhouzhi County, Xi'an City, Shaanxi Province, PR China, leg. Hong-liang Shi (SCAU); 1 male, 1 female, altitude 1300–1500 m, 3.V.2009, Xunyangba Town, Ningshan County, Shaanxi Province, PR China, leg. Yu-fei Li (SCAU); 1 female, same locality and collector, but altitude 1500–1900 m, 8.VI.2014 (SCAU); 2 female, altitude 1500 m, 30.V.2017, Jialingjiang Head Water, Baoji City, Shaanxi Province, PR China, leg. Shu-qin Ji (SCAU); 1 male, altitude 1800 m, 29.IV.2017, Qinghe Forestry Farm, Kang County, Longnan City, Gansu Province, leg. Hao Huang (SCAU), 1 male, same locality and collector, but 1.V.2017 (SCAU); 1 female, same locality and collector, but altitude 1300 m, 3.VI.2017 (SCAU); 3 males, 1 female, altitude 1400 m, 4.VI.1991, Fengxiang County, Mts. Qin Ling, S. Shaanxi, PR China, leg. G.C. Bozano (ZSM).

Diagnosis. *Schistomitra joelmineti* sp. nov. is characterized and distinguished from *S. funeralis* (Figs 6–8, 15–17, 20) by the following characters:

1) the size is larger in both sexes, length of forewing 26–28 mm vs. 25–27 mm in males, 27–30 mm vs. 25 mm in females;
2) the forewing has the discoidal cell totally encircled by darkened veins, while the lower portion of discoidal cell remains pale yellow like its ground color in *S. funeralis*;
3) the blackish postmedian band on forewing upper side is narrower compared to the much wider band in *S. funeralis*;
4) the hind wing upper side has a much reduced blackish pattern in cell Rs and bases of cell 1A+2A and 3A, whereas the blackish pattern is better developed in all these cells in *S. funeralis*;

Figures 1–8. Adults of *Schistomitra* spp. **1–3, 6–7** male **4, 5, 8** female **1–5** *Schistomitra joelmineti* sp. nov. **6–8** *Schistomitra funeralis*. Scale bar: 1 cm.

5) in the male genitalia the uncus is shorter with its tip nearly flat or slightly concave in the middle, while uncus is longer with its tip rounded in *S. funeralis*;
6) the sacculus is longer, and the apex of praesacculus forms a long, sharp, blade-like process pointing dorsally, while in *S. funeralis* the sacculus is shorter, with the apex only forming a short and rounded bulge;

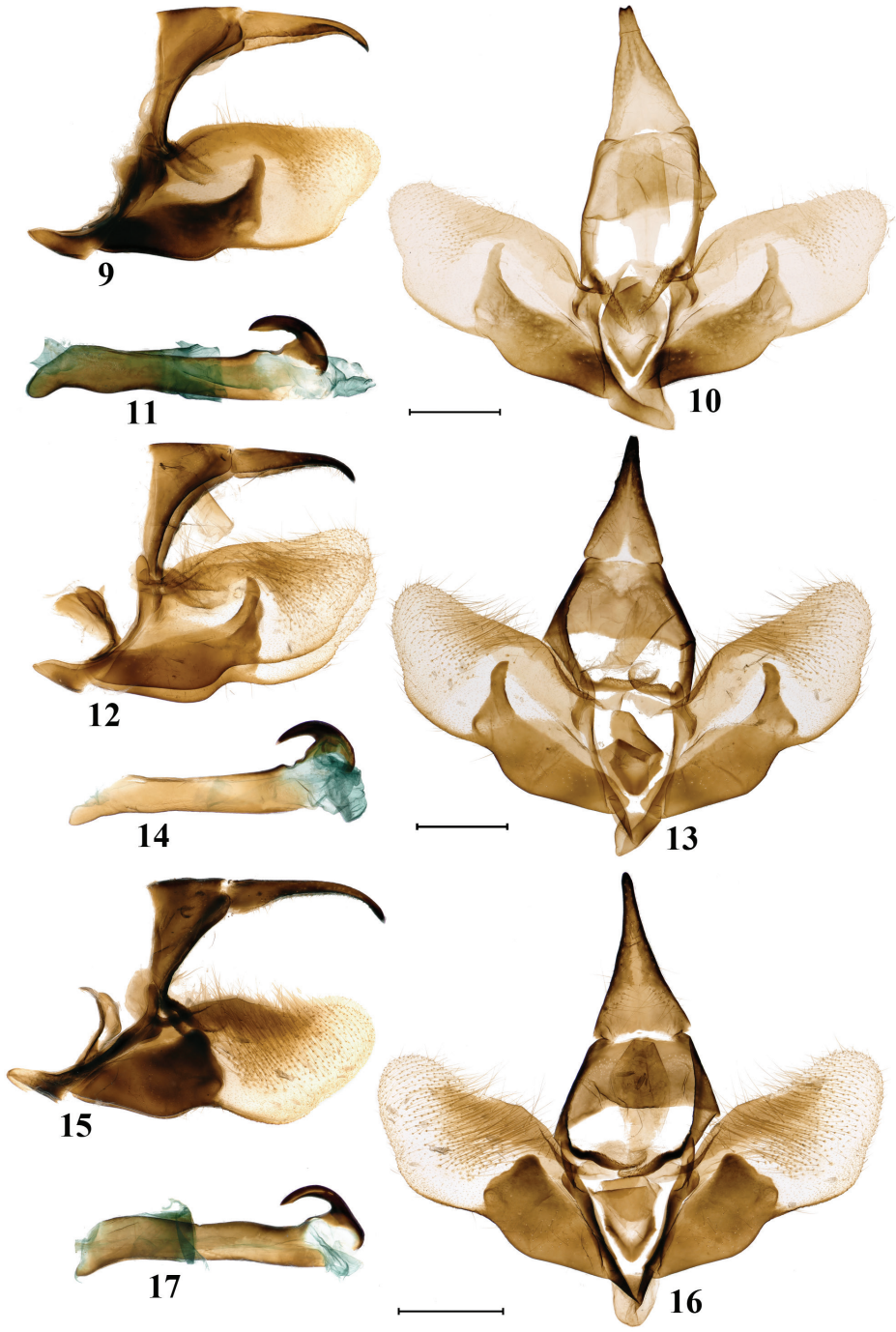
7) the aedeagus is slightly thicker and longer, with the distal shaft more robust and the coecum larger, while the aedeagus is narrower and shorter, with distal shaft slenderer and coecum smaller in *S. funeralis*;
8) in the female genitalia, ductus bursae is more sclerotized, corpus bursae is smaller with a rounded signum, while in those of *S. funeralis* the ductus bursae is more membranous, the corpus bursae is larger, with the signum being elliptical.

Description. ***Male*** (Figs 1–3). Length of forewing 26–28 mm. Head black, frons wide, covered with long blackish hairy scales; vertex covered with long blackish brown hair; compound eye black and large; antenna black, bipectinate. Thorax black; patagia covered with pale yellow hairy scale; tegula black, cephalic part covered with pale yellow hairy scales; abdomen covered with dense black scales dorsally and ventrally with bright yellowish orange rings presenting at intersegmental membranes between each segment of abdomen. Forewing upper side ground color pale yellow, veins all broadly suffused with blackish scales except the base of vein M_2, cilia black. Costa black from base to apex; postmedian band black, running from costal zone to dorsum and extending basally in cell 1A+2A; the pale yellow ground pattern from median to marginal zone is divided by darkened veins and postmedian band into smaller patches of various shape and size. Hindwing upper side ground color pale yellow, cilia black. All veins suffused with blackish scales. A black postmedian band extending from costa to dorsum, varying from fully developed to obsolete.

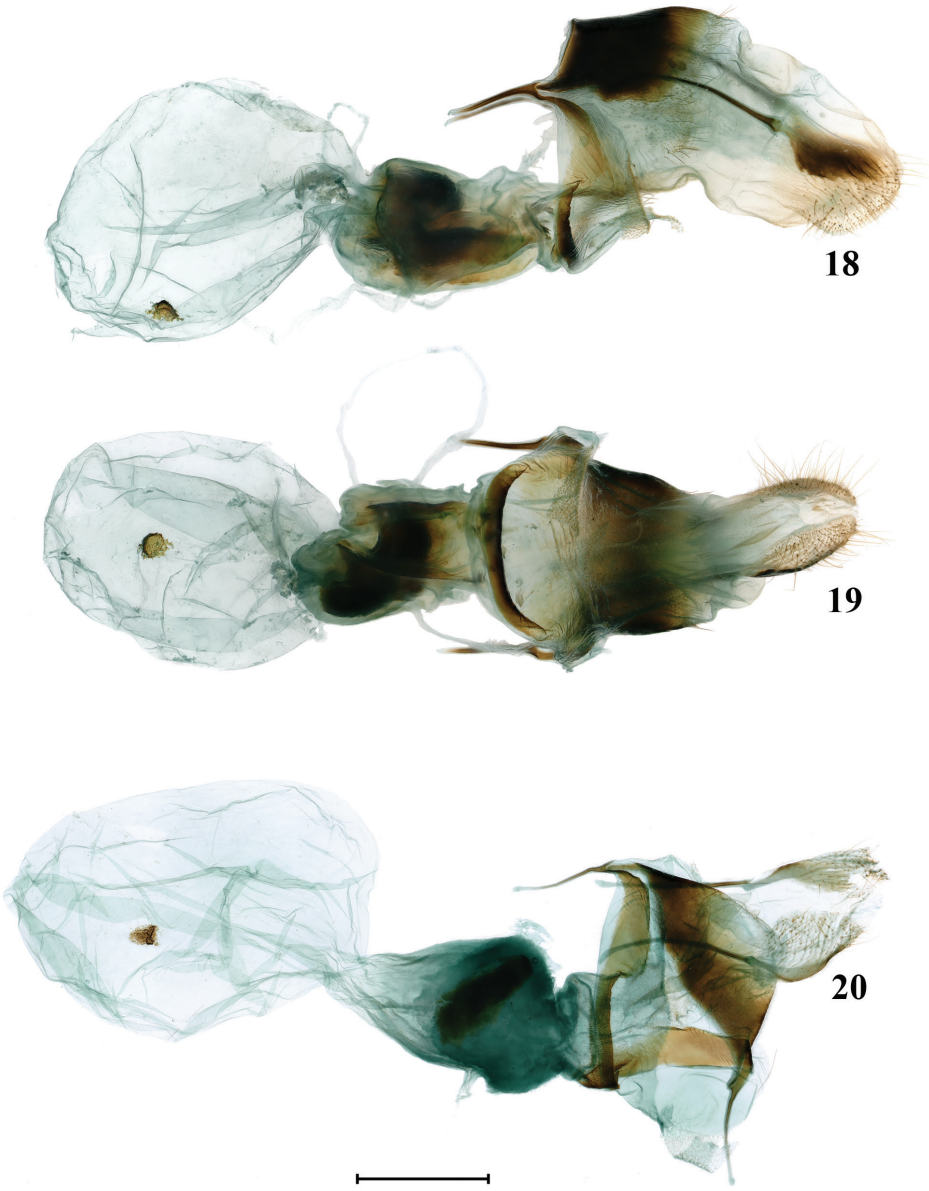
Female (Figs 4, 5). Length of forewing 27–30 mm. Head, thorax and abdomen same as in male, antenna filiform. Forewing broader, termen more rounded, pattern nearly same as in male, only the blackish postmedian band on forewing not continuous. Hindwing slightly broader, other characters same as in male.

Genitalia. ***Male*** (Figs 9–14). Uncus moderately long and triangular, with its tip nearly flat or shallowly concave at the middle. Tegumen broad and short, trapezoid. Subscaphium slightly sclerotized. Gnathos consisted of the two sclerotized arms which connected by membrane medially and dorsally covered by many teeth of different size. Costula at the base of costa, consists of two sclerotized triangular processes connected together by a membrane. Juxta V-shaped, with each lobe extending upwards and ending with a large triangular-like sclerotized plate. Saccus broad and stout, semielliptical. Valva broad and short, concave at ventral margin with inner surface setose at apex. Costa moderately long, strongly sclerotized. Sacculus nearly the same length of costa, strongly sclerotized and slightly broadening at middle portion. Praesacculus short and strongly sclerotized, its apex ending with a long and sharp blade-like process directed dorsally, which slightly varying in width. Aedeagus long and thick, distal shaft strongly sclerotized and horn-shaped, bending at the middle and basally connecting to the dorsal wall of the aedeagus by a sclerotized plate, coecum presents, moderately developed.

Female (Figs 18, 19). Papillae anales slightly sclerotized, rectangular in lateral view, with tip flat. Apophyses posteriores and anteriores sclerotized and slender; and the former are nearly twice the length of the latter. Antrum membranous and broad. Ostium bursae nearly the same width as antrum. Lamella antevaginalis broad, mostly membranous and anteriorly edging with a strongly sclerotized bar. Lamella



Figures 9–17. Male genitalia of *Schistomitra* spp **9–11** holotype of *Schistomitra joelmineti* sp. nov. **12–14** paratype of *Schistomitra joelmineti* sp. nov., from individual in Fig. 2 **15–17** *Schistomitra funeralis* **9, 12, 15** genitalia capsule lateral view **10, 13, 16** genitalia capsule ventral view **11, 14, 17** aedeagus lateral view. Scale bars: 1 mm.



Figures 18–20. Female genitalia of *Schistomitra* spp. **18** *Schistomitra joelmineti* sp. nov. lateral view **19** *ditto*, ventral view **20** *Schistomitra funeralis* ventral view. Scale bar: 1 mm.

postvaginalis obsolete and very slightly sclerotized, elliptical in ventral view. Ductus bursae short and broad, strongly sclerotized. Ductus seminalis very long, arising from ductus bursae. Corpus bursae membranous, large and oval shape. A sclerotized rounded signum presenting at anterior zone of corpus bursae, with numerous spinules on the surface.

Figures 21–23. *Schistomitra joelmineti* sp. nov. living adult and habitat **21** sucking on damp ground **22** resting on leaves **23** habitat of *Schistomitra joelmineti* sp. nov. in Chengguan Town, Ningshan County.

Distribution. Currently this species is restricted to the southern part of Shaanxi Province and Gansu Province.

Etymology. The specific name *joelmineti* is named in honor of Prof. Joël Minet (Paris, France) who contributed greatly to the study of the family Epicopeiidae and kindly provided the first author with valuable literature when he began studying Epicopeiidae.

Biology. This species is univoltine, occurring from late April to early June. Adults are usually found sucking nutrients and water on damp ground (Fig. 21) or resting on leaves (Fig. 22) near the edge of the forest (Fig. 23) at altitude between 800 to 1800 m.

Discussion

Although the external features of adults of *Schistomitra joelmineti* are variable among individuals to some extent, their genitalia are only slightly different in the tip of the uncus, length of the aedeagus, and width of the pointed process in the praesacculus, while they differ greatly from those of *S. funeralis*. Thus, we regard all these individuals from China as a single species.

The genus *Schistomitra* currently shows a disjunct distribution with the discovery of *Schistomitra joelmineti*, with one species found in the mountainous region around Mt. Qinling in Shaanxi Provinceand Gansu Province in China and the other in Honshu, Shikoku, and Kyushu in Japan (Fig. 24). The disjunct distribution might be caused by the distribution pattern of their host plants. The host plant genus *Stewartia* is widely distributed in Honshu, Shikoku, and Kyushu in Japan, the southern part of the Korean Peninsula, as well as in the vast area between Mt. Qinling and Mt. Nanling in China (Li 2011), which could explain the absence of this moth genus in northeastern, northern China and the northern part of the Korean Peninsula. However, it is still a mystery as to why this genus is not found in the southern part of the Korean Peninsula, but this will only be solved with careful and intensive collecting in the suitable habitats, to determine its biogeography. In addition, *S. funeralis* tends to be distributed in mountainous areas with a rather dry climate in Japan, where annual precipitation is no more than 1800 mm (Sugi 1972). Similarly, the mountainous regions in southern Shaanxi and Gansu are also rather cool and dry with an annual precipitation of no more than 1300 mm, similar to the habitats of *S. funeralis* in Japan. Thus, the narrow distribution of *Schistomitra* in southern Shaanxi and Gansu may relate to its intolerance of high temperatures or humid climates; in other words, the hot and humid climate of other regions may have played an important role in preventing the extension of this genus to southern and southeastern China.

Speciation in *Schistomitra* may mostly be the result of isolation mechanisms mentioned above. In addition, the utilization and distribution of different host plants may also contribute to it to some extent. In the phylogenetic tree of *Stewartia* proposed by Li (2011) based on morphological characters, *Stewartia pseudocamellia*, the host plant of *Schistomitra funeralis*, was not recovered in the same clade as the only species of *Stewartia* found in southern Shaanxi, *Stewartia shensiensis* (which might be the candidate host plant of *Schistomitra joelmineti*). In Lepidoptera, a similar case exists in the lycaenid butterfly genus *Sibataniozephyrus* Inomata, 1986, which is widespread in Japan, Taiwan, and the southern, southwestern and central part of mainland China, and diverges into three species utilizing different species of *Fagus* present in each area (Koiwaya 2007). Although Koiwaya suggested that *Sibataniozephyrus lijinae* Hsu, 1995 from mainland China might utilize the same *Fagus* species as *S. kuafui* Hsu & Lin, 1994 from Taiwan, there is still no evidence to support this idea.

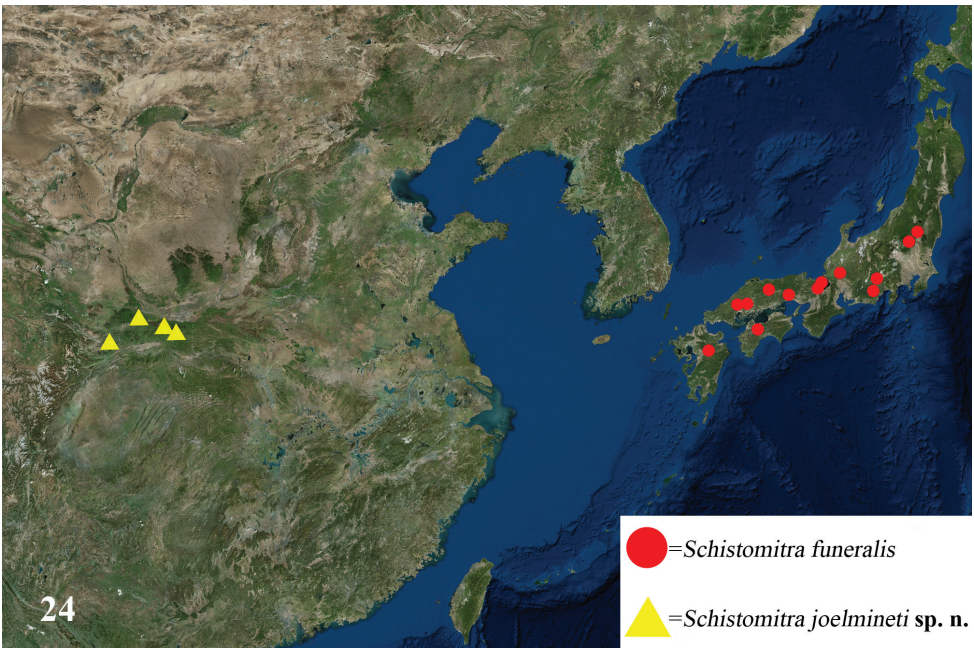


Figure 24. Distribution map of the genus *Schistomitra*. Records of distribution are taken from Sugi (1972), Association of Aso area world agriculture inheritance promotion (2014), and the present study.

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