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Deutsche Entomologische Zeitschrift

An International Journal of Systematic Entomology

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- *Title page*
- *Abstract*
- *Introduction*
- *Materials and Methods*
- *Results*
- *Discussion*
- *Acknowledgements*
- *References*
- *Tables with captions*
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In Focus

The cover picture shows *Derossiella lukici* sp. n.

See paper of **Lohaj R & Delić T** Playing hard to get: two new species of subterranean Trechini beetles (Coleoptera, Carabidae, Trechinae) from the Dinaric Karst

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Abstract & Indexing Information

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Playing hard to get: two new species of subterranean Trechini beetles (Coleoptera, Carabidae, Trechinae) from the Dinaric Karst

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Abstract

Almost 200 years of continuous and systematic research in subterranean habitats of the Dinaric Karst and adjoining areas have resulted in the discovery of more than 400 specialized subterranean beetles. Among these, a special place belongs to the morphologically well distinguished and elusive, so called aphaenopsoid trechine beetles, which are characterized by a prolonged head, pronotum and appendages, and widened, ovoid-shaped elytra. Two new species of aphaenopsoid trechines – *Derossiella lukici* **sp. n.** from two deep pits on Mt Biokovo, Croatia, and *Adriaphaenops petrimaris* **sp. n.** from Pištet 4 Cave, Kameno more, Montenegro – are described, illustrated, and compared with closely related congeners. Identification keys for both genera and an annotated catalogue for all *Adriaphaenops* species, as well as data on the distribution and the ecology of these remarkable species, are provided and discussed.

Introduction

Following the description of the first cave animal, a subterranean beetle *Leptodirus hochenwartii* Schmidt, 1832 (Polak 2005, Moldovan 2012), the western Balkan's Dinaric Karst became a theater of ceaseless discoveries of highly specialized, cave adapted fauna. The so called troglobionts. Here, the richness of subterranean biodiversity exceeds that of similar areas throughout the world; thus, it is considered the world's primary subterranean biodiversity hotspot (Sket et al. 2004, Culver et al. 2006, Sket 2012). Moreover, it is only here that caves (locally called jama, pećina or špilja) having more than 100 troglobiotic species are known to exist (Ozimec and Lučić 2009, Zagmajster et al. in prep). Much of this exceptional richness consists of beetles specialized for living in these

(Bregović and Zagmajster 2016) resource-scarce habitats (Gibert and Deharveng 2002, Culver and Pipan 2009). To date, more than 400 species of troglobiotic beetles have been recognized in the Dinaric Karst and adjoining areas (Bregović and Zagmajster 2016, Zagmajster, personal communication). The vast majority are classified in two subfamilies: Cholevinae (family Leiodidae) and Trechinae (family Carabidae). Even though their natural histories and ecology differ, the two groups show similar distribution patterns, which might suggest that the same mechanisms triggered the emergence of the two species richness peaks in the Dinaric Karst: one in the northwest and the other in the southeast (Zagmajster et al. 2008, Bregović and Zagmajster 2016).

Among the Trechini, a group of morphologically derived and predatory "aphaenopsoid" beetles, characterized by a

prolonged head, pronotum, and appendages, can be easily distinguished (Jeannel 1928, Casale and Laneyrie 1982, Luo et al. 2018). By the beginning of the 20th century, the genus *Aphaenopsis* Müller, 1913 was the only aphaenopsoid trechine genus recorded from the Dinaric Karst. Only two additional genera, *Scotoplanetes* Absolon, 1913 and *Adriaphaenops* Noesske, 1928, were discovered until the employment of vertical caving techniques, which enabled karst researchers to explore deeper sections of the caves. This also offered the possibility to sample new and hardly accessible habitats, i.e. the cave hygropetric (Sket 2004). During the following decades, discoveries of peculiar, yet unrecognized aphaenopsoid beetles were reported from all over the Dinaric Karst. Overall, nine new genera were described (*Dalmataphaenops* Monguzzi, 1993 [junior synonym *Biokovoaphaenopsis radici* Jalžić, 1993]; *Albanotrechus* Casale & Guéorguiev, 1994; *Croatotrechus* Casale & Jalžić, 1999; *Minosaphaenops* Quéinnec, 2008; *Derossiella* Quéinnec, 2008; *Jalzicaphaenops* Lohaj & Lakota, 2010; *Acheroniotes* Lohaj & Lakota, 2010; *Velebitaphaenops* Casale & Jalžić, 2012; and *Velesaphaenops* Ćurčić & Pavićević, 2018) (Quéinnec 2008, Casale et al. 2012, Ćurčić et al. 2018). The newly recognized genera encompassed an entire range of body sizes, from the 4.4 mm long *Croatotrechus* to the gigantic, 14 mm long *Velebitaphaenops* (Casale and Jalžić 1999, Casale et al. 2012). Most of the newly discovered genera remained monotypic, with the exception of the genera *Minosaphaenops* (2 species) and *Acheroniotes* (3 species) (Lohaj and Jalžić 2009, Ćurčić et al. 2018), and seem to represent geographically isolated and morphologically well-defined lineages. Moreover, most of the Dinaric aphaenopsoid trechine genera seem to be ecologically specialized predators and are rarely found. In many cases, species or even genera are single-site endemics known by one or several specimens only, with the only exceptions being the genera *Acheroniotes* and *Dalmataphaenops* (Noesske 1928, Scheibel 1935, Pretner 1959, Pavićević 1990, Monguzzi 1993, Casale and Guéorguiev 1994, Casale and Jalžić 1999, Pavićević 2000, Quéinnec 2008, Quéinnec and Pavićević 2008, Quéinnec et al. 2008, Lohaj and Jalžić 2009, Lakota et al. 2010, Casale et al. 2012, Lohaj and Lakota 2010, Lohaj and Mlejnek 2012, Lohaj et al. 2016, Ćurčić et al. 2018). To date, including the most recently described genus *Velesaphaenops*, the Dinaric aphaenopsoid trechines are classified into twelve genera comprising 28 species.

Herein we describe two recently discovered species of the Dinaric Karst aphaenopsoid trechines. They are representatives of genera with apparently differing or even opposing distribution patterns. One species belongs to the formerly monotypic and narrowly distributed *Derossiella* and the other to the relatively widely distributed and species-rich genus *Adriaphaenops*.

The genus *Derossiella* with its type species, *Derossiella nonveilleri* Quéinnec, 2008, was described based on a single female collected in April 1999 in a nameless pit about 15 m deep, situated ca 500 m south-southeast from

the Balićeva špilja (Kraljeva jama), Balići, Mt Mosor, Croatia (Quéinnec, 2008). The locality was later identified as Mala jama, Jelinac, Džakići, Dugopolje, Croatia (Jalžić et al. 2013). The second specimen of *D. nonveilleri*, a male, was collected in the Drinovčuša jama, Kotlenice, Mt Mosor, Croatia in August 2007 by the Croatian speleobiologist Branko Jalžić (Lohaj and Jalžić 2009). Subsequently, both localities were visited multiple times by B. Jalžić or the second author (T.D.), but without success in finding additional specimens.

An immature female of a new species was first found during speleobiological research in the cave Biokovka, Golubinjak, Mt Biokovo, Croatia in September 2007, by the Croatian speleobiologist Marko Lukić. This specimen was examined by the first author (R.L.) and provisionally placed in the genus *Derossiella*. Further intensive research of the deep subterranean habitats of Mt Biokovo was executed from 2015 to 2017 by members of the Croatian Biospeleological Society, DZRJ Ljubljana, and members of the SubBioLab (Bregović et al. 2015). During one of the visits to the Pretnerova jama, Lokva, Mt Biokovo, Croatia in 2015, biology student Ester Premate found a second immature female at an approximate depth of 120 m. Finally, in June 2017, a male was collected by the second author (T.D.), again in Biokovka, at a depth of ca 300 m. Subsequent examination of all three specimens, including male genitalia, confirmed that they belong to an undescribed species of the genus *Derossiella*, whose description is provided below.

Whereas representatives of the genus *Derossiella* seem to be rare and exceptionally hard to find, almost half of the Dinaric Karst aphaenopsoid trechines, 12 out of 28 described species, are classified within the Southern Dinaric genus *Adriaphaenops*. The first species of the genus, *Adriaphaenops antroherponomimus* (Noesske, 1928), was found during the summer of 1927 in a small cave named Snježnica u Tišovom kršu (synonym = Čatol jama), Mt Bjelašnica, Gacko, Bosnia and Herzegovina by Leo Weirather, a famous Austro-Hungarian speleobiologist and an early explorer of the Dinaric Karst. Just before the Second World War, Oskar Scheibel, an entomologist from Zagreb, Croatia, described two additional species, each based on a single female specimen found in two famous caves. He described *A. pretneri* Scheibel, 1935 from Vjetrenica, Zavala, Popovo polje, Bosnia and Herzegovina, and *A. staudacheri* Scheibel, 1939 from Grbočica, Virpazar, Rijeka Crnojevića in south-eastern Montenegro. The fourth species, *A. stirni* Pretner, 1959, was discovered during the autumn of 1956 by a Slovenian entomologist, Jože Štirn, in Velja peć, a small cave located near Nikšić in Montenegro (Pretner 1959). By the end of the 20th century, speleobiological investigations made on Mt Durmitor, Montenegro led to the discovery of a new species with two subspecies, *A. zupcense zupcense* and *A. zupcense tartariensis* (Pavićević 1990, 2001). Intensive speleobiological investigations in Eastern Hercegovina, in the beginning of the 21st century, resulted in the discovery of two new species, *A. perreaui* Quéinnec & Pavićević, 2008 from Pećina u Mravinjac, Mt Bjelašnica, Trebinje, Bos-

nia and Herzegovina, and *A. kevser* Quéinnec, Pavićević & Ollivier, 2008 from Vilina pećina, Mt Lebršnik, Gacko, Bosnia and Herzegovina. Finally, five new species, *A. albanicus*, *A. jasminkoi*, *A. mlejneki*, *A. njegosiensis*, and *A. rumijaensis*, were found during speleological and speleobiological survey in the central and southern Dinarides (Bosnia and Hercegovina, Montenegro, and Albania) and were described in 2016 (Lohaj et al. 2016).

Recently, during speleobiological research performed by SubBioLab members and cavers from DZRJ Ljubljana in Pištet 4 cave (synonym = PT4), Velji Pištet, Kameno more, Risan, Montenegro in spring 2018, two specimens of the genus *Adriaphaenops* were found by the second author (T.D.). Subsequent examination confirmed that they belong to a new species described below.

Material and methods

Geomorphological framework and locality descriptions

Plate tectonics during Eocene and Miocene triggered uplift of the so called Adriatic carbonate platform, resulting in the formation of the Dinaric Karst, a 650 km long mountain range stretching along the eastern Adriatic Sea coast (Vlahović et al. 2005, Korbar 2009) from the border with the Southern Calcareous Alps to the Albanian coast (Gams 2004). Along the Dinaric Karst, protruding mountain ridges like Mt Biokovo and Orjen (and associated Kameno more) are recognized and accompanied by numerous karstic polje. Both ridges are predominantly formed by Jurassic and Cretaceous limestones and subordinate dolomites (Ad-

amson et al. 2014, Velić et al. 2017), and are characterized by high levels of yearly precipitation (Ranković 1961). Moreover, as a part of the Orjen foothills, Kameno more is considered to be the area receiving the highest amount of precipitation in Europe (Ducić et al. 2012). In addition, both areas are highly karstified and characterized by a lack of surface waters. Another common factor in both areas is the existence of many karst springs with outlets below sea level, so called "vrulje" (Bellafiore et al. 2011, Kuhta et al. 2012), whose origins are connected to oscillations of the sea level during the Miocene and Pleistocene (Bonacci 2015). The rise and fall of glaciers during the Pleistocene largely shaped the surface morphologies of both areas (Hughes et al. 2011, Žebre et al. 2013). Both areas include extensive karstic landscapes with numerous phenomena such as dolines, sinkholes, and a large number of caves. As a result of glacial melt water ingressing deeply into the vadose zone, deep caves were formed. On Mt Biokovo alone, more than 400 caves are known (Vedran Sudar personal communication), and 11 of them have depths exceeding 250 m. Most renowned are the caves of Mokre noge (831 m deep), discovered in 2009, and Amfora (788 m deep). No similar data on the number of caves exists for the areas of Orjen or Kameno more, but some of the deepest caves are of similar depths to those found on Mt Biokovo (e.g. Kozi Dira, 654 m deep, and PT4, 455 m deep). However, due to the thickness of the limestone beds, the large extent of yet unexplored terrain, and hydrological connections with the extensive karstic springs and vruljes in the coastal area, the potential for deep caves in both areas is likely to surpass the depth of 1 km.
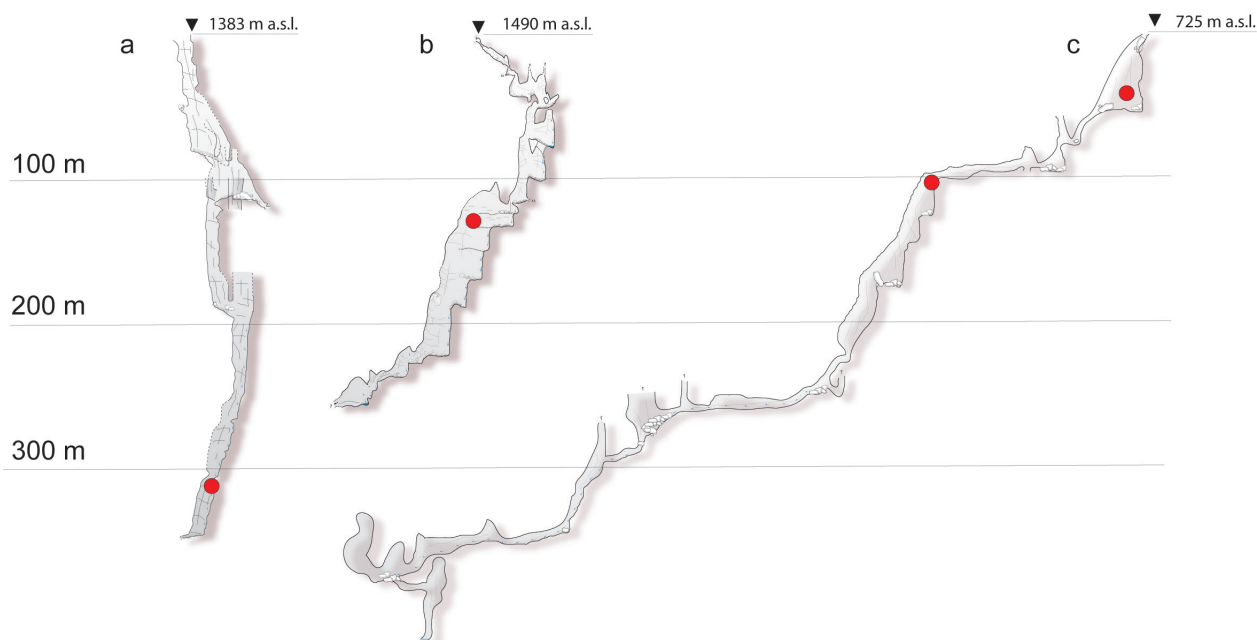
Figure 1. Cross sections of the caves from which the newly described species were collected: **a)** Biokovka, Golubinjak, Mt Biokovo, Croatia; **b)** Pretnerova jama, Lokva, Mt Biokovo, Croatia; **c)** Pištet 4 cave (PT4), Velji Pištet, Kameno more, Risan, Montenegro. Approximate finding localities are presented with red points. The original cave surveys of Biokovka and PT4 were made by Ivan Glavaš and the University of Bristol Spelaeological Society, respectively.

Due to the high endemicity of Biokovo's subterranean fauna, several speleobiological excursions were organized in recent years, culminating with the "1ˢᵗ Biospeleological expedition – Biokovo 2017" (Sudar et al. 2017). The main goal of the expedition was to gather additional distributional data on the poorly known taxa and to execute speleological surveys of some of the deep caves. During four visits in 2017, from April to October, 26 caves were visited, including eight caves exceeding 250 m in depth. Some of the deep caves were visited due to the existence of pre-expedition data on ambiguous trechine belonging to a yet undescribed species of *Derossiella*. These caves include Biokovka, Golubinjak, Vošac, Mt Biokovo, Croatia (43.322197°N, 17.050591°E; 363 m deep) (Fig. 1a) and Pretnerova jama, Lokva, Mt Biokovo, Croatia (43.33945°N, 17.03836°E; 254 m deep) (Fig. 1b) (Bregović et al. 2015). Both caves are characterized by a series of vertical pits ingressing deeply into the vadose zone. Deeper parts of both caves, starting from the approximate depth of 75 m in Pretnerova jama and 200 m in Biokovka, are characterized by films of percolating water flowing over vertical walls; the cave hygropetric. Also, the temperature span was similar in both caves, ranging from about 4 °C in the entrance parts without direct sun influence to 5 °C in the lower parts. Subterranean fauna in both caves was sampled by using baited pitfall traps, hand collecting or by mean of an aspirator. No preserving media was used in the pitfall traps; therefore, the trapped fauna was alive and mainly released upon collecting the traps.

Similarly, the Kameno more area was visited due to the speleobiological potential, the existence of already known and peculiar troglobiotic species such as *Hadesia* cf. *weiratheri* (Perreau and Pavićević 2008), and the existence of caves with the deep vadose pits. Such is also the second deepest cave in the area, Pištet 4 cave (synonym = PT4), Velji Pištet, Kameno more, Risan (42.55183°N, 18.73864°E) (Fig. 1c), whose entrance opens beneath a boulder in the bottom of a collapsed doline. Like the described caves of Mt Biokovo, PT4 is also characterized by the existence of a series of vertical pits interconnected with a stream running through the limestone beds, reaching the phreatic waters at the maximum depth of 455 m. Deeper portions of the cave, starting already at a depth of 60 m, are characterized by the existence of the cave hygropetric. The temperature in the cave was measured only once, at an approximate depth of 200 m, and was 7.4 °C. Detailed descriptions of the cave, including morphology, hydrology, and detailed speleological maps can be found in Binding (2010, 2011). Due to a time constraint, the cave was sampled using hand collecting only.

Laboratory work and morphology

The morphological structures of the beetles were examined using Olympus SZ 60 (Olympus, Tokyo, Japan) and Leica S8 APO (Leica, Wetzlar, Germany) stereoscopic microscopes. Macrophotographs were taken using a Canon 5D Mark II camera. Male and female genitalia were dissected, cleaned, and mounted in Euparal or Dimethyl-Hydantoin formaldehyde (DMHF) on transparent slides, which were later pinned under the specimens. Fine structures of male and female genitalia were studied at magnifications up to 600× by using a Leica DM1000 light microscope (Leica, Wetzlar, Germany). Drawings were made using an attached drawing tube.

Measurements

TL	total body length (measured from the anterior margin of clypeus to the apex of elytra).
L	overall length, from apex of mandibles to apex of elytra, measured along the suture.
HL	head length (measured from the anterior margin of the clypeus to the neck constriction).
HW	maximum width of head.
AL	antennal length (measured from the base of antennal scape to the apex of terminal antennal segment).
PL	Pronotal length (measured along the median line).
PW	Maximum width of pronotum, as greatest transverse distance.
EL	Elytral length (as linear distance measured along the suture from the elytral base to the apex).
EW	Maximum width of elytra.
HL/HW	Ratio head length/maximum width of head.
PL/PW	Ratio length of pronotum/maximum width of pronotum.
EL/EW	Ratio length of elytra/maximum width of elytra.

Forward slash indicates separate labels.

Acronyms

CNHM	Collection of Croatian Natural History Museum, Zagreb, Croatia
PMSL	Collection of Slovenian Natural History Museum, Ljubljana, Slovenia
CRL	Private collection of Roman Lohaj, Slovakia.

Higher classification of the Trechini used here follows Belousov (2017).

Results

Genus *Derossiella* Quéinnec, 2008

Figs 2–5

Derossiella Quéinnec, 2008: 164, by monotypy; type species: *Derossiella nonveilleri* Quéinnec, 2008.

Material examined. Male labelled: Croatia, Split, Mt Mosor, Kotlenice, Tukići, Bradarića staje, Drinovčuša jama, 01.08.2007 B. Jalžić lgt. (white label, printed) / *Derossiella nonveilleri* Quéinnec, 2008, R. Lohaj det. 2008 (white label, printed), CNHM.

Derossiella lukici sp. n.

http://zoobank.org/BCB33301-A988-465D-A0F5-82060EAD16B0
Figs 2–5

Type series. Holotype male labelled: "Croatia, Mt Biokovo, Golubinjak, Biokovka, -300 m, 24.6.2017, T. Delić lgt." (white label, printed) / "DNA extraction RL–07" (orange label, printed) / "HOLOTYPUS *Derossiella lukici* sp. n. Lohaj & Delić des. 2018" (red label, printed), (CNHM, voucher code 600: ZAG; ZEC2, 4194 Coll. Jalžić). Paratypes: one female (right posterior tarsus missing) labelled: "Croatia, Mt Biokovo, Golubinjak, Biokovka, 2.9.2007, M. Lukić lgt." (white label, printed) / "PARATYPUS *Derossiella lukici* sp. n. Lohaj & Delić des. 2018" (red label, printed), (CNHM, voucher code 600: ZAG; ZEC2, 4195 Coll. Jalžić)., one female (last three antennomeres of right antenna missing) labelled: "Croatia, Mt Biokovo, Lokva, Pretnerova, -120 m, 19.05.2015, E. Premate lgt." (white label, printed) / "PARATYPUS *Derossiella lukici* sp. n. Lohaj & Delić des. 2018" (red label, printed), (CRL).

Diagnosis. Medium-sized aphaenopsoid trechine with morphological features fully matching generic description proposed by Quéinnec (2008). Head long, parallel-sided, with complete, deep frontal furrows reaching neck constriction and two pairs of supraorbital setae, posterior setae doubled. Eyes absent, mentum with simple tooth. Aphaenopsoid habitus with very narrow head and pronotum; elytra oblong-oval, 2.6 times wider than head and pronotum. Hind angles of pronotum without setae. Surface completely glabrous, striae absent, elytral chaetotaxy with macrochetae and microchetae. Cuticle depigmented, reddish-yellow, body strongly flattened dorso-ventrally, with very long and slender legs and antennae (Figs 3, 4). Closely related to the type species of the genus, *Derossiella nonveilleri*, from which it differs by paired posterior supraorbital setiferous punctures, differently shaped elytra with higher number of macro- and microchetae, narrower pronotum, as well as by the differently shaped aedeagus.

Description. L: 5.5 mm (PT)–6.0 mm (HT), TL: 4.8 mm (PT)–5.4 mm (HT). Head relatively large, nearly parallel-sided, with maximum width behind middle, distinctly longer than wide (index HL/HW 1.35 (PT)–1.42 (HT), slightly wider than pronotum, sparsely pubescent. Frontal furrows deep, complete, reaching neck constriction, slightly divergent posteriorly. Anterior pair of supraorbital setae situated before middle of head length, posterior supraorbital setae paired, two setae on each side of head situated close to neck constriction. Neck constriction distinct; genae gently convex. Clypeus and labrum with three pairs of setae, outer pairs longer. Antennae length 4.9 mm (HT)–4.3 mm (PT), scape as long as pedicel, almost as long as terminal antennomere.
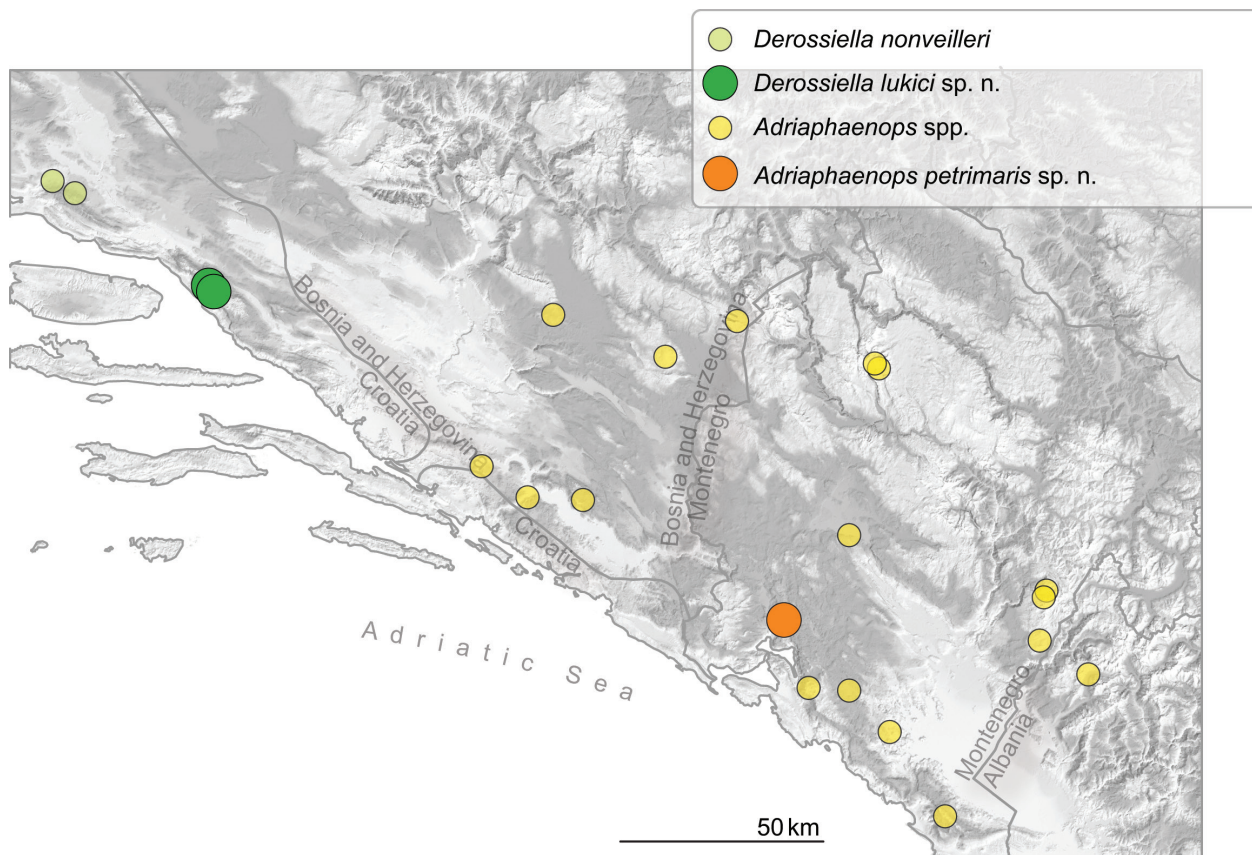
Figure 2. Geographical distribution of the Dinaric aphaenopsoid trechines of the genera *Derossiella* and *Adriaphenops*. Source of data: http://subbio.net/db/

Figure 3. *Derossiella lukici* sp. n. in its habitat in the cave Biokovka, Golubinjak, Mt Biokovo (Photo courtesy of P. Bregović).
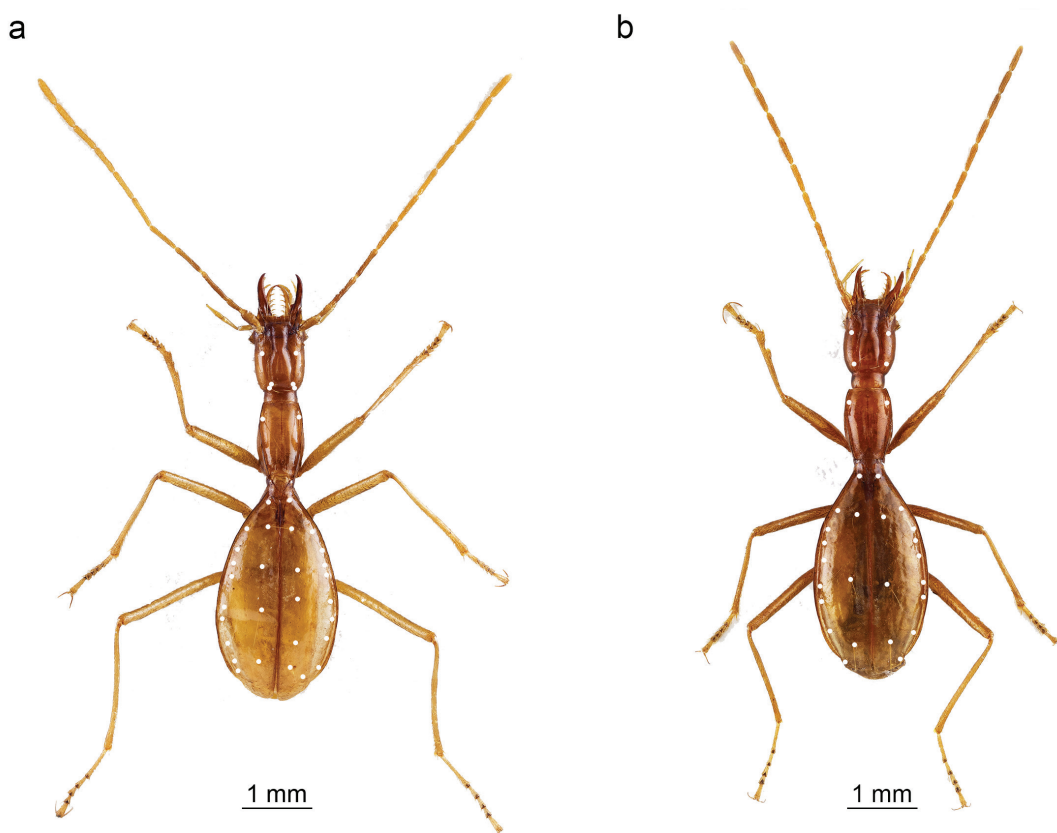
Figure 4. Habitus of *Derosiella* species. *Derossiella lukici* sp. n. **(a)** and *Derossiella nonveilleri* **(b)**. Chetotaxy is presented as white points (photo courtesy of Dušan Beňo).

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a b c d
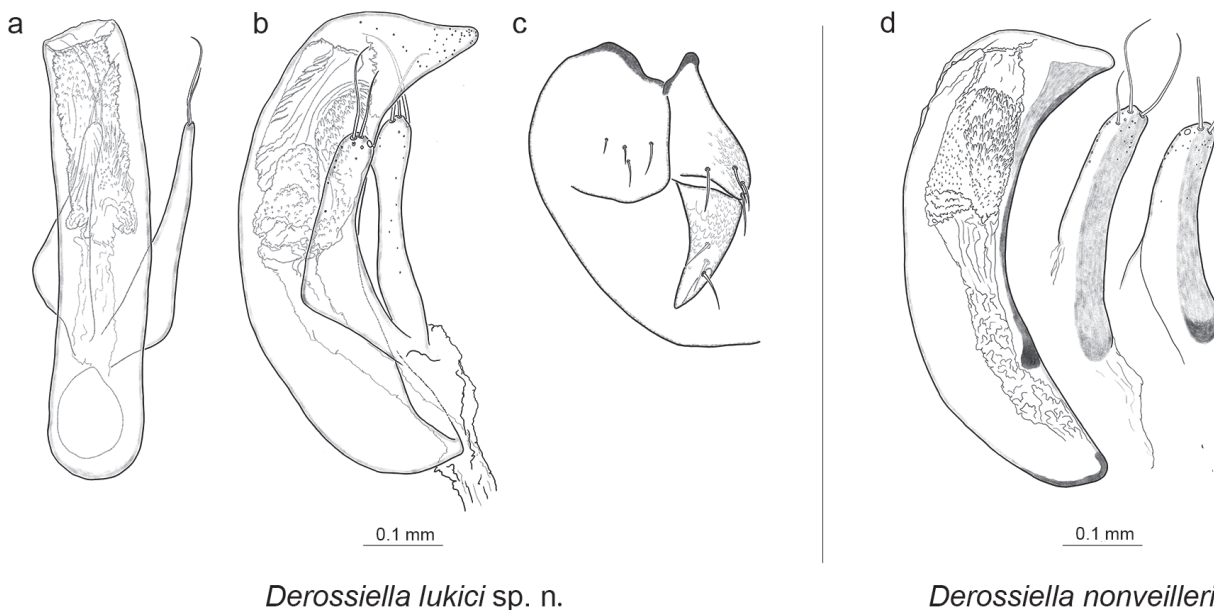
Derossiella lukici sp. n.

Derossiella nonveilleri

Figure 5. Male and female genitalia of *Derossiella* representatives: aedeagus of *D. lukici* sp. n., dorsal view **(a)**; and lateral view **(b)**; female genitalia gonocoxite 1 and 2 (basal and apical segments of gonostylus) copulatory piece of *D. lukici* sp. n. **(c)**; and *D. non-veilleri*, lateral view of male aedeagus with parameres detached **(d)** (illustration by Fedor Čiampor).

Pronotum elongated, slightly longer and narrower than head, with maximum width in anterior third, index PL/PW 1.75 (PT)–1.83 (HT), only slightly narrowed anteriorly, posterior part distinctly narrower than anterior. Surface glabrous, median furrow distinct, visible in whole pronotal length. Propleura visible from dorsal aspect in basal two-thirds. Anterior angles of pronotum not protruding, posterior angles obtuse. Lateral furrows well developed, deep, with one pair of anterolateral setae, situated in the apical fifth of pronotal length.

Elytra subovate elongate, distinctly longer than wide, index EL/EW 1.74 (PT)–1.85 (HT), with maximum width in posterior third; elytral surface glabrous, without pubescence; striae absent. Stria 3 with 4–5 (3–4 discal and one preapical) macrochetae and 3 or 4 microchetae situated between macrochetae, stria 5 with 4 or 5 microchetae (Fig. 4). Humeral group of umbilicate pores not aggregated, first anterior pore of humeral group isolated and situated at level of the first discal seta.

Legs long, slender, densely pubescent. First two tarsomeres of male protarsi distinctly dilated and protracted at their internal margins. Tarsal claws very long and slender, without traces of denticulation on their internal sides.

Male genitalia. Aedeagus (Fig. 5) 0.58 mm long, relatively robust, regularly wide, lacking apical constriction, laterally flattened. Parameres relatively long and slender, longer than half of the length of aedeagus. Apex very short, tip obtuse. Each paramere at apex with three setae, two long, and one short.

Female genitalia as in Figure 5.

Etymology. Patronymic, dedicated to our dear friend Marko Lukić (Zagreb, Croatia), enthusiastic speleologist and speleobiologist, taxonomic specialist on subterranean Collembola, and collector of the first specimen of the new species.

Differential diagnosis. *Derossiella lukici* sp. n. is closely related to the type species of the genus, *Derossiella nonveilleri*. However, these two species can be easily recognized using the following key:

1(2) Head with 2 posterior supraorbital setiferous punctures on each side, which are very close to each other. Elytra with maximum width in the posterior third. Putative stria 3 with 4 or 5 macrochetae and 4–6 microchetae, putative stria 5 with 3 or 4 microchetae (Fig. 4). Pronotum narrower, index PL/PW: 1.75–1.83, anterior angles not protruding. Aedeagus (Fig. 5) shorter, more robust. L: 5.5–6.0 mm. Croatia, Mt Biokovo......................................*Derossiella lukici* sp. n.

2(1) Head with only 2 posterior supraorbital setiferous puncture on each side. Elytra with maximum width in middle. Putative stria 3 with 3 macrochetae and 2 microchetae between each macrochetae, putative stria 5 with 1 microcheta in basal fourth (see Fig. 4). Pronotum wider, index PL/PW: 1.43–1.44, anterior angles slightly protruding. Aedeagus (Fig. 5) longer and slenderer. L: 5.4–5.8 mm. Croatia, Mt Mosor........................*Derossiella nonveilleri* Quéinnec, 2008

Distribution. So far this species is known from the two pits on Mt Biokovo, the type locality, Biokovka, Golubinjak and Pretnerova jama, Lokva. All three specimens were found in deeper parts of the caves, attaining depths of 120 to 300 m. They were all found walking on the "moon-milk", a white, pastelite material consisting of microbiologically transformed microcrystalline calcites with high water content (60–90%), and near the cave hygropetric.

Associated subterranean coleopteran fauna observed in the pits:

1　　　　　Biokovka, Golubinjak, Biokovo, Croatia:
Carabidae: Trechinae
　　Neotrechus dalmatinus (Miller, 1861)
Leiodidae: Cholevinae
　　Leptomeson biokovensis Giachino, Bregović & Jalžić, 2012
　　Radziella styx Casale & Jalžić, 1988
　　Speoplanes giganteus biocovensis Müller, 1934

2　　　　　Pretnerova jama, Lokva, Biokovo, Croatia:
Carabidae: Trechinae
　　Dalmataphaenops chiarae Monguzzi, 1993
Carabidae: Sphodrini
　　Laemostenus cavicola (Schaum, 1858)
Leiodidae: Cholevinae
　　Leptomeson biokovensis Giachino, Bregović & Jalžić, 2012
　　Radziella styx Casale & Jalžić, 1988
　　Speoplanes giganteus biocovensis Müller, 1934
Staphylinidae: Pselaphinae
　　Pselaphinae gen.

Genus *Adriaphaenops* Noesske, 1928

Adriaphaenops Noesske, 1928: 5, type species: *Trechus antroherponomimus* Noesske, 1928 by monotypy, type locality: Čatol jama des Bjelasica-Gebirges (weitere Umgebung von Gacko) im nord-ostherzegowinischen Karstlande.

Aphaenopsis (sg. *Adriaphaenops*) Jeannel, 1928: 793, Pretner 1959: 79, Casale and Laneyrie 1982: 159, Vigna Taglianti and Sciaky 1988: 166, Pavićević 1990: 365.

Aphaenops (sg. *Adriaphaenops*) Scheibel, 1935: 34, Pavićević 2001: 33.

Adriaphaenops Sciaky & Vigna Taglianti, 1990: 171, Monguzzi 1993: 238, Casale and Guéorguiev 1994: 421, Drovenik and Peks 1994: 43, Moravec et al. 2003: 289, Quéinnec 2008: 157, Quéinnec and Pavićević 2008: 144, Quéinnec et al. 2008: 154, Lakota et al. 2010: 100, Lohaj and Lakota 2010: 78.

Revision. Lohaj et al. 2016.

Adriaphaenops petrimaris sp. n.

http://zoobank.org/7C58EE0D-541B-4C5A-9937-CCDE8AAF01C5
Figs 2, 6, 7, 8, 9

Type series. Holotype male labelled: "MONTENEGRO, Risan, Velji Pištet, Kameno more, cave Pištet 4 (PT4), (18.73864°E, 42.55183°N), - 40 m, 3.5.2018, T. Delić lgt." (white label, printed) / "DNA extraction XA475" (white

Figure 6. *Adriaphaenops petrimaris* sp. n. in its natural habitat in Pištet 4 cave, Velji Pištet, Kameno more, Risan.

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9
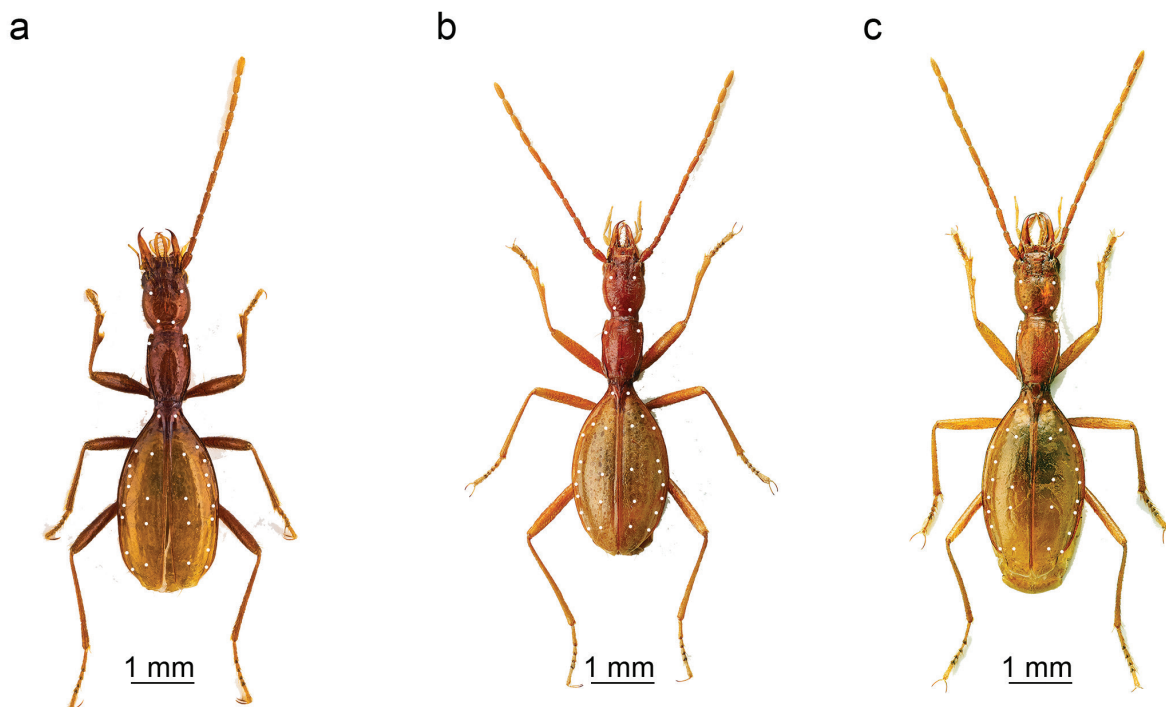
Figure 7. Habitus of morphologically similar *Adriaphaenops* species. *Adriaphaenops petrimaris* sp. n. **(a)**, *Adriaphaenops rumijaensis* **(b)** and *Adriaphenops kevser* **(c)**. Chetotaxy is presented as white points (photo courtesy of Dušan Beňo).

label, printed) / "HOLOTYPUS *Adriaphaenops petrimaris* sp. n. Lohaj & Delić des. 2018" (red label, printed) (PMSL, voucher code Coleoptera–11519). Paratype one female (left antenna missing), labelled: MONTENEGRO, Risan, Velji Pištet, Kameno more, cave Pištet 4 (PT4), (18.73864°E, 42.55183°N), - 100 m, 2.5.2018, T. Delić lgt." (white label, printed) / "PARATYPUS *Adriaphaenops petrimaris* sp. n. Lohaj & Delić des. 2018" (red label, printed) (CRL).

Diagnosis. A medium-sized trechine beetle with aphaenopsoid features: head and pronotum elongate; elytra ovoid, strongly narrowed at the base, obviously wider than head and pronotum; body depigmented, strongly flattened, covered with sparse pubescence (Figs 6, 7). This new species is mainly characterized by the presence of four pairs of dorsal setae (three discal and one preapical) on elytra. This character is so far present only in presumably closely related species, *A. kevser* and *A. rumijaensis*; see identification key below.

Description. L: 5.0 mm (HT)–5.4 mm (PT), TL: 4.7 mm (HT)–5.1 mm (PT). Head relatively large, rounded, with maximum width behind middle, distinctly longer than wide (index HL/HW 1.23 (HT)–1.33 (PT), slightly wider than pronotum, sparsely pubescent. Frontal furrows weakly impressed, short, ending in the front half of head. Two pairs of long supraorbital setae present; neck constriction distinct; genae gently convex. Clypeus and labrum with three pairs of setae, outer pairs longer. Antennae length 3.3 mm (HT)–3.4 mm (PT), scape as long as pedicel, almost as long as terminal antennomere.

Pronotum elongate, slightly longer and wider than head, with maximum width in middle, only very slightly narrowed anteriorly, basal part distinctly narrower than anterior (index PL/PW 1.66 (HT)–1.57 (PT)), sparsely pubescent, setae long, suberect; median furrow weakly marked, visible in the middle part of pronotum. Propleura visible from dorsal aspect only in basal half. Anterior angles of pronotum distinctly protruding, obtuse, posterior angles obtuse. Lateral furrows developed, deep, with one pair of anterolateral setae, situated in apical fourth of pronotal length.

Elytra subovate elongate, distinctly longer than wide (index EL/EW 1.74 (HT)–1.78 (PT)), with maximum width in middle; elytral surface covered with very sparse, long and erect pubescence; striae absent. Site of stria 3 with four (three discal and one preapical) setae, humeral group of umbilicate pores not aggregated, first anterior pore of humeral group isolated and situated before the level of the first discal seta. Pore 5 located nearer to pore 6 than to pore 4.

Legs long, slender, densely pubescent. First two tarsomeres of male protarsi distinctly dilated and protracted at their internal margins. Tarsal claws very long and slender, without traces of denticulation on their internal sides.

Male genitalia (Fig. 8): aedeagus very long and slender, gradually narrowed towards apex in lateral aspect, sagittal aileron large, endophallus without distinct copulatory piece. Parameres long and slender, with two long setae at apex. Female genitalia as in Figure 9.

Etymology. Topotypic, referring to the toponym where the Pišet 4 cave is situated, Kameno more (in English, Sea of stone and in Latin, Mare petris).

Differential diagnosis. Genus *Adriaphaenops* currently comprises 13 described species, including *A. petrimaris* sp. n.

This species, *A. kevser*, and *A. rumijaensis* form a group of species with four discal setae (three dorsal and one preapical) on elytra, with elytral pubescence in all three species sparser in comparison to the other species (Fig. 7). *A. petrimaris* morphologically resembles *A. kevser*, described from Mt Lebršnik, Bosnia & Hercegovina. These two species can be easily recognized by the shape of head, pronotum, and aedeagus (Figs 7, 8) (see identification key below).

Distribution. So far this species is known only from the type locality, Pištet 4 cave (synonym = PT4), Kameno more, Risan, Montenegro. Both specimens, HT and PT, were found walking on the wet and damp vertical cave walls at the depth of 40 and 100 m.

Associated subterranean fauna observed in the pit:

Carabidae: Trechinae:
Neotrechus suturalis ssp. (Schaufuss, 1864)
Neotrechus paganettii ssp. (Ganglbauer, 1896)
Leiodidae: Cholevinae:
Blattochaeta sp.
Anthroherpon sp.
Hadesia cf. *weiratheri* Zariquiey, 1927
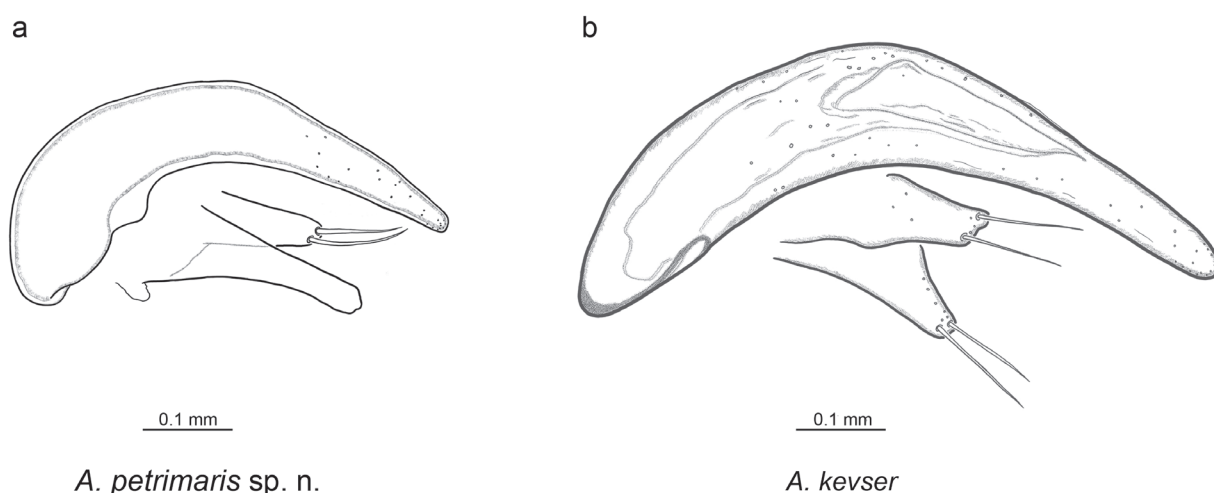
Figure 8. Male genitalia of *Adriaphaenops petrimaris* sp. n. **(a)** and similarly looking *A. kevser* **(b)** (illustrations by Fedor Čiampor).
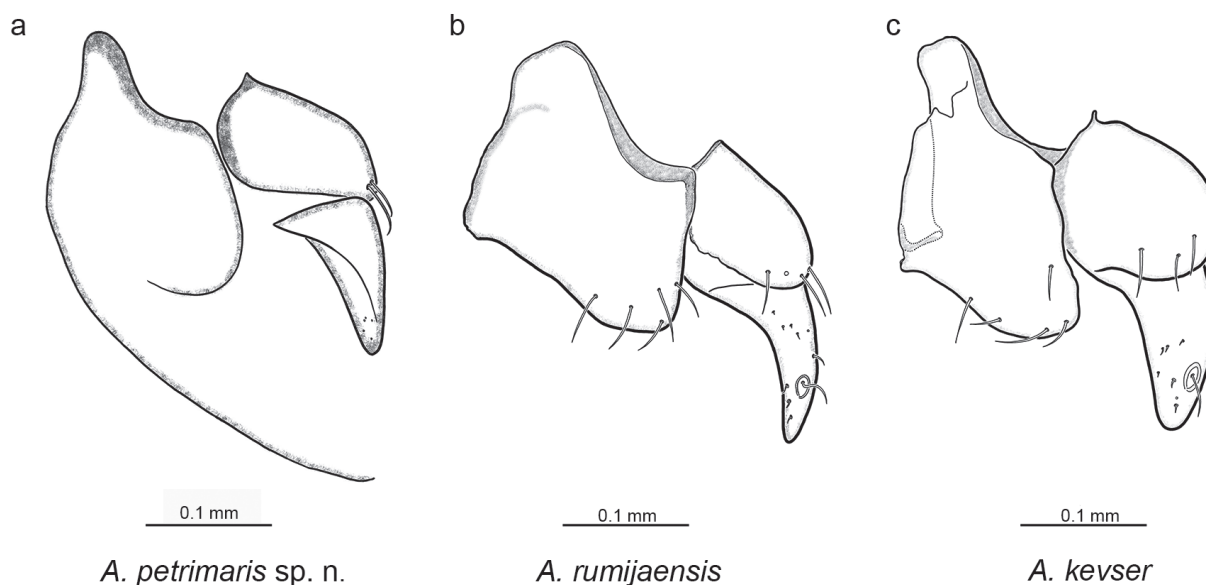
Figure 9. Female genitalia; gonocoxite 1 and 2 (basal and apical segments of gonostylus) of *Adriaphaenops petrimaris* sp. n. **(a)**, *A. rumijaensis* **(b)**, and *A. kevser* **(c)** (illustrations by Fedor Čiampor).

Identification key to the species of the genus *Adriaphaenops* Noesske (for the drawings and details, see Lohaj et al. 2016)

1(6)   Head almost rounded, wider 2

2(5)   Head with 2 pairs of supraorbital setae 3

3(4)   Clypeus with 4 pairs of setae, pronotum wider, index PL/PW 1.21, base of pronotum as wide as anterior part L: 4.65–5 mm. BiH, Hercegovina, Popovo polje ....9. *A. pretneri* Scheibel, 1935

4(3)   Clypeus with 3 pairs of setae, pronotum narrower, index PL/PW 1.42, base of pronotum narrower than anterior part. L: 5.5 mm. BiH, Hercegovina, Nevesinje.. 3. *A. jasminkoi* Lohaj et al., 2016

5(2)   Head without supraorbital setae or these setae are indistinguishable from head pubescence L: 4.6 mm. BiH, Hercegovina, Turica, Mt Bjelašnica...7. *A. perreaui* Quéinnec & Pavićević, 2008

6(1)   Head elongate or parallel-sided, distinctly narrower 7

7(12)   Elytra with 4 pairs of discal setae (3 dorsal and 1 preapical), only very sparsely pubescent 8

8(11)   Pronotum widest in anterior third/middle. Ultimate segment of maxillar palpi distinctly shorter than penultimate 9

9(10)   Pronotum widest in anterior third, distinctly narrowed anteriorly, head narrower. Aedeagus wider in lateral view, apex widely rounded (Fig. 8) L: 4.8–5.7 mm. BiH, Hercegovina, Mt Lebršnik... .... 4. *A. kevser* Quéinnec, Pavićević & Ollivier, 2008

10(9)   Pronotum widest in middle, only very slightly narrowed anteriorly, head more rounded. Aedeagus narrower in lateral view, apex pointed (Fig. 7). L: 5.0–5.4 mm. Montenegro, Risan, Kameno more ....8. *A. petrimaris*, sp. n.

11(8)   Pronotum widest in anterior fourth. Ultimate segment of maxillar palpi as long as penultimate. L: 5.05–5.4 mm. Montenegro, Mt Rumija .... 10. *A. rumijaensis* Lohaj et al., 2016

12(7)   Elytra with 3 pairs of discal setae (two dorsal and one preapical), densely pubescent... 13

13(16)   Head without supraorbital setae or these setae are very short, indistinguishable from head pubescence............. 14

14(15)   Clypeus with 4 pairs of setae. Smaller species, L: 3.8 mm. Montenegro, Virpazar, Trnovo.................................... .... 11. *A. staudacheri* Scheibel, 1939

15(14)   Clypeus with three pairs of setae. Larger species L: 4.9 mm. Montenegro, Cetinje. 6. *A. njegosiensis* Lohaj et al., 2016

16(13)   Head with one or two pairs of long supraorbital setae 17

17(20)   Head with only posterior pair of supraorbital setae, anterior pair absent 18

18(19)   Clypeus with four pairs of setae, frontal furrows longer, exceeding half length of head, anterior angles of pronotum rounded. L: 4.7–5.75 mm. Montenegro, Kučke planine Mts ....5. *A. mlejneki* Lohaj et al., 2016

19(18)   Clypeus with three pairs of setae, frontal furrows distinctly shorter than half length of head, anterior angles of pronotum pointed. L: 4.65 mm. Albania, Shkodër, Boga.. 1. *A. albanicus* Lohaj et al., 2016

20(17)   Head with both anterior and posterior pairs of supraorbital setae 21

21(22)   Clypeus with 3 pairs of setae, head wider, index HL/HW 1.10–1.15, posterior angles of pronotum protruding, acute. L: 3.5–5.1 mm. Montenegro, Mt Durmitor... 13. *A. zupcense* Pavićević, 1990

22(21)   Clypeus with 4 pairs of setae, head narrower, index HL/HW 1.33–1.36, posterior angles of pronotum not protruding, obtuse... 23

23(24)   Head parallel-sided, pronotum narrower, index PL/PW 1.5, with maximum width in anterior fourth. L:4.7–4.85 mm. BiH, Hercegovina, Gacko, Mt Bjelašnica ....2. *A. antroherponomimus* (Noesske, 1928)

24(23)   Head slightly rounded, pronotum wider, index PL/PW 1.35, with maximum width in anterior third. L: 5–5.35 mm. Montenegro, Nikšić...12. *A. stirni* (Pretner, 1959)

Annotated catalogue of the genus *Adriaphaenops* Noesske

1   *albanicus* Lohaj, Lakota, Quéinnec, Pavićević & Čeplík, 2016: 518 (*Adriaphaenops*). Type locality: Albania, District Shkodër, V. Boga, Mts Thatë, Grotte No. 25.
    Distribution: Albania, Prokletije Mts.

2   *antroherponomimus* Noesske, 1928: 7 (*Trechus*). Type locality: Čatol jama des Bjelasica-Gebirges (weitere Umgebung von Gacko) im nordostherzegowinischen Karstlande [= Sniježnica, Tišov krš]). Distribution: Bosnia and Hercegovina, Mt Bjelašnica near Gacko.

3   *jasminkoi* Lohaj, Lakota, Quéinnec, Pavićević & Čeplík, 2016: 520 (*Adriaphaenops*). Type locality: Bosnia and Hercegovina, Nevesinje, Bišina village, Novakuša (Novakova) pećina.
    Distribution: Bosnia and Hercegovina, Nevesinje.

4   *kevser* Quéinnec, Pavićević & Ollivier, 2008: 154 (*Adriaphaenops*). Type locality: Vilina pećina, alt. 1840 m a.s.l., Lebršnik planina, eastern Hercegovina, Bosnia and Hercegovina)
    Distribution: Bosnia & Hercegovina, Mt Lebršnik.

5   *mlejneki* Lohaj, Lakota, Quéinnec, Pavićević & Čeplík, 2016: 524 (*Adriaphaenops*). Type locality: Montenegro, Žijovo Mts, Šila Mt env., Gornje Stravče, Katun Guzovalja, 1690 m a.s.l.,

Prometheus abyss (−130 m). Other localities: Montenegro, Žijovo, Borova jama 1, Borova jama 2, Snježna jama, Milići-Miliči snježnica.
Distribution: Montenegro, Kučke planine Mts (=Žijovo Mts).

6   *njegosiensis* Lohaj, Lakota, Quéinnec, Pavićević & Čeplík, 2016: 526 (*Adriaphaenops*). Type locality: Cetinjska pećina, Cetinje, Montenegro. Other localities: Lovćen Mts, Štirovnik, Dvogrla jama (synonym = Kétlyukú-barlang), −130 m (T. Delić lgt., new locality).
Distribution: Montenegro, Mt Lovćen.

7   *perreaui* Quéinnec & Pavićević, 2008: 144 (*Adriaphaenops*) Type locality: Pećina u Mravinjac, alt. 1000 m a.s.l., Turica, Motka, Bjelašnica planina, Bosnia and Hercegovina.
Distribution: Bosnia and Hercegovina, Mt Bjelašnica near Turica, above Popovo polje.

8   *petrimaris* sp. n. (*Adriaphaenops*). Type locality: Montenegro, Risan, Kameno more, Velji Pištet, Pištet 4 cave (synonym = PT4) (42.55183°N, 18.73864°E).
Distribution: Montenegro, Risan, Kameno more.

9   *pretneri* Scheibel, 1935b: 35 (*Adriaphaenops*). Type locality: Windhohle bei Zavala, Herzegowina [= Vjetrenica pećina]. Another locality: Popovo polje, Turkovići, Žira jama (Lohaj et al. 2017).
Distribution: Bosnia and Hercegovina, Popovo polje.

10   *rumijaensis* Lohaj, Lakota, Quéinnec, Pavićević & Čeplík, 2016: 522 (*Adriaphaenops*). Type locality: Montenegro, Virpazar, Mt Rumija, ca 1100 m a.s.l. Phoenix (cave) (−70 m).
Distribution: Montenegro, Mt Rumija.

11   *staudacheri* Scheibel, 1939: 372 (*Adriaphaenops*). Type locality: in der "Grbovica", etwa 500 Meter langen Höhle am Rande des Polje von Trnovo, bei Virpazar in Montenegro [= Grbočica pećina]
Distribution: Montenegro, Virpazar.

12   *stirni* Pretner, 1959: 83 (*Aphaenopsis*). Type locality: Velja Peć appelatur apud Carev most in margine meridiano regionis Nikšićko polje (Respublica Montenegro)
Distribution: Montenegro, Nikšić.

13   *zupcense zupcense* Pavićević, 1990: 365 (*Aphaenopsis*). Type locality: Durmitor: pećina u Zupcima (Sedleni do, 1900–2000 m a.s.l.)

14   *zupcense tartariensis* Pavićević, 2001: 35 (*Aphaenops*). Type locality: Montenegro, Mt Durmitor, Jama na Vjetrenim Brdima ("Pit on the Windy Hills"), 2196 m a.s.l. (entrance).
Distribution: Montenegro, Mt Durmitor.

Discussion

The vast landscape of the Dinaric Karst is characterized by the existence of numerous karstic fields and mountain ridges reaching well above 2000 m a.s.l. While most of the lowland areas, including most of the karstic fields, were intensively sampled already in the early days of speleobiology, high mountainous areas received far less attention, mostly due to their physical remoteness and the challenging logistical demands intrinsic to their exploration. However, in the last 25 years many new beetle species and even genera have been found and described from such areas (Monguzzi 1993, Casale et al. 2012, Lohaj et al. 2016). Their discovery was largely dependent on the improvements of caving techniques, which enabled speleological surveys and speleobiological sampling in the deep vadose caves of the Dinaric Karst that reach a maximum depth of 1471 m (Lukina jama–Trojama system, Nothern Velebit, Croatia) (Bakšić et al. 2013).

Sixteen of 30 Dinaric aphaenopsoid trechines, including those described here, were discovered in vertical pits. Moreover, if we consider only those species discovered after 1980, 16 of 23 species (70%) were discovered in caves where vertical caving equipment is needed. The rest were predominantly discovered in remote and hardly accessible karstic areas, while only a few of them were found after systematic sampling of already known caves. Along with the aphaenopsoid trechine beetles discovered throughout the Dinaric Karst, new species and genera of Cholevinae were also discovered. Some genera include morphologically and ecologically specialized hygropetricolous Cholevinae: *Radziella* Casale & Jalžić, 1988; *Tartariella* Nonveiller & Pavićević, 1999; *Croatodirus* Casale, Giachino & Jalžić, 2000; *Nauticiella* Moravec & Mlejnek, 2002; *Velebitodromus* Casale, Giachino & Jalžić, 2004 and *Kircheria* Giachino & Vailati, 2006. All of these filter-feeding genera are dependent on the constant influx of percolating waters in the vadose zone, which enables functioning of the cave hygropetric (Sket 2004, Giachino and Vailati 2006).

Genera morphologically similar to the Dinaric aphaenopsoid trechines are also found among subterranean trechines distributed in the Alps or Pyrenees (Faille et al. 2013). Common morphology of these genera is characterized by elongated appendages, head, and a pronotum, with ovoid and basally strongly narrowed elytra, which are wider than the head or pronotum. Such morphological characteristics are present also in other groups of Balkan, American, and Asian specialized Carabidae (Gómez et al. 2016, Luo et al. 2018, Vrbica et al. 2018) and are probably a consequence of directional selection driving the convergent evolution of elaborated traits in the subterranean fauna. However, such morphological derivations still lack a proper evolutionary or functional explanation (but see Luo et al. 2018).

Representatives of the Dinaric aphaenopsoid trechines are generally hard to find, inaccessible, and mostly known from a few individuals caught by hand or, as in several cases, "accidentally" by long-term pitfall trapping. The only exceptions to this rule are representatives of the genera *Acheroniotes* (Lohaj and Lakota 2012) and *Dalmataphaenops* (our own unpublished data). The lat-

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ter genera are known to locally form large populations. Although the Dinaric aphaenopsoid trechines are often considered to be specialized predators (Quéinnec 2008), little is known about their biology or their role in the subterranean communities. Moreover, as they are not prone to pit-fall trapping, most of our knowledge on their biology and behavior is based on scarce field observations. At present, we are not aware of their phylogenetic relations and biogeography or evolutionary trends, as only several samples of Dinaric taxa were included into phylogenetic analyses on the continental scale (Faille et al. 2013). Some of the genera, like *Scotoplanetes* (Lakota et al. 2010), and the species of *Derossiella* described above, have elongate legs and claws. Also, when compared to other aphaenopsoid genera in the Dinaric Karst, these genera are characterized by thin integument (Quéinnec 2008). These characters can to some extent be connected with specialization to the habitat these animals most probably live in. Most representatives of these genera, including the specimens described here as *D. lukici* sp. n., were collected directly from 'moonmilk' or the cave hygropetric (Lakota et al. 2010, our data). Such morphological adaptations offer possibilities to hypothesize the adaptive value of these characters to predation on specialized taxa found in the cave hygropetric (hygropetricolous beetles, springtails, leeches, and crustaceans). Unfortunately, such hypotheses remain untested as most of the specimens were preserved in low concentration ethanol or even vinegar, causing degradation of DNA material and minimizing the possibilities for later DNA isolation of the gut content.

Another interesting hypothesis to be tested is the adaptive value of divergent morphological characters, as *Derossiella* and *Adriaphaenops* are known to exist in sympatry with other specialized aphaenopsoid trechines, *Dalmataphaenops* and *Scotoplanetes*, respectively. This raises the question of niche differentiation among the specialized subterranean beetles, similarly to what was already shown in other subterranean taxa (Trontelj et al. 2012, Vergnon et al. 2013). However, with the extremely low number of specimens and the already mentioned lack of a phylogenetic context for the Dinaric aphaenopsoid trechines we are unable to place such hypotheses in their proper evolutionary context. Although data on the Dinaric aphaenopsoid trechines are lacking, only the publication of all known data will enable recognition of the distributional patterns of the group, the mechanisms underlying these patterns, general biology of the taxa, and the potential need to employ suitable conservation policies.

Acknowledgements

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Redescriptions of thirteen species of chewing lice in the *Brueelia*-complex (Phthiraptera, Ischnocera, Philopteridae), with one new synonymy and a neotype designation for *Nirmus lais* Giebel, 1874

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Abstract

Thirteen species of chewing lice in the *Brueelia*-complex are redescribed and illustrated. They are: *Brueelia blagovescenskyi* Balát, 1955, ex *Emberiza schoeniclus* (Linnaeus, 1758); *B. breueri* Balát, 1955, ex *Chloris chloris* (Linnaeus, 1758); *B. conocephala* (Blagoveshchensky, 1940) ex *Sitta europaea* (Linnaeus, 1758); *B. ferianci* Balát, 1955, ex *Anthus trivialis* (Linnaeus, 1758); *B. glizi* Balát, 1955, ex *Fringilla montifringilla* Linnaeus, 1758; *B. kluzi* Balát, 1955, ex *Fringilla coelebs* Linnaeus, 1758; *B. kratochvili* Balát, 1958, ex *Motacilla flava* Linnaeus, 1758; *B. matvejevi* Balát, 1981, ex *Turdus viscivorus* Linnaeus, 1758; *B. pelikani* Balát, 1958, ex *Emberiza melanocephala* Scopoli, 1769; *B. rosickyi* Balát, 1955, ex *Sylvia nisoria* (Bechstein, 1792); *B. vaneki* Balát, 1981, ex *Acrocephalus schoenobaenus* (Linnaeus, 1758); *Guimaraesiella haftorni* (Balát, 1958) ex *Turdus iliacus* Linnaeus, 1758; *G. lais* (Giebel, 1874) ex *Luscinia megarhynchos* (Brehm, 1831). Redescriptions are made from type material where available. Holotypes are identified in Balát's material when possible, and lectotypes are designated for *B. blagovescenskyi*, *B. breueri*, *B. glizi*, *B. ferianci*, *B. kluzi*, *B. kratochvili*, *B. pelikani*, and *B. rosickyi*; a neotype of *Nirmus lais* Giebel, 1874 is designated. *Brueelia weberi* Balát, 1982, is placed as a synonym of *Brueelia conocephala* (Blagoveshchensky, 1940).

Introduction

Correct identification of chewing lice (Phthiraptera) to species level is often hampered by inadequate species descriptions. During work on a recent revision of the species-rich *Brueelia*-complex (Gustafsson and Bush 2017), it became apparent that the majority of the described species in this group are impossible to identify without comparison with type material. Several recent publications have provided redescriptions of some key taxa (e.g., Mey and Barker 2014, Valim and Cicchino 2015, Gustafsson and Bush 2017, Mey 2017, Gustafsson

et al. 2018a); however, the majority of the proposed species in this complex are still poorly described and only partially illustrated.

To partially address the difficulties in identifying lice in this complex, we here redescribe 13 species of chewing lice in the *Brueelia*-complex: 10 species in the genus *Brueelia* Kéler, 1936 and two species in the genus *Guimaraesiella* Eichler, 1949. Redescriptions of 10 of these species are based on type material, complemented in some cases by non-type material. In most species, the present status of Balát's specimens is addressed, including notes on specimens that must be regarded as lost. To

stabilize the nomenclature and anchor the descriptions and illustrations here to specific specimens, we also designate a number of lectotypes and paralectotypes from Balát's syntype series.

In addition, we redescribe *Nirmus lais* Giebel, 1874, based on specimens in Balát's collection, and designate one of these as the neotype of this species. Moreover, we here consider one proposed species name, *Brueelia weberi* Balát, 1982, as a synonym of an older species name, *Degeeriella conocephala* Blagoveshtchensky, 1940. We take the opportunity to redescribe *D. conocephala* as well, based on non-type specimens in Balát's collection.

With these redescriptions, only one species of *Brueelia* and *Guimaraesiella* described by Balát remain without modern redescriptions: *Guimaraesiella tovornikae* (Balát, 1981). We were unable to find any specimens of *G. tovornikae* at the Moravian Museum, and the types must therefore be assumed to be lost. Gustafsson and Bush (2017) saw specimens identified as this species in the Brelih Collection at the Slovenian Museum of Natural History (Ljubljana, Slovenia) but did not redescribe this species.

Material and methods

We examined slide-mounted specimens in František Balát's collection deposited at the Moravian Museum, Brno (MMBC). In addition, we examined some specimens from the Natural History Museum, London, United Kingdom (NHML), the Slovenian Museum of Natural History, Ljubljana, Slovenia (PMSL), and the Museum of Natural History, University of Wrocław, Poland (MNHW). We typically only illustrated and measured specimens at the MMBC; other specimens were only examined visually. In some cases, we were unable to illustrate, for example, male genitalia accurately, even if specimens in other collections were better preserved than the ones at the MMBC. Specimens were examined in an Olympus CX31 microscope. Illustrations were drawn by hand, using a drawing tube fitted to the microscope. Line drawings were scanned, collated, and edited in GIMP (http://www.gimp.org). Grey lines in all illustrations denote the approximate extent of dark pigmentation on heads, tergopleurites, and female subgenital plates; these patterns typically differ slightly between specimens of the same species and sometimes between sides of the same specimen.

Measurements were made in Quick PHOTO MIKRO 3.1 (Promicra, Prague, Czechia). Measurements are given in millimetres for the following dimensions: AW = abdominal width (at segment V); HL = head length (at midline); HW = head width (at temples); PRW = prothoracic width (at posterior end); PTW = pterothoracic width (at posterior end); TL = total length (at midline). Terminology of chaetotaxy and morphological structures follows Gustafsson and Bush (2017), and include: *aps = accessory post-spiracular seta*; *mms = marginal mesometanotal setae*; *pst1–2 = parameral setae 1–2*; *pts = post-temporal*

seta; *ss = sutural setae*; *vms = vulval marginal setae*; *vos = vulval oblique setae*; *vss = vulval submarginal setae*. Counts of *vos* include the distal *vos* typically situated median to the *vss*. Setal characters are given in *italics*.

Host taxonomy follows Clements et al. (2018). The species treated here are ordered according to host family.

Note on Balát's type series

In the original descriptions of most of the species redescribed here, Balát explicitly mentioned a single male and a single female as type specimens but listed all other specimens examined as "other material". Article 72.4.6 of the International Code of Zoological Nomenclature (1999) states that if an author establishing a new species-group taxon uses the term "type" or its equivalents for some specimens, but also lists other specimens, these additional specimens are excluded from the type series. Balát appears to have been unaware of this, and labeled several non-type slides as "paratypes", including some slides deposited in other collections. These specimens have no special status, and are not either paratypes or paralectotypes.

Systematics

PHTHIRAPTERA Haeckel, 1896
Ischnocera Kellogg, 1896
Philopteridae Burmeister, 1838
***Brueelia*-complex**

Brueelia Kéler, 1936

Philopterus Nitzsch, 1818: 288 (*in partim*).
Nirmus Nitzsch, 1818: 291 (*in partim*).
Degeeriella Neumann, 1906: 60 (*in partim*).
Painjunirmus Ansari, 1947: 285.
Allobrueelia Eichler, 1951: 36 (*in partim*).
Nigronirmus Złotorzycka, 1964: 248.
Spironirmus Złotorzycka, 1964: 261.
Serinirmus Soler Cruz, Rodríguez, Florido-Navío and Muñoz Parra, 1987: 244.

Type species. *Brueelia rossittensis* Kéler, 1936: 257 [= *Nirmus brachythorax* Giebel, 1874: 134] (by original designation).

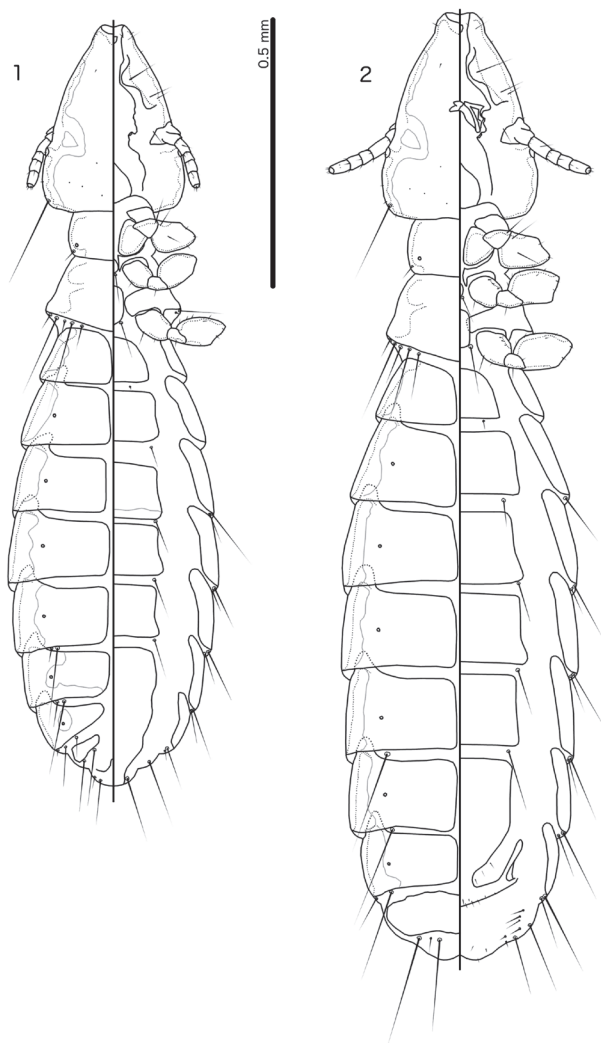### *Brueelia blagovescenskyi* Balát, 1955
Figs 1–5

Brueelia blagovescenskyi Balát, 1955: 504.

Type host. *Emberiza schoeniclus* (Linnaeus, 1758), reed bunting (Emberizidae).
   Type locality. Hodonín, "Kapřiska", Czechia.
   Description. *Both sexes.* Head trapezoidal (Fig. 3), lateral margins of preantennal area concave distally and convex proximally, frons widely concave. Marginal cari-

Figures 1, 2. *Brueelia blagovescenskyi* Balát, 1955, ex *Emberiza schoeniclus* (Linnaeus, 1758) **1** Male habitus, dorsal and ventral views **2** Female habitus, dorsal and ventral views.

Figures 3–5. *Brueelia blagovescenskyi* Balát, 1955, ex *Emberiza schoeniclus* (Linnaeus, 1758) **3** Female head, dorsal and ventral views **4** Male genitalia, dorsal view **5** Female subgenital plate and vulval margin, ventral view.

na slender, much displaced at osculum. Ventral anterior plate small, shield-shaped. Head chaetotaxy and pigmentation pattern as in Figure 3. Preantennal nodi not bulging. Preocular nodi slightly larger than post-ocular nodi. Marginal temporal carina slender, with undulating median margins. Gular plate slender, lanceolate. Thoracic and abdominal segments and pigmentation patterns as in Figures 1, 2; sternites V–VI and subgenital plates medium brown in both sexes.

Male. Thoracic and abdominal chaetotaxy as in Figure 1; due to thickness of cover glass on single examined male, smaller setae (e.g., *ss*) not visible, and may be overlooked. Mandibles distorted in single examined male, and not illustrated. Male genitalia of single examined male partially obscured by gut content, and shape of basal apodeme unknown. Proximal mesosome near quadratic (Fig. 4), mesosomal lobes relatively small, gonopore wider than long. Parameres broadly elongated distally (Fig. 4). Measurements (*n* = 1): TL = 1.43; HL = 0.35; HW = 0.27; PRW = 0.17; PTW = 0.25; AW = 0.37.

Female. Thoracic and abdominal chaetotaxy as in Figure 2. Subgenital plate pentagonal (Fig. 5), with broad connection to cross-piece. Vulval margin convergent to median point, with 3 short, slender *vms* and 3–5 short, thorn-like *vss* on each side; 4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (*n* = 2): TL = 1.79–1.80; HL = 0.39–0.40; HW = 0.30–0.31; PRW = 0.20; PTW = 0.29–0.30; AW = 0.45–0.48.

Type material. Lectotype ♂, Hodonín, "Kapřiska", Czechia, 2 Apr. 1949, F. Balát, 404a (MMBC). **Paralectotypes**. 1♀, same data as lectotype, 404b (MMBC).

Non-types. 1♀, same data as lectotype, 404c (MMBC).

Remarks. Balát (1955) mentioned a type male and female on slide no. 404. The same handwritten notes are on slides 404a and 404b. As Balát (1955) did not explicitly designate a holotype, both examined type specimens mentioned in original description represent syntypes. We hereby designate the male on slide 404a as the lectotype of *B. blagovescenskyi*. The other syntype becomes a paralectotype. In addition, Balát (1955) mentioned two females and 15 nymphs from the same host species as other (non-type) material. Except one female on slide

404c, these have not been found in the MMBC collection, and must be assumed to be lost. Our redescription of this species is therefore based only on the lectotype and paralectotype, and the single non-type female.

The lectotype male and paralectotype female (404a–b) are mounted on slides using a second slide used as a cover slide, which blurs the outline of the thoracic and abdominal plates and prevents using higher magnifications. Accurate illustration of the male genitalia is impossible without remounting the specimen, which was not attempted; the genitalia are therefore illustrated approximately. Moreover, smaller setae are very hard to see, and especially smaller abdominal setae of the male may have been overlooked. The female 404b lacks a subgenital plate. For the head and female illustrations, the non-type female specimen (slide 404c) was used. Fresh collections are needed to establish the correct abdominal and leg chaetotaxy of males of this species, as well as the shape of the male genitalic elements.

Brueelia pelikani Balát, 1958
Figs 6–12

Brueelia pelikani Balát, 1958: 414.

Type host. *Emberiza melanocephala* Scopoli, 1769, black-headed bunting (Emberizidae).

Type locality. Sliven, Bulgaria.

Description. *Both sexes.* Head slender, rounded dome-shaped (Fig. 8). Marginal carina slender much displaced at osculum. Ventral anterior plate small, shield-shaped. Head chaetotaxy and pigmentation pattern as in Fig. 8. Preantennal nodi not bulging. Preocular nodi slightly larger than postocular nodi. Marginal temporal carina slender, with undulating median margin. Gular plate broadly triangular, with rounded anterior margins. Thoracic and abdominal segments and pigmentation patterns as in Figures 6, 7; sternal plates get progressively browner in more posterior segments, and subgenital plate of both sexes medium brown.

Male. Thoracic and abdominal chaetotaxy as in Figure 6; *ss* visible only on tergopleurites VI–VII in one male, but distal tergopleurites distorted in both examined males and *ss* on other segments may be overlooked. Basal apodeme slender, with concave lateral margins (Fig. 9). Proximal mesosome gently rounded (Fig. 10). Mesosomal lobes wide, high convergent distally; rugose area limited to distal margin. Gonopore longer than wide. Penile arms not extending distal to mesosome. Parameres moderate in width, much elongated distally (Fig. 11); *pst1–2* not visible in examined specimens. Measurements (*n* = 3): TL = 1.46–1.52; HL = 0.35; HW = 0.25; PRW = 0.17–0.18; PTW = 0.25–0.26; AW = 0.32–0.36.

Female. Thoracic and abdominal chaetotaxy as in Figure 7. Subgenital plate pentagonal (Fig. 12), with broad connection to cross-piece. Vulval margin convergent to rounded median point, with 2 or 3 short, slender *vms* and
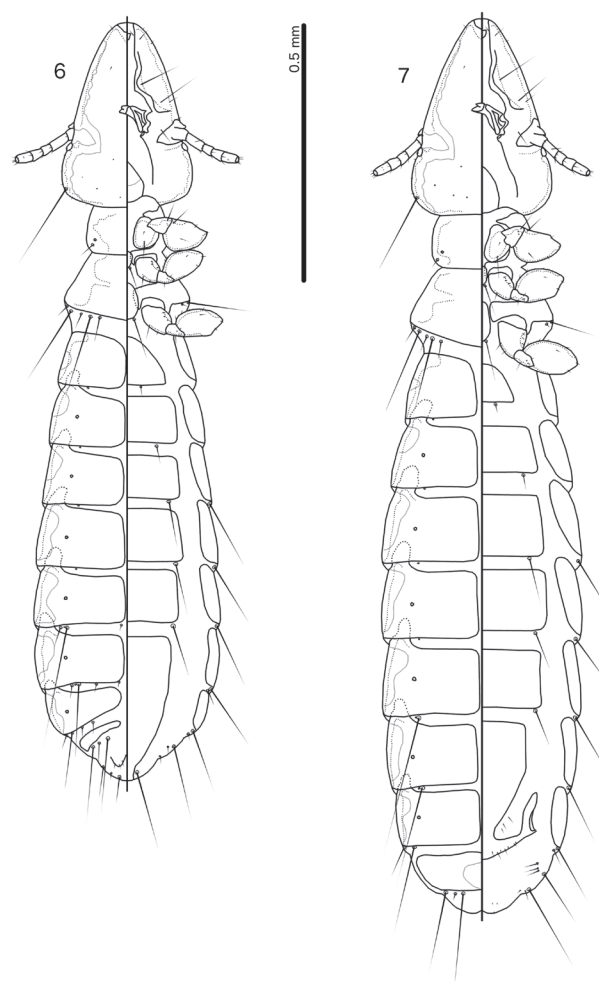
Figures 6, 7. *Brueelia pelikani* Balát, 1958, ex *Emberiza melanocephala* Scopoli, 1769 **6** Male habitus, dorsal and ventral views **7** Female habitus, dorsal and ventral views.

3 short, thorn-like *vss* on each side; 2–4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (*n* = 7, except PTW where *n* = 6, and AW where *n* = 5): TL = 1.62–1.84; HL = 0.36–0.38; HW = 0.26–0.28; PRW = 0.18–0.19; PTW = 0.27–0.28; AW = 0.37–0.41.

Type material. Lectotype ♂, Sliven, Bulgaria, 24 May 1957, F. Balát, 969a (MMBC), **Paralectotypes.** 5♀, same data as lectotype, 969a–c (MMBC). 1♂, Sliven, Bulgaria, 26 May 1957, F. Balát, 934 (MMBC). 1♀, Kap Maslennos, Bulgaria, 5 June 1957, F. Balát, 980 (MMBC). 1♂, 1♀, same data as lectotype, 969d, Brit. Mus. 1958-452 (NHML).

Remarks. Balát (1958) did not designate a holotype for *B. pelikani*, but he mentioned that he had examined 3 males, 8 females, and 12 nymphs from 3 hosts; collectively these form the syntype series. The text "Type male and female" is written by hand on the label of slide 969a, and "paratypes" on slides 969b–c. Another slide (969d) with 1♂, 1♀ deposited at the NHML (Brit. Mus. 1958-452) is marked "paratypes". Presently, five slides with a total of two males, six females, and one nymph are de-

Dtsch. Entomol. Z. 63 (1) 2019, 17–39

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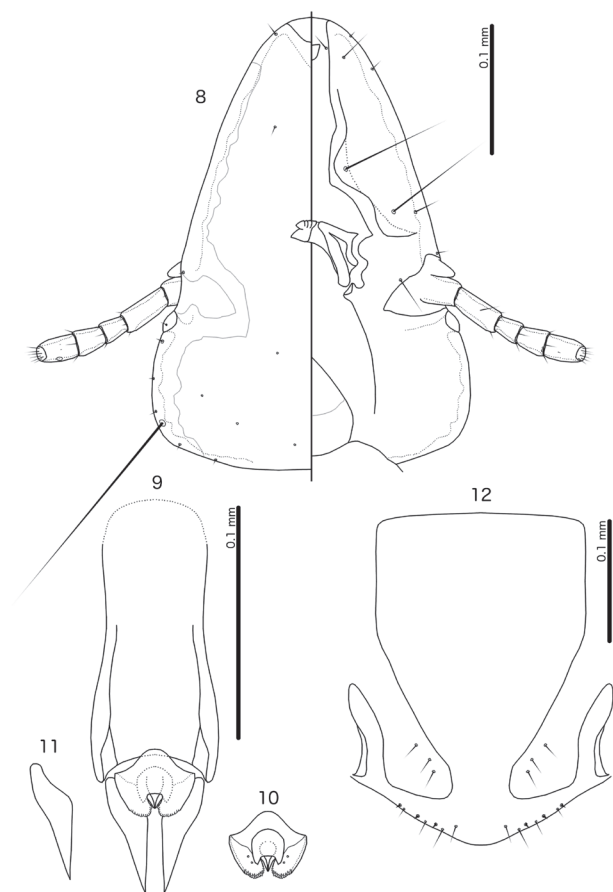**Figures 8–12.** *Brueelia pelikani* Balát, 1958, ex *Emberiza melanocephala* Scopoli, 1769 **8** Male head, dorsal and ventral views **9** Male genitalia, dorsal view **10** Male mesosome, ventral view **11** Male paramere, dorsal view **12** Female subgenital plate and vulval margin, ventral view.
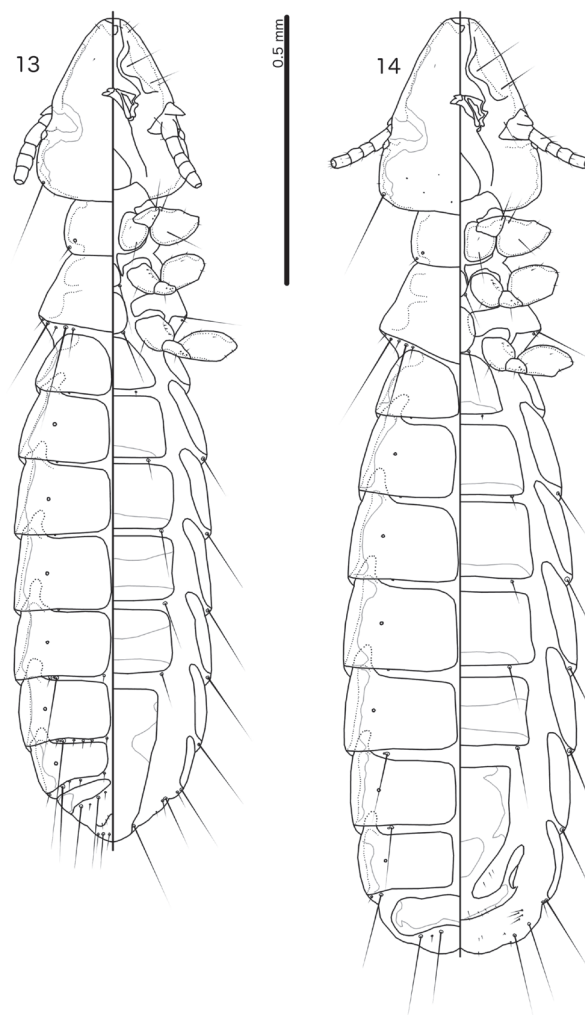
Figures 13–14. *Brueelia breueri* Balát, 1955, ex *Chloris chloris* (Linnaeus, 1758). **13** Male habitus, dorsal and ventral views; **14** Female habitus, dorsal and ventral views.

posited at the MMBC. All specimens other than these and the two specimens at the NHML have been lost. To settle the identity of this species, we hereby designate the male on slide 969a as the lectotype of *B. pelikani*. The other syntypes become paralectotypes.

The abdomen of this lectotype male is unfortunately disrupted distally, which has affected the genitalia. In the paralectotype male 934, the mesosome is partially obscured by gut content, and the shape of the proximal mesosome cannot be seen clearly. We have illustrated the mesosome as seen in the lectotype, but the other genital elements as seen in the paralectotype male (934).

Brueelia breueri Balát, 1955

Figs 13–19

Brueelia breueri Balát, 1955: 505.

Type host. *Chloris chloris* (Linnaeus, 1758), European greenfinch (Fringillidae).

Type locality. Gabčíkovo, Slovakia.

Description. *Both sexes.* Head flat dome-shaped (Fig. 15), lateral margins of preantennal area slightly convex, frons broadly concave. Marginal carina narrow, deeply displaced and widened at osculum, median margin undulating. Ventral anterior plate small, shield-shaped. Head chaetotaxy and pigmentation patterns as in Figure 15; head sensilla and *pts* not visible in examined specimens. Preantennal nodi not bulging. Preocular nodi much larger than postocular nodi. Marginal temporal carina moderate in width, with undulating median margin. Gular plate lanceolate, slender. Thoracic and abdominal segments and pigmentation patterns as in Figures 13, 14.

Male. Thoracic and abdominal chaetotaxy as in Figure 13. Basal apodeme with deeply concave lateral margins (Fig. 16). Proximal mesosome roughly quadratic, with rounded corners, small (Fig. 17). Mesosomal lobes wide, highly convergent distally; rugose area limited to distal margin. Gonopore wider than long. Penile arms not reaching distal margin of mesosome. Parameres slender (Fig. 18), distal part elongated; *pst1–2* not visi-
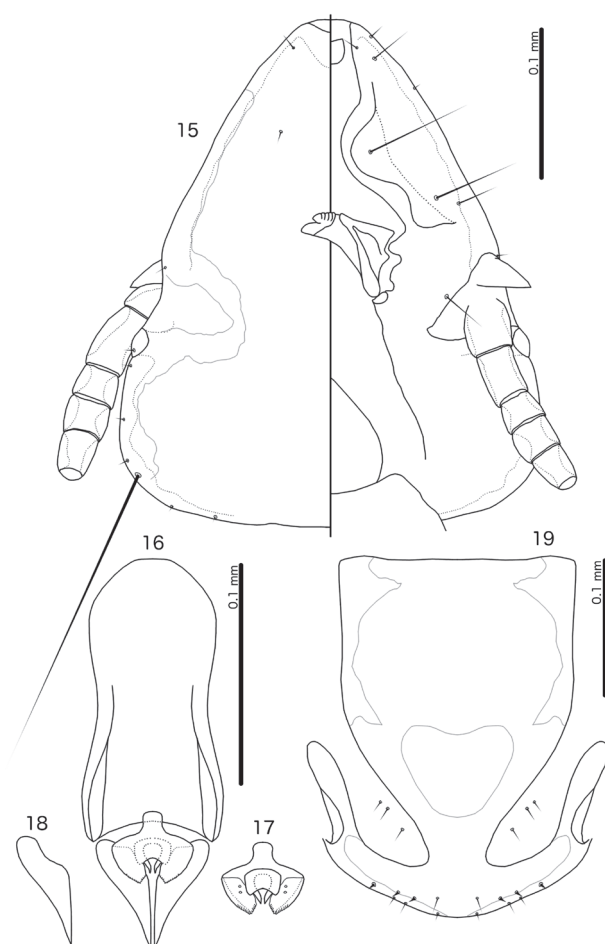
Figures 15–19. *Brueelia breueri* Balát, 1955, ex *Chloris chloris* (Linnaeus, 1758) **15** Male head, dorsal and ventral views **16** Male genitalia, dorsal view **17** Male mesosome, ventral view **18** Male paramere, dorsal view **19** Female subgenital plate and vulval margin, ventral view.

ble in examined specimen. Measurements ($n = 3$, except HW where $n = 2$): TL = 1.29–1.55; HL = 0.31–0.34; HW = 0.28; PRW = 0.15–0.18; PTW = 0.24–0.30; AW = 0.32–0.37.

Female. Thoracic and abdominal chaetotaxy as in Figure 14. Subgenital plate rounded pentagonal (Fig. 19), with broad connection to cross-piece; pigmentation patterns as in Figure 19. Vulval margin gently rounded, with 3 short, slender *vms* and 3 or 4 short, thorn-like *vss* on each side; 3 or 4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements ($n = 6$): TL = 1.59–1.95; HL = 0.35–0.38; HW = 0.28–0.32; PRW = 0.18–0.20; PTW = 0.27–0.32; AW = 0.38–0.47.

Type material. Lectotype ♂ Gabčíkovo, Slovakia, 25 Mar. 1954, F. Balát, 676 (MMBC). **Paralectotype.** 1♀, Podunajské Biskupice, Slovakia, 20 July 1953, F. Balát, 1118a (MMBC).

Non-types. 1♀, same data as lectotype, 676 (MMBC). 1♂, same data as lectotype, Brit. Mus. 1955-662 (NHML). 1♂, 2♀, same data as paralectotypes,1118b, c (MMBC). 5♀, Neslovice, Czechia, 6 Aug. 1958, F. Balát 1179 (MMBC). 1♂, 1♀, Brno, Czechia, 9. Jan. 1960, F. Balát, 1327 (MMBC). 1♀, same data as paralectotypes, Brit. Mus. 1955-662 (NHML).

Remarks. Balát (1955) designated a male from Gabčíkovo and a female from Podunajské Biskupice as types; these are therefore syntypes. The word "type" is written in pencil on the slides 676 and 1118a in the MMBC collection. In addition, Balát mentioned seven females and one male from the same two hosts, and one female from Tormafölek (Zala m., Hungary, 4 Apr. 1952, leg. Georg Breuer; not at MMBC) as "other material", which do not comprise type material. Presently, there are 4 slides of *B. breueri* with a total of two males and four females deposited at MMBC. The other four females, including that from Hungary, are lost. Therefore, to settle the identity of this species, we hereby designate the male on slide 676 as the lectotype of *B. breueri*. The other syntypes become paralectotypes. Some specimens deposited in the NHML are called "paratypes", are not type specimens, as they are not referred to as such in the original publication.

Both antennae of the lectotype male are folded underneath the head and seemingly squashed. We have here reversed the dorsal view of the antenna and illustrated it in a more natural position; the antenna in the ventral view is illustrated as in the specimen. However, in both cases the antennae are likely narrower than illustrated here. As both antennae are displaced, the precise location of antennal setae cannot be established, and these have therefore not been illustrated here. Additional material is needed to fully redescribe *B. breueri*.

Brueelia glizi **Balát, 1955**
Figs 20–26

Brueelia glizi Balát, 1955: 509.

Type host. *Fringilla montifringilla* Linnaeus, 1758, brambling (Fringillidae).

Type locality. Hodonín, Czechia.

Description. ***Both sexes.*** Head flat dome-shaped (Fig. 22), lateral margins of preantennal area slightly convex, frons broadly flattened to slightly concave. Marginal carina narrow, deeply displaced at osculum, median margin undulating. Ventral anterior plate small, shield-shaped. Head chaetotaxy and pigmentation patterns as in Figure 22. Preantennal nodi not bulging. Preocular nodi larger than postocular nodi. Marginal temporal carina moderate in width, median margin undulating. Gular plate slender, lanceolate. Thoracic and abdominal segments and pigmentation patterns as in Figures 20, 21.

Male. Thoracic and abdominal chaetotaxy as in Figure 20. Male genitalia asymmetrical in single examined male, and here illustrated as seen in lectotype, in dorso-lateral view. Basal apodeme slender, with concave
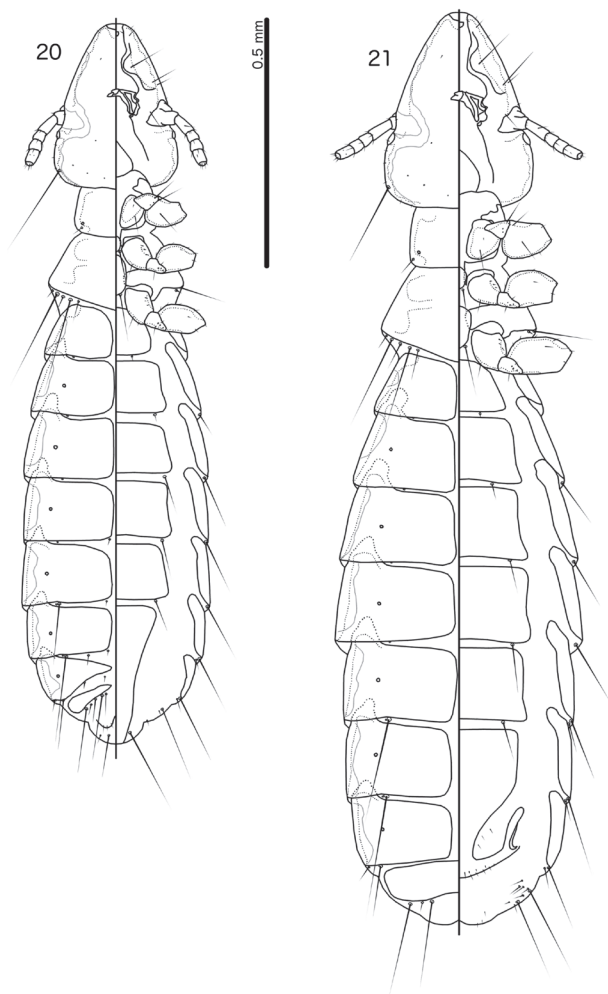
Figures 20, 21. *Brueelia glizi* Balát, 1955, ex *Fringilla montifringilla* Linnaeus, 1758 **20** Male habitus, dorsal and ventral views **21** Female habitus, dorsal and ventral views.
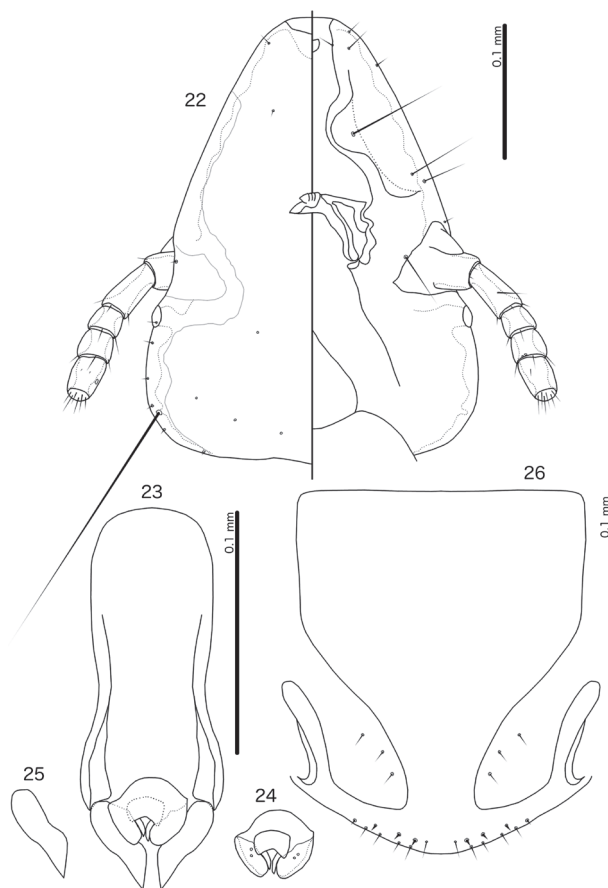
Figures 22–26. *Brueelia glizi* Balát, 1955, ex *Fringilla montifringilla* Linnaeus, 1758 **22** Male head, dorsal and ventral views **23** Male genitalia, dorsal view, except mesosome which is distorted in specimen and here illustrated in dorso-lateral view **24** Male mesosome, ventro-lateral view **25** Male paramere, dorsal view **26** Female subgenital plate and vulval margin, ventral view.

lateral margins (Fig. 23). Proximal mesosome distorted in syntype, but seemingly gently rounded (Fig. 24). Mesosomal lobes broad, convergent distally; rugose area not visible, likely limited. Gonopore wider than long. Parameres partially everted in single syntype male, and true shape may be slightly different than what is illustrated (Fig. 25); *pst1–2* not visible. Measurements ($n = 1$): TL = 1.46; HL = 0.33; HW = 0.25; PRW = 0.17; PTW = 0.26; AW = 0.36.

Female. Thoracic and abdominal chaetotaxy as in Figure 21. Subgenital plate funnel-shaped, with broad connection to cross-piece (Fig. 26). Vulval margin gently rounded, with 4 or 5 short, slender *vms* and 3 or 4 short, thorn-like *vss* on each side; 4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements ($n = 7$): TL = 1.70–1.90; HL = 0.38–0.39; HW = 0.29–0.31; PRW = 0.20–0.22; PTW = 0.30–0.31; AW = 0.43–0.48.

Type material. Lectotype 1♂, Hodonín, Czechia, 10 Feb. 1952, F. Balát, 672a (MMBC). **Paralectotype.** 1♀, same data as lectotype, 672a (MMBC).

Non-type material. 6♀, same data as lectotype, F. Balát, 647, 672b–c (MMBC). 1♀, same data as lectotype, Brit. Mus. 1955-662 (NHML). 1♂, 1♀, same data as lectotype, no. 734 (MNHW).

Remarks. Balát (1955) designated one male and one female on slide 672 as types, but did not explicitly designate either of these as holotype; these therefore constitute the syntype series. The specimens are designated as "types" on the handwritten label. Another nine females and two nymphs were mentioned from the same host specimen, and one female from a different host specimen. Presently, four slides with one male, seven females and one nymph are present at the MMBC; the remaining specimens must be regarded as lost. To settle the identity of *B. glizi*, we hereby designate the male on slide 672a as the lectotype, and the female on the same slide as paralectotype. Specimens deposited at the NHML and MNHW are labeled "paratypes", but these are not mentioned as paratypes in the original description, and thus do not have type status.

Additional material is necessary to describe the male genitalia accurately.
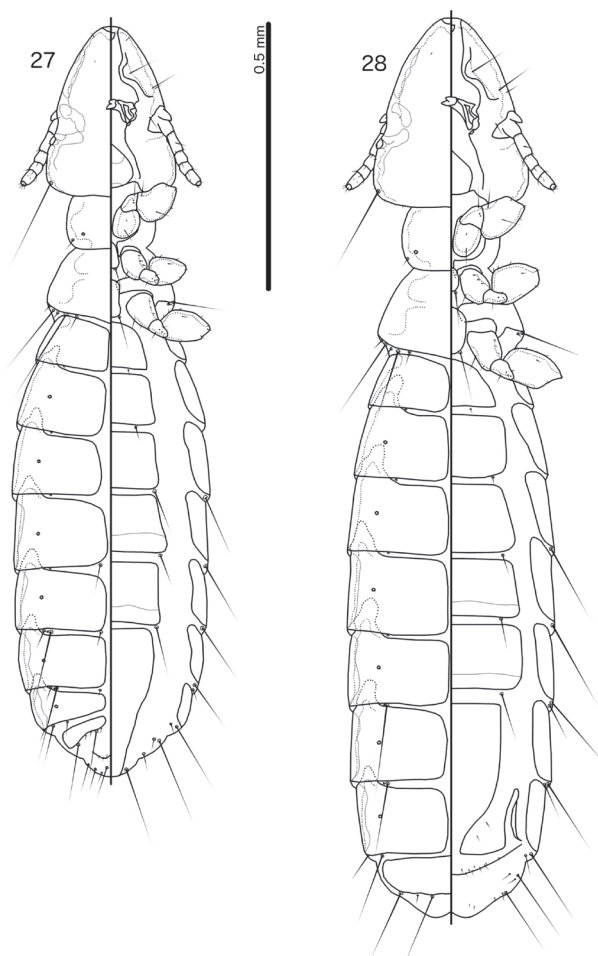
Figures 27, 28. *Brueelia kluzi* Balát, 1955, ex *Fringilla coelebs* Linnaeus, 1758 **27** Male habitus, dorsal and ventral views **28** Female habitus, dorsal and ventral views.
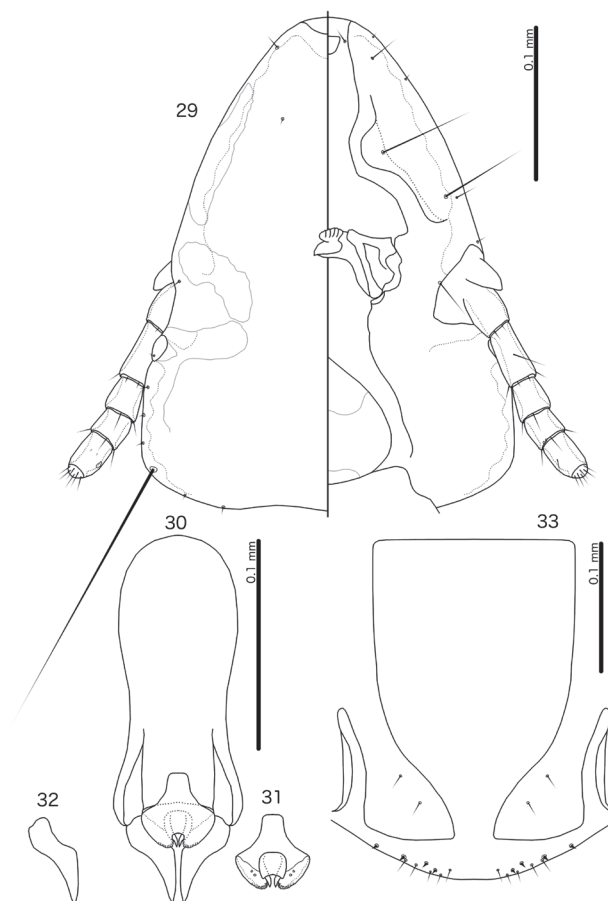
Figures 29–33. *Brueelia kluzi* Balát, 1955, ex *Fringilla coelebs* Linnaeus, 1758 **29** Male head, dorsal and ventral views **30** Male genitalia, dorsal view **31** Male mesosome, ventral view **32** Male paramere, dorsal view **33** Female subgenital plate and vulval margin, ventral view.

Brueelia kluzi Balát, 1955

Figs 27–33

Brueelia kluzi Balát, 1955: 512.

Type host. *Fringilla coelebs* Linnaeus, 1758, chaffinch (Fringillidae).

Type locality. Lednice, Czechia.

Description. *Both sexes.* Head flat-dome shaped (Fig. 29), lateral margins of preantennal area convex, frons rounded to slightly flattened. Marginal carina moderate in width, shallowly displaced and widened at osculum, median margin undulating. Ventral anterior plate small, shield-shaped. Head chaetotaxy and pigmentation patterns as in Figure 29; head sensilla and *pts* not visible in examined specimens. Preantennal nodi with slight median bulge. Preocular nodi larger than post-ocular nodi. Marginal temporal carina moderate in width, undulating. Gular plate not entirely clear in examined specimens, but roughly lanceolate. Thoracic and abdominal segments and pigmentation patterns as in Figures 27, 28.

Male. Thoracic and abdominal chaetotaxy as in Figure 27; *ss* not visible on tergopleurite VIII in any examined male, but likely present if more specimens are examined. Basal apodeme not clearly visible in any examined males, and here illustrated approximately (Fig. 30); seemingly slender, with lateral margins concave. Proximal mesosome elongated, trapezoidal with concave lateral margins (Fig. 31). Mesosomal lobes broad, highly convergent distally; rugose area limited to distal margin. Gonopore longer than wide. Parameres slender, elongated distally (Fig. 32); *pst1–2* not visible in examined males. Measurements (n = 4): TL = 1.32–1.41; HL = 0.31–0.32; HW = 0.24–0.25; PRW = 0.15–0.17; PTW = 0.23–0.25; AW = 0.30–0.36.

Female. Thoracic and abdominal chaetotaxy as in Figure 28. Subgenital plate roughly rectangular, with narrow connection to cross-piece (Fig. 33). Vulval margin rounded laterally, but roughly flat or slightly rounded medially, with 4 short, slender *vms* and 4 or 5 short, thorn-like *vss* on each side; 3 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements

(n = 11): TL = 1.59–1.76 (1.68); HL = 0.35–0.37 (0.36); HW = 0.27–0.29 (0.28); PRW = 0.18–0.20 (0.19); PTW = 0.27–0.29 (0.28); AW = 0.35–0.41 (0.39).

Type material. Lectotype 1♂, Lednice, Czechia, 26 Mar. 1953, F. Balát, 1138 (MMBC). **Paralectotype.** 1♀, same data as lectotype (MMBC).

Non-type material. 3♂, 8♀, same data as lectotype (MMBC). 1♀, Točná, Czechia, 23 May 1938, leg. K. Pfleger, Pfl13 (MMBC). 1♀, Skanör, Sweden, 12 Nov. 1963, F. Balát, 1315 (MMBC). 1♀, Břeclav - Kančí obora, Czechia, 22 May 1953, F. Balát, 1477 (MMBC).

Remarks. Balát (1955) did not explicitly designate a holotype, but mentioned one male and one female on slide 15/53 (= number on host's ring, current slide number 1138) as types; these comprise the syntype series. This is confirmed by Balát's handwritten notes on the slide label. In addition, he mentioned three males and eight females from the same host specimen, and one female from a different host as additional material. These are all present in the Balát collection at the MMBC. We hereby select the male on slide 1138 as the lectotype, and one of the females on the same slide as a paralectotype. These have been marked on the slide with dark spots.

All examined specimens in Brno are poorly cleared, and many are still attached to feather fragments that further obscure the morphology. As a result, thoracic and abdominal chaetotaxy and plates are not always clearly visible, and are here illustrated as accurately as possible. Vulval setae only clearly visible in one female, and range of variation may be greater than given above if more specimens are examined.

Brueelia conocephala (Blagoveshtchensky, 1940)
Figs 34–40

Degeeriella conocephala Blagoveshtchensky, 1940: 64.
Brueelia conocephalus (Blagoveshtchensky, 1940); Hopkins and Clay 1952: 54.
Brueelia conocephala (Blagoveshtchensky, 1940); Gustafsson and Bush 2017: 39.
Brueelia weberi Balát, 1982: 44, **new synonymy.**

Type host. *Sitta europaea caucasica* Reichenow, 1901, Eurasian nuthatch (Sittidae).

Type locality. Alexeyevka, Talysh Lowlands, Lenkoran province [= Lankaran], Azerbaijan.

Other hosts. *Sitta europaea caesia* Wolf, 1810. *Sitta europaea rubiginosa* Tschusi & Zarodny, 1905. *Parus major* Linnaeus, 1758. See Gustafsson et al. (2018b) for a discussion on the type host of this species.

Description. *Both sexes.* Head rounded triangular (Fig. 36), lateral margins of preantennal area more or less straight, in some specimens slightly concave or convex, frons narrowly concave. Marginal carina broad, widening slightly in anterior third, with undulating median margins. Ventral anterior plate shield-shaped, with anterior margin slightly concave. Head chaetotaxy and
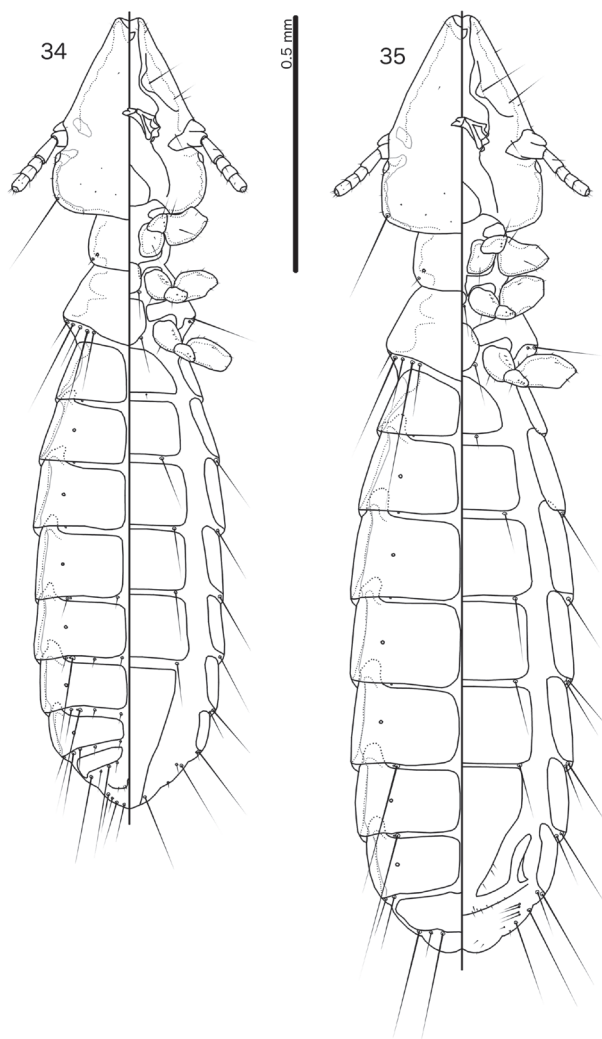
Figures 34, 35. *Brueelia conocephala* (Blagoveshchensky, 1940) ex *Sitta europaea* (Linnaeus, 1758) **34** Male habitus, dorsal and ventral views **35** Female habitus, dorsal and ventral views.

pigmentation patterns as in Figure 36. Preantennal nodi not bulging. Pre-ocular nodi much larger than postocular nodi. Marginal temporal carina moderate in width, with undulating median margin. Gular plate diffuse in most examined specimens, but seemingly rounded lanceolate. Thoracic and abdominal segments and pigmentation patterns as in Figures 34, 35.

Male. Thoracic and abdominal chaetotaxy as in Figure 34. Basal apodeme of more or less even width, lateral margins only slightly concave (Fig. 37). Proximal mesosome rounded trapezoidal, with concave lateral margins (Fig. 38). Mesosomal lobes broad, with almost parallel lateral margins; rugose area extensive along distal margin. Gonopore semi-oval, about as wide as long. Penile arms almost reach distal margin of mesosome. Parameres slender proximally, broad at mid-point, and tapering distally, elongated (Fig. 39); *pst1–2* as in Figure 39. Measurements ex *Sitta europaea caesia* (n = 13): TL = 1.39–1.53 (1.49); HL = 0.38–0.40 (0.39); HW = 0.27–

0.30 (0.29); PRW = 0.16–0.18 (0.17); PTW = 0.25–0.29 (0.27); AW = 0.31–0.39 (0.36). Measurements ex *Parus major major* (*n* = 1): TL = 1.47; HL = 0.37; HW = 0.29; PRW = 0.18; PTW = 0.26; AW = 0.36.

Female. Thoracic and abdominal chaetotaxy as in Figure 35. Subgenital plate shaped as in Figure 40, with broad connection to cross-piece. Vulval margin convergent to median point or slightly rounded medially. Vulval chaetotaxy different but overlapping between material from the two host species: 3–5 short, slender *vms* and 2–4 short, thorn-like *vss* on each side in specimens from *Sitta europaea caesia*, but 3 or 4 short, slender *vms* and 3 or 4 short, thorn-like *vss* on each side in specimens from *Parus major major*. Material from both host species has 3 or 4 short, slender *vos* on each side of subgenital plate, with distal 1 *vos* median to or only slightly anterior to *vss*. Measurements ex *Sitta europaea caesia* (*n* = 24, except PRW where *n* = 23): TL = 1.68–1.92 (1.79); HL = 0.42–0.44 (0.43); HW = 0.31–0.34 (0.33); PRW = 0.18–0.21 (0.20); PTW = 0.28–0.33 (0.31); AW = 0.35–0.47 (0.43). Measurements ex *Parus major major* (n = 5): TL = 1.81–1.95; HL = 0.41–0.44; HW = 0.33–0.35; PRW = 0.20–0.22; PTW = 0.30–0.33; AW = 0.43–0.49.

Type material. Holotype ♀ of *Brueelia weberi*, Serrahn, [Kreis Neustrelitz, Germany], 7 Oct. 1977, F. Balát, 1448 (MMBC). **Paratypes** of *Brueelia weberi*: 1♀, same data as holotype, F. Balát, 1449 (MMBC). 1♂, 3♀, Chropyně, Czechia, 3 Nov. 1977, F. Balát, 1381a–d (MMBC).

Non-type material. Ex *Sitta europaea caesia*: 10♂, 19♀, Košice, Slovakia, 5 Nov. 1953, F. Balát, 1080 (MMBC). 1♂, Lednice – Kančí obora, Czechia, 10 Jun. 1953, F. Balát, 1079 (MMBC). 1♀, Hodonín, Czechia, 12. Feb. 1954, F. Balát, 1078 (MMBC). 2♂, 4♀, Hodonín, Czechia, 24 Nov. 1952, F. Balát, 651 (MMBC).

Remarks. Balát (1982) explicitly designated the female on slide 1448 as the holotype *Brueelia weberi*, and several other specimens as paratypes. This is confirmed in his handwritten notes on the slides. All specimens are present in the MMBC collection, with the exception that there is only one slide marked "Pfl90". However, this female and one of the paratype males (slide 1411) represent a separate species (see below) and have, therefore, been excluded from the paratypes.

We have examined Balát's type and non-type material identified as *B. weberi*, and compared these with his extensive collection of *B. conocephala* from *Sitta europaea caesia*. No diagnostic characters that could separate these two species have been found, and most measurements for specimens from *P. major* fall within the range of the measurements for specimens from *S. europaea*. We therefore consider *B. weberi* to be a synonym of *B. conocephala*. There is enough variation in the head shape and measurements of Balát's specimens of *B. conocephala* to accommodate the perceived differences in dimensions reported by Balát (1982), and the reported differences in the shape of the parameres can be ascribed to individual variation or artificial differences due to mounting.
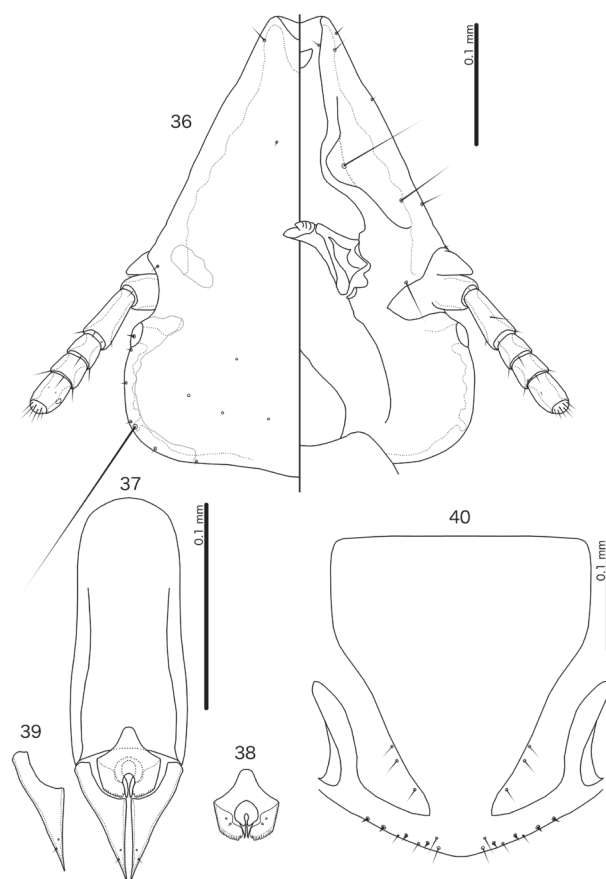
Figures 36–40. *Brueelia conocephala* (Blagoveshchensky, 1940) ex *Sitta europaea* (Linnaeus, 1758) **36** Male head, dorsal and ventral views **37** Male genitalia, dorsal view **38** Male mesosome, ventral view **39** Male paramere, dorsal view **40** Female subgenital plate and vulval margin, ventral view.

Balát collected *B. weberi* from several localities, and it would appear that this species is well established on the host, *Parus major*. This is in contrast to the only other material known from birds in the *P. major*-complex reported by Gustafsson et al. (2018b). They described two species of *Brueelia* (*B. picea* Gustafsson et al. 2018b and *B. nazae* Gustafsson et al. 2018b) which they did not consider to be closely related to *B. conocephala*. However, all material Gustafsson et al. (2018b) examined was from non-European members of the *P. major*-complex.

Interestingly, the "paratype" male on slide 1411 (Břeclav – Kančí obora, Czechia, 5 Mar. 1954, F. Balát, 1411, MMBC) and "paratype" female on slide Pfl90 (Chuchle, Czechia, 28 Jan. 1938, K. Pfleger, Pfl90, MMBC) represent a different, undescribed, species of *Brueelia*. The male specimen is similar to *B. nazae* in head shape, but more similar to *B. picea* in the shape of the genitalia; the abdominal chaetotaxy is different from both species, with *aps* on abdominal segment IV (absent in both *B. picea* and *B. nazae*). The female specimen is slightly different in head shape from the male specimen, and may represent a different species. We do not describe this species here, as more material is needed to sort out whether both spe-

cies of *Brueelia* actually occur on *P. major* in Europe, or whether Pfleger's and Balát's material originated in contaminations or stragglers.

Brueelia ferianci Balát, 1955
Figs 41–47

Brueelia ferianci Balát, 1955: 508.
Nigronirmus ferianci (Balát, 1955); Złotorzycka 1964: 250.

Type host. *Anthus trivialis trivialis* (Linnaeus, 1758), tree pipit (Motacillidae).

Type locality. Nesyt, Czechia.

Description. *Both sexes.* Head trapezoidal (Fig. 43), lateral margins of preantennal area convex proximally and concave distally, frons broadly flattened to slightly concave. Marginal carina broad, irregular, narrowing conspicuously near *dsms*, deeply displaced and much widened at osculum. Ventral anterior plate elongated. Head chaetotaxy and pigmentation patterns as in Figure 43. Preantennal nodi wide, slightly bulging. Pre- and postocular nodi large. Marginal temporal carina wide, with undulating median margin. Gular plate rounded triangular. Thoracic and abdominal segments and pigmentation patterns as in Figures 41, 42.

Male. Thoracic and abdominal chaetotaxy as in Figure 41. Basal apodeme with concave lateral margins (Fig. 44). Proximal mesosome short but broad (Fig. 45), roughly trapezoidal with concave lateral margins. Mesosomal lobes wide, medially bent and convergent distally; rugose area extensive over ventral surface of distal mesosome. Gonopore semi-oval, longer than wide. Parameres broad, elongated distally (Fig. 46); *pst1–2* as in Figure 46. Measurements (*n* = 11, except TL where *n* = 10): TL = 1.36–1.52 (1.41); HL = 0.32–0.36 (0.34); HW = 0.26–0.29 (0.27); PRW = 0.17–0.19 (0.18); PTW = 0.24–0.26 (0.25); AW = 0.29–0.35 (0.32).

Female. Thoracic and abdominal chaetotaxy as in Figure 42. Subgenital plate quadratic or widening slightly distally, connection to cross-piece moderate in width; pigmentation pattern as in Figure 47. Vulval margin gently rounded, in some specimens bulging slightly in median section, with 2–6 short, slender *vms* and 3 or 4 short, thorn-like *vss* on each side; 3–5 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (*n* = 98, except TL and AW where *n* = 96, and PTW where *n* = 97): TL = 1.68–2.05 (1.83); HL = 0.36–0.41 (0.38); HW = 0.29–0.39 (0.31); PRW = 0.19–0.23 (0.20); PTW = 0.26–0.34 (0.30); AW = 0.35–0.51 (0.41).

Type material. Lectotype ♂, Nesyt, Czechia, 8 Apr. 1953, F. Balát, 1062 (MMBC). **Paralectotype.** 1♀, same data as holotype (MMBC).

Non-type material. 1♂, 6♀, same data as holotype, F. Balát, 1062, 1127, 1177 (MMBC). 1♀, same data as holotype, Brit. Mus. 1955-662 (NHML). 2♀, Hodonín, Czechia, 16 Aug. 1949, F. Balát, 553 (MMBC). 1♀, Liteň, Czechia, 20 May 1938, K. Pfleger, Pfl14 (MMBC). 2♀,
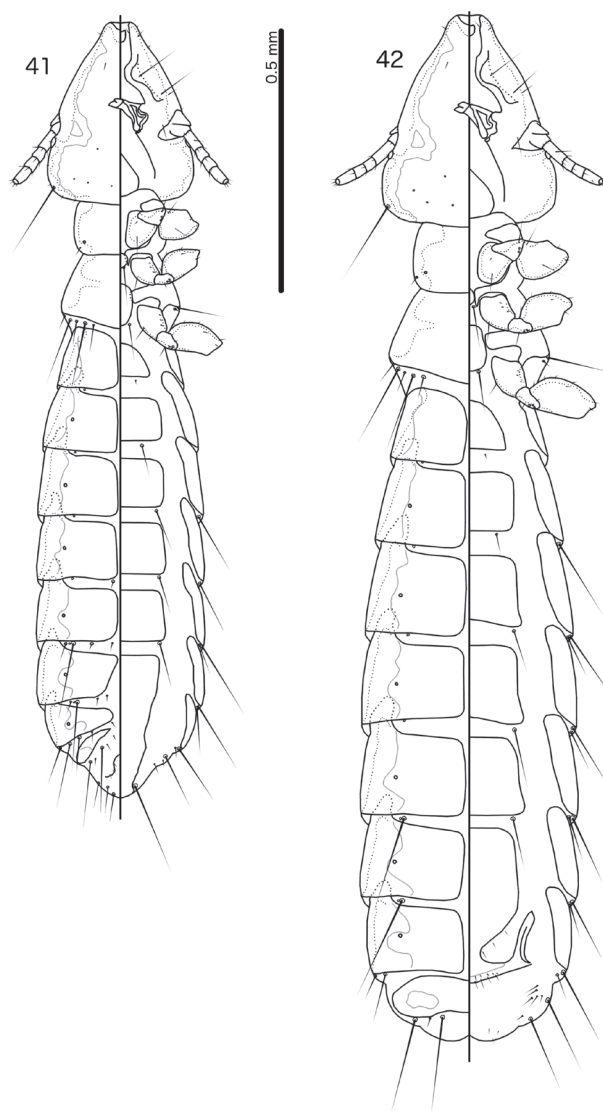
Figures 41, 42. *Brueelia ferianci* Balát, 1955, ex *Anthus trivialis* (Linnaeus, 1758) **41** Male habitus, dorsal and ventral views **42** Female habitus, dorsal and ventral views.

Kuřim, Czechia, 12 May 1955, F. Balát, 714 (MMBC). 1♀, Falsterbo, Sweden, 17 Sep. 1963, F. Balát, 1272 (MMBC). 2♀, Hodonín, Czechia, 16 Aug. 1949, F. Balát, 553 (MMBC). 4♂, 6♀, Goljaki, Trnovski Gozd, Slovenia, 18 June 1965, S. Brelih, 11521–11530 (PMSL); 1♂, 2♀, "S. Spain", Spain, 27 Apr. 1961, Varma Coll. No. A310, Brit. Mus. 1962-325 (NHML); 6♂, 79♀, Morocco, Oct. 1938, R. Meinertzhagen, 11773, 11976 (NHML).

Remarks. Balát (1955) did not explicitly designate a holotype for *B. ferianci*, but mentioned a male and a female as types. On slide no. 1062, which contains three specimens, the male is circled; on the label, the ♂ is circled within a box that reads "Typ ♂ a ♀". We therefore consider this to be an indication that Balát considered this to be the holotype. However, as he did not explicitly name it as such in the original publication, it is a syntype, not a holotype. We hereby designate this male the lectotype, and
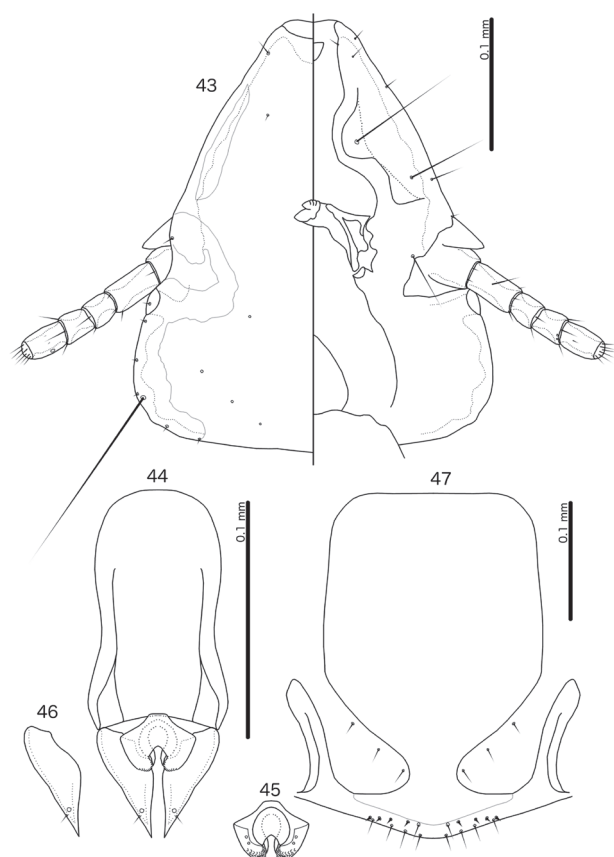
Figures 43–47. *Brueelia ferianci* Balát, 1955, ex *Anthus trivialis* (Linnaeus, 1758) **43** Male head, dorsal and ventral views **44** Male genitalia, dorsal view **45** Male mesosome, ventral view **46** Male paramere, dorsal view **47** Female subgenital plate and vulval margin, ventral view.

the female syntype thus becomes a paralectotype. Presently, all material listed by Balát (1955) is at the MMBC, except one female at the NHML and one female we have not been able to locate; this specimen must be regarded as lost. Another three females (slide no. 1177) were collected from the same host species at the same day on the same location as holotype, but according to ring number (42/53) these lice are from another host specimen that is not mentioned in original paper. The specimen deposited at NHML is labeled "paratype", but has no type status.

The width of the frons differs somewhat between different specimens. The head is here illustrated from the holotype, whereas the full-body illustration is from a more narrow-headed specimen, to illustrate the variation in this species. Most specimens examined are more similar to the narrow-headed illustration. We do not presently consider these differences to be of any taxonomic importance, as the specimens we have examined are otherwise similar. However, fresh material from a number of host subspecies and populations may reveal that the material we have examined represents multiple species. Antennae in holotype and paratype males folded under the head, and here illustrated based on non-type material.

Brueelia kratochvili Balát, 1958
Figs 48–54

Brueelia kratochvili Balát, 1958: 413.
Nigronirmus kratochvili (Balát, 1958); Złotorzycka 1964: 250.

Type host. *Motacilla flava feldegg* Michahelles, 1830, yellow wagtail (Motacillidae).

Type locality. Burgas, Bulgaria.

Other hosts. *Motacilla flava* Linnaeus, 1758, yellow wagtail. *Motacilla tschutschensis macronyx* (Stresemann, 1920), Eastern yellow wagtail. *Motacilla alba* Linnaeus, 1758, white wagtail, **new host record**.

Description. *Both sexes.* Head slender, trapezoidal (Fig. 50), lateral margins of preantennal area convex proximally and slightly concave distally, frons concave. Marginal carina of moderate width, narrowing conspicuously at *dsms*, much displaced and widened at osculum. Ventral anterior plate small, rounded rectangular, hard to see in many specimens. Head chaetotaxy and pigmentation patterns as in Figure 50. Preantennal nodi moderate, not bulging. Pre- and postocular nodi moderate. Marginal temporal carina of moderate width, with median margin undulating. Gular plate lanceolate. Thoracic and abdominal segments and pigmentation patterns as in Figures 48, 49.

Male. Thoracic and abdominal chaetotaxy as in Figure 48. Basal apodeme constricted at about midpoint (Fig. 51). Proximal mesosome large (Fig. 52), gently rounded. Mesosomal lobes broad, highly convergent distally; rugose area extensive in distal end. Gonopore semi-oval, longer than wide. Parameres broad, extended distally (Fig. 53); *pst1–2* as in Figure 53. Measurements ex *Motacilla flava feldegg* (*n* = 8): TL = 1.55–1.72; HL = 0.33–0.35; HW = 0.26–0.28; PRW = 0.18–0.19; PTW = 0.26–0.28; AW = 0.31–0.37. Measurements ex *Motacilla flava* ssp. (*n* = 7): TL = 1.58–1.74; HL = 0.32–0.35; HW = 0.25–0.28; PRW = 0.18–0.20; PTW = 0.25–0.29; AW = 0.32–0.36.

Female. Thoracic and abdominal chaetotaxy as in Figure 49. Subgenital plate rounded rectangular, with narrow connection to cross-piece (Fig. 54). Vulval margin gently rounded, with 3 or 4 short, slender *vms* and 3–5 short, thorn-like *vss* on each side; 5 or 6 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements ex *Motacilla flava feldegg* (*n* = 10): TL = 1.88–2.06 (2.00); HL = 0.35–0.39 (0.37); HW = 0.29–0.32 (0.31); PRW = 0.20–0.22 (0.21); PTW = 0.28–0.32 (0.30); AW = 0.39–0.44 (0.42). Measurements ex *Motacilla flava* ssp. (*n* = 20, except TL, HW and AW where n = 19): TL = 1.80–20.8 (1.97); HL = 0.340.38 (0.36); HW = 0.28–0.31 (0.29); PRW = 0.18–0.22 (0.21); PTW = 0.27–0.33 (0.30); AW = 0.39–0.44 (0.41). Measurements ex *Motacilla tschutchensis macronyx* (*n* = 1): TL = 1.89; HL = 0.36; HW = 0.29; PRW = 0.20; PTW = 0.30; AW = 0.40.

Type material. Lectotype ♂, Burgas, Bulgaria, 29 May 1957, F. Balát, 917a (MMBC). **Paralectotypes.** 2♂, 5♀, same data as lectotype, F. Balát, 917a–b, 945a–c

Dtsch. Entomol. Z. 63 (1) 2019, 17–39

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Figures 50–54. *Brueelia kratochvili* Balát, 1958, ex *Motacilla flava* Linnaeus, 1758 **50** Male head, dorsal and ventral views **51** Male genitalia, dorsal view **52** Male mesosome, ventral view **53** Male paramere, dorsal view **54** Female subgenital plate and vulval margin, ventral view.

Figures 48, 49. *Brueelia kratochvili* Balát, 1958, ex *Motacilla flava* Linnaeus, 1758 **48** Male habitus, dorsal and ventral views **49** Female habitus, dorsal and ventral views.

(MMBC). 1♂, 1♀, same data as lectotype, F. Balát, 945d, Brit. Mus. 1958-425 (NHML). 1♀, same data as lectotype, F. Balát (PMSL).

Non-type material. **Ex *Motacilla flava* ssp.:** 4♂, 4♀, Velké Kapušany, Slovakia, 18 Apr. 1959, F. Balát, 1485, 1486, 1487, 1488 (MMBC). 3♂, 14♀, Metkovic, Croatia, 23 Apr. 1963, A. Lesinger, 6285–6290, 8415–8428 (PMSL). 1♂, Dubrovnik, Croatia, 1 Apr. 1968, A. Lesinger, 11420 (PMSL). 1♀, Burgas, Bulgaria, 29 May 1957, F. Balát (PMSL). 1♀, Bharatpur, Rajasthan, India, 4 Oct. 1969, X1E-1006, 24295 on reverse (NHML). 1♀, Muang Bung Boraphet, Nakhon Sawan Province, Thailand, 15 Mar. 1968, X1E-702 (NHML). 2♂, 2♀, Bahig, Egypt, 25 Aug. 1968, OMS-4468 (NHML). 1♀, Mishmar HaNegev [?], Israel, 29 Aug. 1960, 1167-1174, Brit. Mus. 1961-403 (NHML).

Ex *M. tschutschensis macronyx*: 1♀, Bangkok, Thailand, 18 Sep. 1964, H.E. McClure, H-0953 (NHML).

Ex *M. alba*: 2♂, 1♀, Krišovská Liesková - Krížany, Slovakia, 14 Apr. 1959, F. Balát, 1215, 1216, 1217 (MMBC).

Remarks. Balát (1958) did not designate any type specimens, and all specimens he mentioned are therefore syntypes. The words "Type male and female" is handwritten on the label of slide 917a, and we therefore designate the male on this slide as the lectotype (this male has been marked with a dark spot on the slide); all other specimens mentioned by Balát (1958) thus become paralectotypes. All material is present at the MMBC except for the slides at the NHML and PSML listed above, as well as a slide with a single male we have been unable to trace; it should be regarded as lost.

In addition, there are two slides at MMBC (1485 and 1486) marked 'Type male" and "Type female" on the labels. However, these were collected a year after the publication of *B. kratochvili*, and can thus not be part of the type series. The slides from *Motacilla alba* are also labeled "Type male" (slide no. 1215), "Paratype male" (slide no. 1216), and "Type female" (slide no. 1217), but

no species name based on these specimens have ever been published. The specimens from *Motacilla alba* are here deemed to be conspecific with *M. kratochvili* from *M. flava*. There are no significant differences in head shape, male genitalia, or abdominal chaetotaxy between material from the two host species, but females from *M. alba* have slightly different vulval chaetotaxy from that described above (4 *vos*, 3 or 4 *vms*, 5–7 *vos* on each side). These setal numbers overlap, and we therefore consider *M. alba* to be a new host record of *B. kratochvili*.

Notably, specimens from Asian subspecies of *M. alba* we have seen differ from the present material in the extent of head pigmentation, the male abdominal chaetotaxy, and the shape of the male genitalia, including both the parameres and the mesosome. These populations may represent a different species of *Brueelia*, and are not included under *B. kratochvili* here.

Brueelia rosickyi Balát, 1955

Figs 55–61

Brueelia rosickyi Balát, 1955: 517.

Type host. *Sylvia nisoria* (Bechstein, 1792), barred warbler (Sylviidae).

Type locality. Těšice u Hodonína, Czechia.

Description. *Both sexes.* Head slender, rounded triangular (Fig. 57), lateral margins of preantennal area convex, frons narrowly concave. Marginal carina slender, deeply displaced at osculum, median margin slightly undulating. Ventral anterior plate not visible. Head chaetotaxy and pigmentation patterns as in Figure 57. Preantennal nodi not bulging. Pre- and postocular nodi small, of roughly similar size. Marginal temporal carina of moderate width, median margin undulating. Gular plate broadly lanceolate. Thoracic and abdominal segments and pigmentation patterns as in Figures 55, 56.

Male. Thoracic and abdominal chaetotaxy as in Figure 55. Basal apodeme widening distally, with lateral margins slightly concave at mid-point (Fig. 58). Proximal mesosome large, trapezoidal with slightly concave lateral margins (Fig. 59). Mesosomal lobes slender, converging distally; rugose area extensive along distal margin. Parameres slender, elongated (Fig. 60); *pst1–2* as in Figure 60. Measurements (*n* = 3): TL = 1.28–1.36; HL = 0.33–0.35; HW = 0.22–0.24; PRW = 0.15–0.16; PTW = 0.23–0.24; AW = 0.33–0.35.

Female. Thoracic and abdominal chaetotaxy as in Figure 56. Subgenital plate pentagonal, with narrow connection to cross-piece (Fig. 61). Vulval margin convergent to rounded median point, with 3–5 short, slender *vms* and 3 or 4 short, thorn-like *vss* on each side; 2 or 3 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (*n* = 17): TL = 1.57–1.77 (1.66); HL = 0.36–0.38 (0.37); HW = 0.25–0.28 (0.26); PRW = 0.16–0.18 (0.17); PTW = 0.25–0.28 (0.26); AW = 0.36–0.42 (0.39).
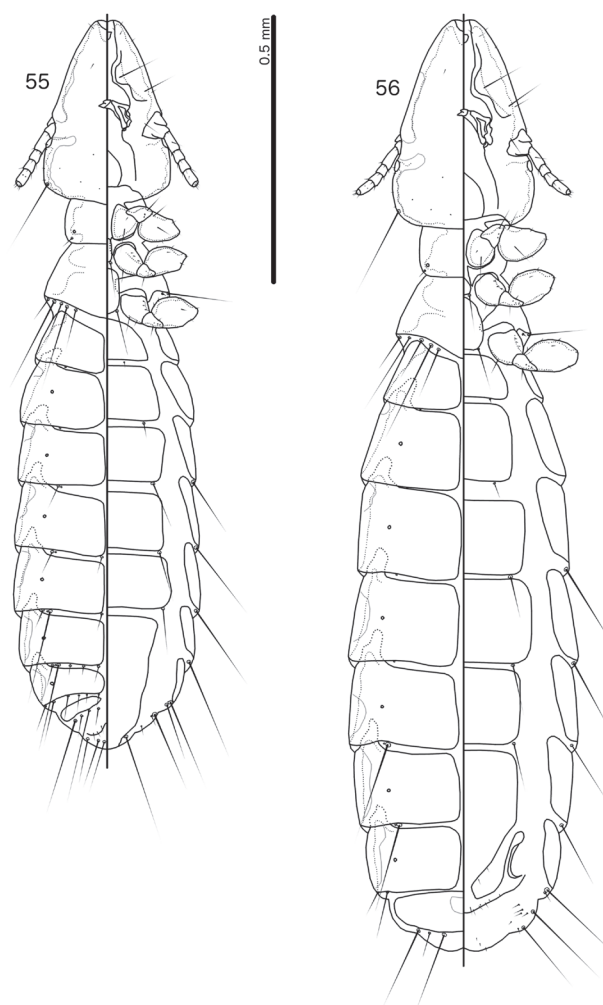
Figures 55, 56. *Brueelia rosickyi* Balát, 1955, ex *Sylvia nisoria* (Bechstein, 1792) **55** Male habitus, dorsal and ventral views **56** Female habitus, dorsal and ventral views.

Type material. Lectotype ♂, Těšice u Hodonína, Czechia, 15 May 1953, F. Balát, 1133a (MMBC). **Paralectotype.** 1♀, same data as lectotype, 1133b (MMBC).

Non-type material. 1♂, 14♀, same data as lectotype, F. Balát, 1133c–q (MMBC). 1♂, 2♀, Járok u Nitry, Slovakia, 17 June 1953, F. Balát, 1070 (MMBC). 1♀, Liteň, Czechia, 19 May 1938, K. Pfleger (MMBC).

Remarks. Balát (1955) did not designate any holotype, but mentioned a male and a female as "types"; these two specimens comprise the syntype series. The specimens on slides 1133a and 1133b are marked accordingly in handwriting, and the male is here designated the lectotype with the female becoming the paralectotype. All other specimens mentioned by Balát as additional specimens have no type status. Slide 1133d is marked "allotype female" and slides 1133e–n are marked "paratypes", but this does not seem to be in Balát's hand. Presently, 20 slides with a total of four males and 18 females are deposited at the MMBC. We have been unable to trace the remaining one male and three females and consider them to be lost.

Figures 57–61. *Brueelia rosickyi* Balát, 1955, ex *Sylvia nisoria* (Bechstein, 1792) **57** Male head, dorsal and ventral views **58** Male genitalia, dorsal view **59** Male mesosome, ventral view **60** Male paramere, dorsal view **61** Female subgenital plate and vulval margin, ventral view.
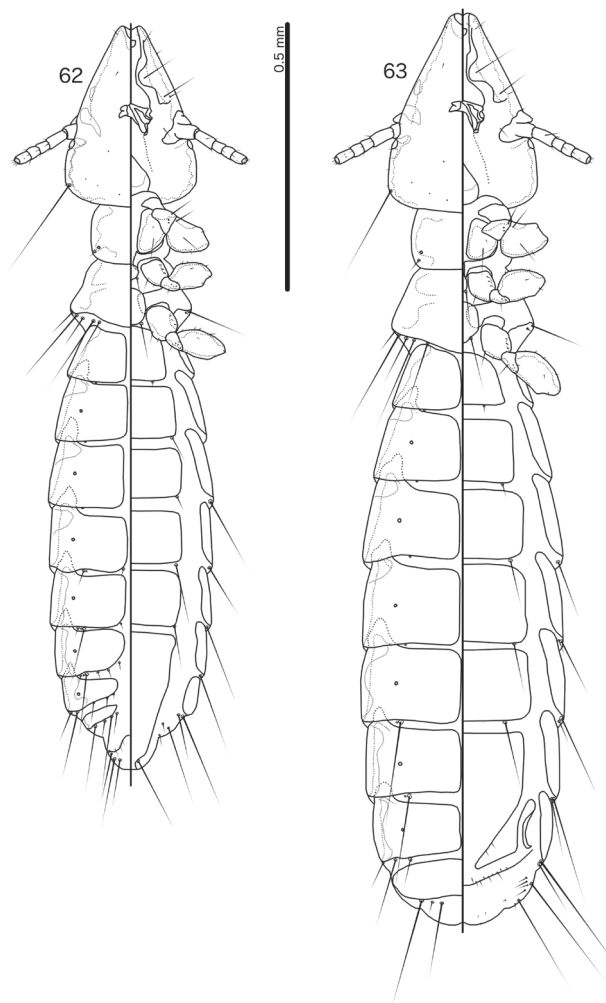
Figures 62–63. *Brueelia vaneki* Balát, 1981, ex *Acrocephalus schoenobaenus* (Linnaeus, 1758) **62** Male habitus, dorsal and ventral views **63** Female habitus, dorsal and ventral views.

Brueelia vaneki Balát, 1981

Figs 62–68

Brueelia vaneki Balát, 1981: 277.

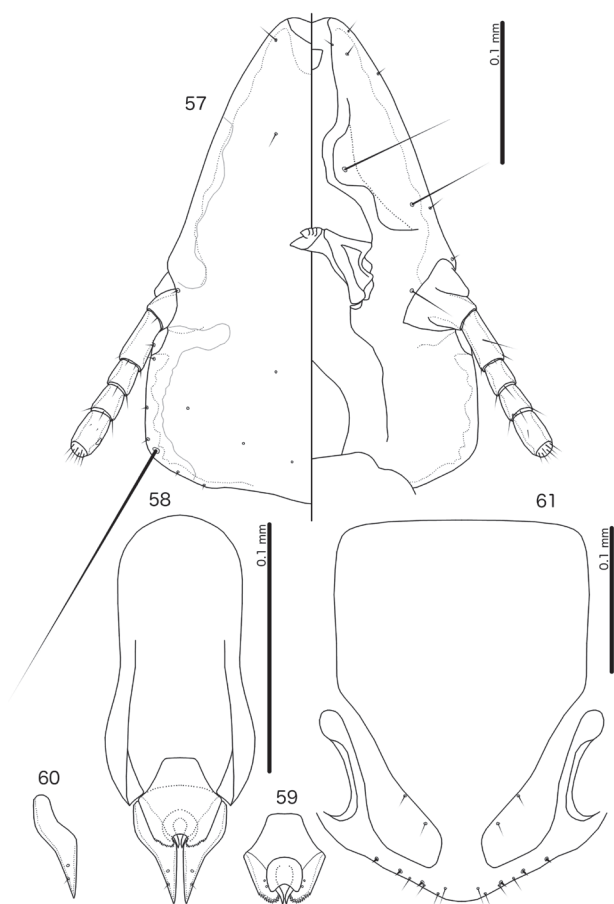**Type host.** *Acrocephalus schoenobaenus* (Linnaeus, 1758), sedge warbler (Acrocephalidae).

Type locality. Velký Dvůr u Pohořelic, Czechia.

Description. *Both sexes.* Head elongated, rounded-trapezoidal (Fig. 64), lateral margins of preantennal area convex proximally and concave distally, frons narrowly concave. Marginal carina moderate in width, with undulating median margin, deeply displaced at osculum. Ventral anterior plate small, shield-shaped. Head chaetotaxy and pigmentation patterns as in Figure 64. Preantennal nodi not bulging. Pre- and postocular nodi of roughly equal size. Marginal temporal carina of moderate width, median margin undulating. Gular plate lanceolate. Thoracic and abdominal segments and pigmentation patterns as in Figures 62 and 63.

Male. Thoracic and abdominal chaetotaxy as in Figure 62. Male genitalia slightly distorted, and proximal mesosome not clearly visible; here illustrated in dorso-lateral view as seen in single examined specimen. Basal apodeme broad, anterior end not visible in specimen (Fig. 65). Proximal mesosome seemingly broad and trapezoidal (Fig. 66). Mesosomal lobes broad, rounded; rugose area extensive along distal margin. Gonopore distorted, but seemingly semi-oval, about as wide as long. Parameres slender, elongated distally (Fig. 67); only *pst1* visible in specimen, as in Figure 67. Measurements (*n* = 1): TL = 1.40; HL = 0.34; HW = 0.25; PRW = 0.16; PTW = 0.23; AW = 0.31.

Female. Thoracic and abdominal chaetotaxy as in Figure 63; holotype has 5 *mms* on one side and 7 *mms* on the other; we have here illustrated only 5, as this is the normal amount in *Brueelia* and the number found in the examined non-type females. Female subgenital plate is almost completely translucent and exact limits very hard to ascertain; apparently broadly pentagonal, with connection to cross-piece moderate in width (Fig. 68). Vulval margin rounded, with slight bulge in median section; 3
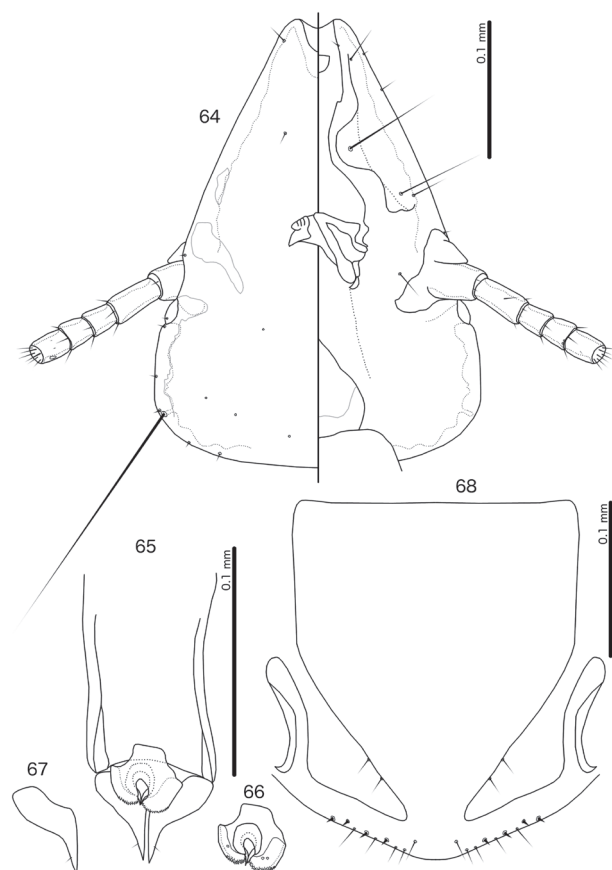
Figures 64–68. *Brueelia vaneki* Balát, 1981, ex *Acrocephalus schoenobaenus* (Linnaeus, 1758) **64** Male head, dorsal and ventral views **65** Male genitalia, dorsal view, except mesosome which is distorted in specimen and here drawn in dorso-lateral view **66** Male mesosome, ventro-lateral view **67** Male paramere, dorsal view **68** Female subgenital plate and vulval margin, ventral view.

or 4 short, slender *vms* and 3 or 4 short, thorn-like *vss* on each side; 3 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to or only slightly anterior to *vss*. Measurements (*n* = 2): TL = 1.42–1.72; HL = 0.34–0.38; HW = 0.25–0.27; PRW = 0.17–0.19; PTW = 0.24–0.26; AW = 0.34–0.39.

Type material. Holotype ♀, Velký Dvůr u Pohořelic, Czechia, 18 June 1978, F. Balát, 1519 (MMBC). **Paratypes.** 1♂, same data as holotype, F. Balát, 1507 (MMBC). 2♀, Hodonín, Czechia, Aug. 1951, F. Balát, 614 (MMBC).

Remarks. Balát (1981) explicitly designated a holotype (female on slide 1519), which is also marked accordingly on the label in handwriting. All other specimens were explicitly designated paratypes. Presently, there are four slides with this material at the MMBC, comprising one male and three females; the remaining two males and two nymphs mentioned by Balát are not in the MMBC, and must be regarded as lost. In addition, slide 1520, which supposedly contained a male of this species, is empty.

Brueelia matvejevi Balát, 1981
Figs 69–75

Brueelia matvejevi Balát, 1981: 278.

Type host. *Turdus viscivorus* Linnaeus, 1758, mistle thrush (Turdidae).

Type locality. Zabljak, Montenegro.

Description. *Both sexes.* Head flat dome-shaped (Fig. 71), lateral margins of preantennal area convex, frons flat to slightly concave. Marginal carina moderate in width, median margin slightly undulating, deeply displaced and widened at osculum. Ventral anterior plate small, shield-shaped with concave anterior margin. Head chaetotaxy and pigmentation patterns as in Figure 71; pigmentation very uniform, and difference between different areas slight. Preantennal nodi slightly bulging. Pre- and postocular nodi large. Marginal temporal carina wide, with undulating median margin. Gular plate broad, with concave lateral margins. Thoracic and abdominal segments as in Figures 69 and 70. Thoracic and abdominal pigmentation more or less uniform, and not denoted in Figures 69, 70.

Male. Thoracic and abdominal chaetotaxy as in Figure 69; *aps* on tergopleurites V–VI absent in some specimens, and only present on one side of tergopleurite VI in holotype. Basal apodeme with shallowly concave lateral margins (Fig. 72). Proximal mesosome as in Figure 73. Mesosomal lobes wide, converging distally, with extensive rugose area in distal end. Gonopore large, crescent-shaped. Parameres stout, elongated distally (Fig. 74); *pst1–s* as in Figure 74. Measurements (*n* = 12): TL = 1.47–1.64 (1.56); HL = 0.33–0.37 (0.35); HW = 0.28–0.32 (0.30); PRW = 0.19–0.22 (0.21); PTW = 0.28–0.31 (0.30); AW = 0.37–0.44 (0.41).

Female. Thoracic and abdominal chaetotaxy as in Figure 70. Subgenital plate rounded pentagonal (Fig. 75), with connection to cross-piece moderate in width. Vulval margin gently rounded to flattened medianly, with 4 or 5 short, slender *vms* and 2 or 3 short, thorn-like *vss* on each side; 3 or 4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (*n* = 15): TL = 1.53–1.93 (1.73); HL = 0.35–0.41 (0.38); HW = 0.28–0.35 (0.32); PRW = 0.20–0.24 (0.22); PTW = 0.28–0.35 (0.32); AW = 0.40–0.51 (0.46).

Type material. Holotype ♂, Žabljak, Montenegro, 3 July 1958, S. Brelih (6342), F.B. 1523 (MMBC). **Paratypes.** 1♀ same collection data as holotype, S. Brelih (6344), F.B. 1524. 3♂, 1♀ Brno – Obora, Czechia, 15 Jun. 1954, F. Balát, 1416, 1417a, b, 1419.

Non-types examined. **Ex *Turdus viscivorus viscivorus*:** 2♂, 2♀, Crno Jez, Durmitor, Montenegro, 8 July 1958, S. Brelih, 333, 1990, 1992–1993 (PMSL); 6♂, 10♀, Crno Jez, Durmitor, Montenegro, 3 July 1958, S. Brelih, 428–429, 628–629, 1997–1998, 6338–6339, 6341, 6343, 6345–6347, 6350–6352 (PMSL); 1♀, Crna Gora, Zabljak, Montenegro, 1 Mar. 1958, S. Brelih (NHML).

Remarks. Balát (1981) explicitly designated the male on slide 1523 (Brelih's collection number 6342) as the holotype, and this is confirmed by the handwritten note on
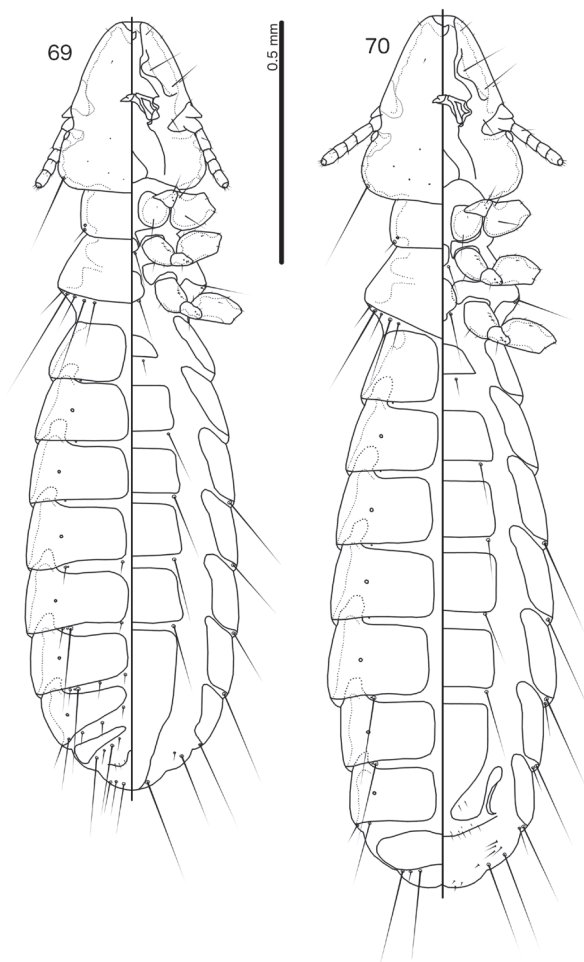
Figures 69, 70. *Brueelia matvejevi* Balát, 1981, ex *Turdus viscivorus* Linnaeus, 1758 **69** Male habitus, dorsal and ventral views **70** Female habitus, dorsal and ventral views.
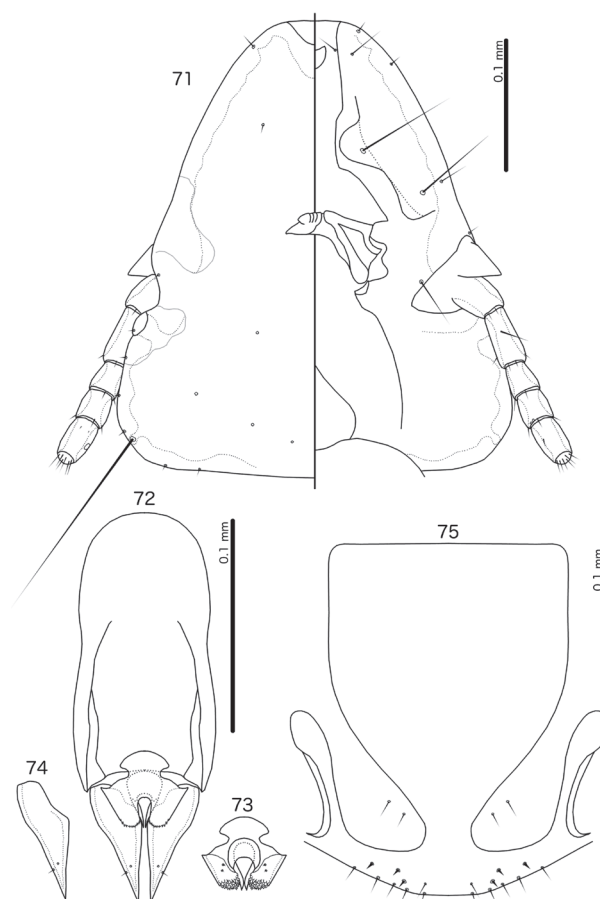
Figures 71–75. *Brueelia matvejevi* Balát, 1981, ex *Turdus viscivorus* Linnaeus, 1758. **71** Male head, dorsal and ventral views **72** Male genitalia, dorsal view **73** Male mesosome, ventro-lateral view **74** Male paramere, dorsal view **75** Female subgenital plate and vulval margin, ventral view.

the slide label. Another female from the same host specimen (slide no. 1524; Brelih's collection number 6344), and 20 males, 26 females, and 6 nymphs were designated as paratypes. Presently, six slides with the holotype and five paratypes are at the MMBC. All other specimens are missing from the MMBC, and must be regarded as lost.

Guimaraesiella Eichler, 1949

Nirmus Nitzsch, 1818: 291 (*in partim*).
Degeeriella Neumann, 1906: 60 (*in partim*).
Brueelia Kéler, 1936: 257 (*in partim*).
Xobugirado Eichler 1949: 13.
Allobrueelia Eichler, 1951: 36 (*in partim*).
Allobrueelia Eichler, 1952: 74 (near-verbatim redescription).
Allonirmus Złotorzycka, 1964: 263.
Nitzschnirmus Mey & Barker, 2014: 101.

Type species. *Docophorus subalbicans* Piaget, 1885: 6 [= *Docophorus papuanus* Giebel, 1879: 475], by original designation.

Guimaraesiella haftorni (Balát, 1981)
Figs 76–82

Allobrueelia haftorni Balát, 1981: 280.
Guimaraesiella haftorni (Balát, 1981); Gustafsson and Bush 2017: 222.

Type host. *Turdus iliacus* Linnaeus, 1758. redwing (Turdidae).

Type locality. Sokolnice, Czechia.

Description. *Both sexes.* Head broad, rounded dome-shaped (Fig. 78), lateral margins of preantennal head convex, frons broadly concave. Marginal carina broad, with undulating median margin. Dorsal and ventral anterior plates and exact extent of dorsal preantennal suture not clear in examined specimens, and illustrated tentatively. Head chaetotaxy as in Figure 78. Preantennal nodi bulging. Pre- and postocular nodi of roughly equal size. Marginal temporal carina of moderate width, median margin undulating slightly. Gular plate not visible in examined material, and not illustrat-
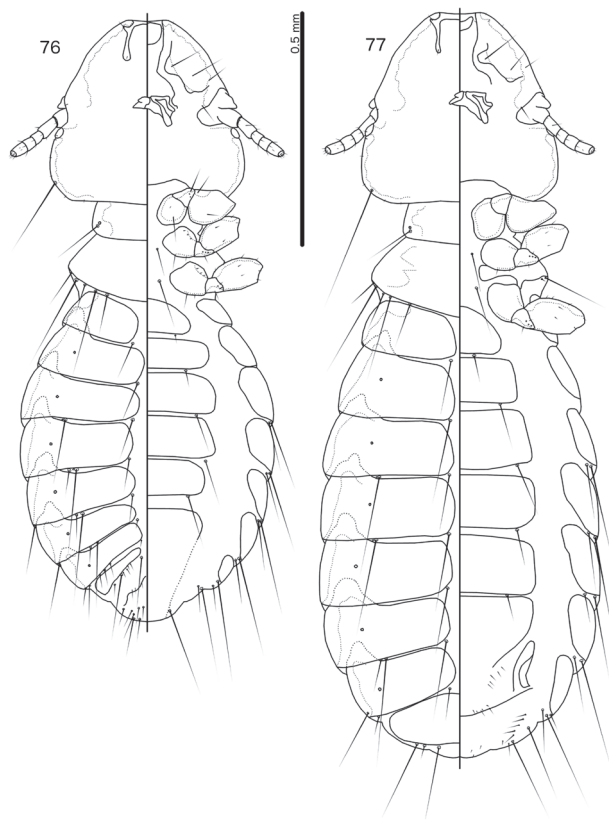
Figures 76, 77. *Guimaraesiella haftorni* (Balát, 1958) ex *Turdus iliacus* Linnaeus, 1758. **76** Male habitus, dorsal and ventral views **77** Female habitus, dorsal and ventral views.

Figures 78–82. *Guimaraesiella haftorni* (Balát, 1958) ex *Turdus iliacus* Linnaeus, 1758 **78** Male head, dorsal and ventral views **79** Male genitalia, dorsal view **80** Male mesosome, ventral view **81** Male paramere, dorsal view **82** Female subgenital plate and vulval margin, ventral view.

ed. Thoracic and abdominal segments as in Figures 76 and 77. Pigmentation artificially altered, and true pigmentation patterns unknown.

Male. Thoracic and abdominal chaetotaxy as in Figure 76. Basal apodeme widening proximally, with slightly concave lateral margins (Fig. 79). Proximal mesosome widening slightly proximally (Fig. 80). Ventral sclerite rectangular, slender. Mesosomal lobes slender, convergent distally, seemingly not fused in distal end. Mesosomal chaetotaxy as in Figure 80. Moderate rugose area anterior to reverse drop-shaped gonopore. Parameral heads roughly widely rectangular (Fig. 81); parameral blades slender, elongated; *pst1–2* not visible in specimens. Measurements (*n* = 2): TL = 1.25–1.26; HL = 0.37–0.38; HW = 0.39–0.41; PRW = 0.24; PTW = 0.32–0.35; AW = 0.51–0.52.

Female. Thoracic and abdominal chaetotaxy as in Figure 77. Holotype with 5 *mms* on one side, and 7 *mms* on the other; we here illustrated only 5, which is the typical number in *Guimaraesiella*. Tergopleurite VI without post-spiracular setae in holotype, but this is likely an anomaly as these setae occur in all other *Guimaraesiella*; *ss* on tergopleurite VIII only present on one side. Subgenital plate not clear in specimen, seemingly wide anteriorly (Fig. 82); distal shape unknown. Vulval margin gently rounded, somewhat flattened medially, with 2 short, slender *vms* and 2 or 3 short, thorn-like *vss* on each

side; 4–6 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (*n* = 1): TL = 1.71; HL = 0.44; HW = 0.47; PRW = 0.28; PTW = 0.42; AW = 0.64.

Type material. Holotype ♀, Sokolnice, Czechia, 1 Apr. 1958, F. Balát, 1242 (MMBC). **Paratypes.** 2♂, same collection data as holotype, F. Balát, 1240, 1241 (MMBC).

Remarks. Balát (1981) explicitly designated the female on slide 1242 as the holotype, and the specimens on slides 1240 and 1241 as paratypes. This is confirmed by the handwritten notes on the slide labels. All specimens are present in the MMBC. Balát (1981) stated that both paratype males were immature. This is incorrect, as both males are adult. However, all three known specimens are poorly cleared, and many details cannot be seen properly, including the meso- and metasterna, metepisterna, proepimera, the gular plate, many leg setae, and the distal section of the subgenital plate of both sexes. More specimens of *G. haftorni* are needed to completely redescribe and reillustrate this species.

The *Guimaraesiella* of European thrushes are all morphologically very similar, differing mainly in the male genitalia and the head shape. Moreover, we have seen

some specimens of *Guimaraesiella* from non-type host species in European material (D. Gustafsson unpublished data). Unless these records are the result of contamination or misidentification of the host, this may suggest that at least some European species of *Guimaraesiella* occur on more than one host species. Relying on host relationships to obtain the species identity of *Guimaraesiella* samples from thrushes may thus be unreliable. However, almost all species of *Guimaraesiella*, including those from thrushes, are poorly described, and presently unidentifiable. Redescriptions of *Guimaraesiella amsel* (Eichler, 1951), *Guimaraesiella marginata* (Burmeister, 1838), *Guimaraesiella turdinulae* (Ansari, 1956), and *Guimaraesiella viscivori* (Denny, 1842) are urgently needed to establish the species limits in this group.

Guimaraesiella lais (Giebel, 1874)
Figs 83–89

Nirmus .... Giebel, 1866: 366 [species 25].
Nirmus lais Giebel, 1874: 143.
Degeeriella lais Giebel, 1874; Harrison 1916: 116.
Brueelia lais (Giebel), 1874; Hopkins and Clay 1952: 57.
Brueelia (*Allobrueelia*) *lais* (Giebel); Balát 1955: 503.
Allonirmus lais (Gieb.); Złotorzycka 1977: 45.
Guimaraesiella lais (Giebel, 1874); Gustafsson and Bush 2017: 222.
Allobrueelia lais (Giebel, 1874); Mey 2017: 177.

Type host. *Luscinia megarhynchos* (Brehm, 1831), common nightingale (Muscicapidae).

Type locality. None given in original, but likely Germany. Neotype (designated herein) is from Nejdek u Lednice, Czechia.

Description. *Both sexes.* Head broad, rounded pentagonal (Fig. 85), lateral margins of preantennal area convex, frons broadly concave. Marginal carina moderate in width, with undulating median margin. Exact posterior extent of dorsal preantennal suture not clear in examined specimens, but suture does not appear to reach *ads*. Ventral anterior plate with deeply concave anterior margin. Head chaetotaxy and pigmentation patterns as in Figure 85; pigmentation of preantennal head rather uniform. Preantennal nodi with slight median bulge. Preocular nodi larger than postocular nodi. Marginal temporal carina thin, of more or less equal width. Gular plate short, broad, with median point. Thoracic and abdominal segments and pigmentation patterns as in Figures 83, 84.

Male. Sternites II–IV partially ruptured and displaced in neotype, and here illustrated approximately. Thoracic and abdominal chaetotaxy as in Figure 83; neotype has no setae on dorsal side of abdominal segment XI, but this is likely an anomaly. Male genitalia partially obscured by gut content. Basal apodeme widens proximally, with slightly concave lateral margins in distal half (Fig. 86). Proximal mesosome widening proximally, with concave lateral margins (Fig. 87). Ventral sclerite obscured by gut
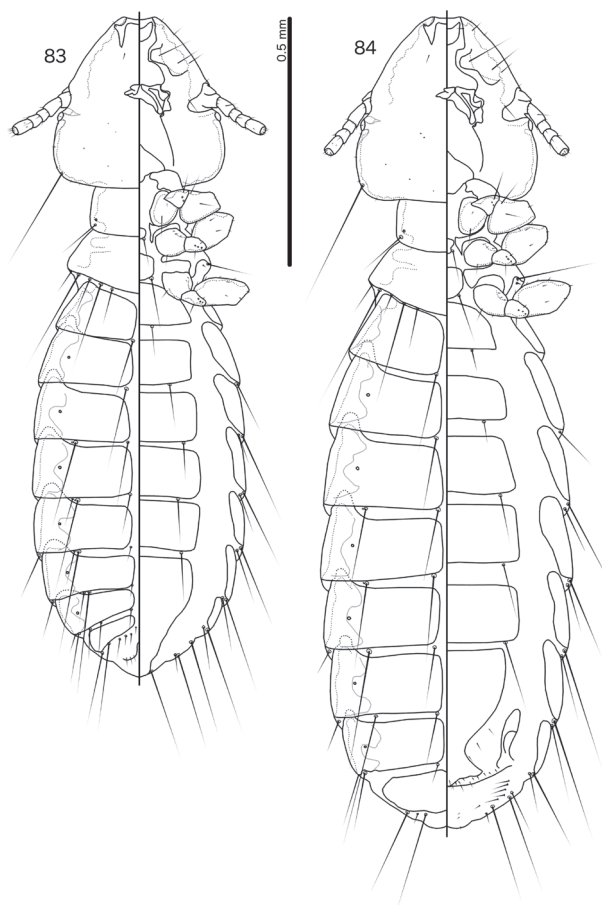
Figures 83, 84. *Guimaraesiella lais* (Giebel, 1874) ex *Luscinia megarhynchos* (Brehm, 1831) **83** Male habitus, dorsal and ventral views **84** Female habitus, dorsal and ventral views.

content, and illustrated approximately; seemingly narrowly rectangular. Mesosomal lobes slender, converging in distal end, fused distally. Mesosomal chaetotaxy as in Figure. 87. Rugose area absent. Gonopore almost terminal, semi-oval. Parameral heads large (Fig. 88), parameral blades of approximately uniform width in proximal half, tapering in distal half, with *pst1–2* as in Figure 81. Measurements ($n = 1$): TL = 1.32; HL = 0.34; HW = 0.33; PRW = 0.21; PTW = 0.30; AW = 0.43.

Female. Thoracic and abdominal chaetotaxy as in Figure 84. Examined specimens poorly cleared, and exact shape of distal subgenital plate not clear, and here illustrated as accurately as possible; seemingly rounded-triangular, with broad distal section, including wide lateral submarginal bulges (Fig. 89). Vulval margin flattened medially, with 3 or 4 short, slender *vms* and 8 short, thorn-like *vss* on each side; 3 or 4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements ($n = 3$): TL = 1.61–1.66; HL = 0.36–0.38; HW = 0.35–0.37; PRW = 0.21–0.22; PTW = 0.31–0.34; AW = 0.46–0.51.

Type material. Neotype 1♂, Nejdek u Lednice, Czechia, 6 May 1953, F. Balát, 1114 (MMBC). **Neoparatypes:** 3♀, same data as neotype, 1113, 1114 (MMBC).

Remarks. Gustafsson and Bush (2017) included *Nirmus lais* Giebel, 1874, in *Guimaraesiella* Eichler, 1949, without comment; they did not examine any specimens of this species. The placement of this species in *Guimaraesiella* followed Balát (1955), who placed it in *Allobrueelia* Eichler, 1951, a synonym of *Guimaraesiella*, and Złotorzycka (1977), who placed it in *Allonirmus* Złotorzycka, 1964, also a synonym of *Guimaraesiella*. However, they overlooked that Giebel (1874) stated that this species was close to *Nirmus intermedius* Nitzsch [in Giebel], 1866, which Gustafsson and Bush (2017) placed in *Brueelia* Kéler, 1936. This apparent contradiction requires some additional discussion.

Giebel's description of *N. lais* was based on a single female, and does not contain any specific character that can be used to place *N. lais* in either *Brueelia* or *Guimaraesiella* with certainty. Giebel (1874) did not illustrate this species. Giebel (1866) recorded lice from the same host merely as "*N ...*" [species 25 under the genus *Nirmus*], but lists specimens from *Erithacus rubecula* (Linnaeus, 1758) under the same heading; the lice from *E. rubecula* were later (Giebel 1874) described as *Nirmus tristis* Giebel, 1874, which was also placed in *Guimaraesiella* in the revision of Gustafsson and Bush (2017).

Giebel's (1874) statement that *N. lais* is similar to *N. intermedius* is unreliable, as his other statements about similarity between louse species are often confusing. For instance, on the page before the description of *N. lais*, Giebel (1874: 142) stated that *Nirmus intermedius* is similar to *Nirmus ruficeps* Nitzsch [in Giebel], 1866, and *N. limbatus* Burmeister, 1838. The former species is a head louse, now placed in the genus *Rostrinirmus* Złotorzycka, 1964, whereas the latter is an uncommonly wide-headed and large-bodied member of *Brueelia* s. str. *Brueelia intermedia*, by contrast, is a slender-headed species of *Brueelia*, quite unlike both *N. ruficeps* and *N. limbatus*. This issue is further confused by Giebel's statement that *N. intermedius* is similar to *N. merulensis* Denny, 1842, differing only in the proportions of the antennae and the prothorax. Gustafsson and Bush (2017) placed *N. merulensis* in the genus *Turdinirmus* Eichler, 1951, a genus superficially similar to *Guimaraesiella*, but very different from species of *Brueelia* known from thrushes in size, head shape, and head structure. It is therefore not at all clear what specimens Giebel actually examined, and what he means by "similar".

Apart from the specimens listed here, we have been unable to locate any specimens of *Brueelia*-complex lice from *L. megarhynchos* in any of the museum collections we have searched (see list in Gustafsson and Bush 2017). In particular, Giebel's original specimen appears to have been destroyed in the war (Clay and Hopkins 1955). Moreover, Balát's (1955) report appears to be the only subsequent report of any species of louse in the *Brueelia*-complex from *L. megarhynchos*. Eichler [in Niethammer] (1937; not seen) and Séguy (1944) reported *N. lais* from *Luscinia luscinia* (Linnaeus, 1758); we have not seen these specimens. It is not clear from Séguy's
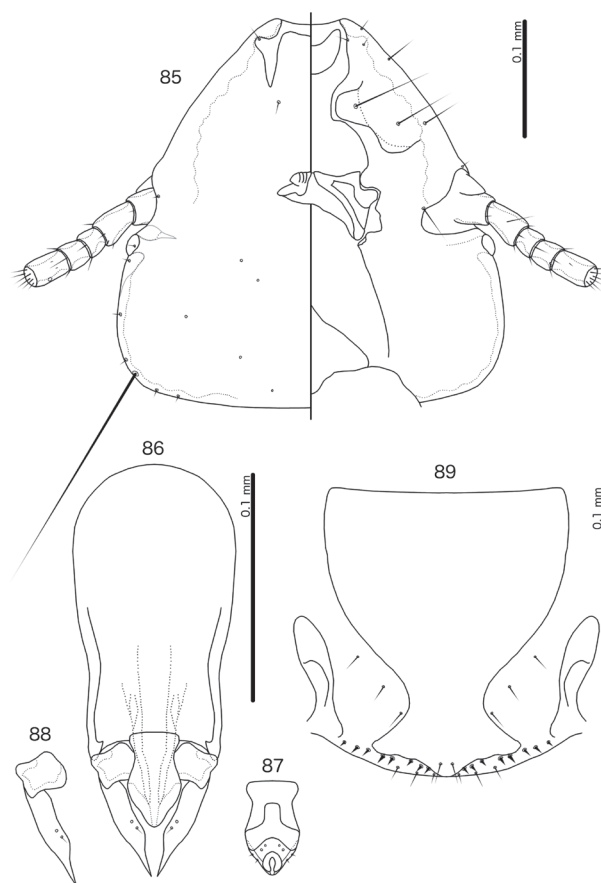
Figures 85–89. *Guimaraesiella lais* (Giebel, 1874) ex *Luscinia megarhynchos* (Brehm, 1831) **85** Male head, dorsal and ventral views **86** Male genitalia, dorsal view **87** Male mesosome, ventral view **88** Male paramere, dorsal view **89** Female subgenital plate and vulval margin, ventral view.

(1944) short description whether his specimens represent the same species as Giebel's *N. lais*, or whether this identity is assumed based on the close relationship between the host species.

Złotorzycka (1977: figs 149–152) illustrated the head, ventral anterior plate, male genitalia, and pleurites of *N. lais*, but indicated that this species was not known from Poland (ibid.: 10). It is therefore uncertain where the material she based her illustration on originated, nor where this specimen is located today. Złotorzycka's illustrations are rarely very informative, especially those of male genitalia. However, the specimens we have examined are largely concordant with the illustrations of Złotorzycka (1977).

To stabilize the nomenclature of the lice found on thrushes and flycatchers, we here designate a neotype for *Nirmus lais* Giebel, 1874, from Balát's specimens. These specimens all belong to *Guimaraesiella* (sensu Gustafsson and Bush 2017), and our neotype designation thus conforms to the placement of this species in *Guimaraesiella* by Gustafsson and Bush (2017), in *Allobrueelia* [= *Guimaraesiella*] by Balát (1955) and Mey (2017), and in *Allonirmus* by Złotorzycka (1977). More-

over, this conforms to Giebel's (1866) earlier placement of Nitzsch's material from *L. luscinola* [= *L. megarhynchos*; but given as *Sylvia luscinia* by Giebel (1866)] with his material from *E. rubecula*, which represents *Guimaraesiella tristis*.

Guimaraesiella tovornikae (Balát, 1981)

Allonirmus tovornikae Balát, 1981: 281.
Nigronirmus atricapillae Soler-Cruz et al., 1984: 147.
Brueelia atricapillae Soler-Cruz et al., 1984; Price et al. 2003: 153 (nec *B. atricapilla* Cicchino, 1983: 290).
Brueelia neoatricapillae Price, Hellenthal & Palma, 2003 [in Price et al.: 153].
Guimaraesiella tovornikae (Balát, 1981); Gustafsson and Bush 2017: 222.

Type host. *Sylvia atricapilla* (Linnaeus, 1758), blackcap (Sylviidae).

Type locality. Antošovice, Czechia.

Remarks. Balát (1981) reported four males and three females of this species from three localities in Czechia and Yugoslavia. The male on slide 1383 was explicitly designated as holotype, and the other specimens as paratypes. Unfortunately, these slides cannot be found at the MMBC, and we have been unable to trace them elsewhere. The type material of this species must be regarded as lost.

This is unfortunate, as *A. tovornikae* is considered to be a senior synonym of *Nigronirmus atricapillae* Soler-Cruz et al., 1984, from the same host (Gustafsson and Bush 2017). While this synonymy should not be controversial, considering the morphological similarities of the two species, any neotype designation for *A. tovornikae* will need to take the synonymy with *N. atricapillae* into consideration. For this, fresh material is needed.

Discussion

Dalgleish and Price (2003) stated that the only way to realistically deal with a super-species-rich genus like *Myrsidea* Waterston, 1915, is to circumscribe each revision to species of lice from the same host family; this practice is generally followed by taxonomists working on *Myrsidea* (e.g., Price and Johnson 2006, Sychra and Literák 2008, Kounek et al. 2011). Taken as a whole, the *Brueelia*-complex is more species-rich than *Myrsidea*, and the host range of the *Brueelia*-complex is similar to that of the genus *Myrsidea*. Any approach likely to make species identification and description within the *Brueelia*-complex easier is thus appealing. Is the approach used for *Myrsidea* then applicable to the *Brueelia*-complex as well?

In a wider perspective, using this approach in the *Brueelia*-complex is not without problems. Gustafsson and Bush (2015) and Gustafsson et al. (2018b) showed several examples of morphologically similar species of *Brueelia* occurring on different host families, and, conversely, species of *Brueelia* occurring on the same host family being morphologically different.

The species redescribed here show similar patterns. Most taxa treated here are fairly typical species for their respective host families. For instance, both *B. ferianci* and *B. kratochvili* have the head shape typical of *Brueelia* species parasitizing boreal (but not tropical or southern; Gustafsson and Bush in prep.) motacillids. The extensive dark pigmentation patterns of *B. breueri* are also typical of the species of *Brueelia* parasitizing many boreal fringillids.

However, the head shape of *B. blagovescenskyi* (Fig. 4) is more similar to *Brueelia* species on boreal motacillids (e.g., Fig. 50) than it is to *B. pelikani* from another emberizid host (Fig. 8). The same head shape is found in some undescribed species from cisticolid hosts (Gustafsson and Bush in prep.). Similarly, the lack of *aps* on male tergopleurites VI–VII in *B. glizi* (Fig. 20) is more similar to some species of *Brueelia* on North American passerellids (Gustafsson and Bush in prep.) than it is to any species of *Brueelia* known from fringillids.

Descriptions of new species in large genera like *Brueelia* and *Guimaraesiella* thus need to be done with caution, as the close relatives may parasitize different host families (Gustafsson and Bush 2015, Bush et al. 2016). A simple comparison of a potential new louse species with only species found on the same host family may therefore not be sufficient. Unfortunately, of the 426 species of lice in this complex recognized by Gustafsson and Bush (2017; additional species have since been described by Mey 2017, Gustafsson et al. 2018a, b, c, 2019), less than half are identifiable from their original descriptions. Moreover, there are no published suggestions for species groups in *Brueelia* and *Guimaraesiella* to consult. Apart from species description and illustration, future taxonomic work on the *Brueelia*-complex should include attempts to delimit species groups within the larger genera of the complex (*Brueelia, Guimaraesiella*). In addition, it is vital that more already described species within this complex are examined critically and redescribed whenever possible.

Acknowledgements

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Type catalogue of the thick-headed flies (Diptera, Conopidae) in the collection of the Museum für Naturkunde Berlin

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http://zoobank.org/40FA7125-B15A-4678-843C-2B3D67B66344

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Abstract

Type material of thick-headed flies (Diptera, Conopidae) in the collection of the Museum für Naturkunde Berlin (ZMHB) is documented. The entire collection holds primary type material (i.e. holotypes, lectotypes, syntypes) of 73 species. Five *Conops* species with previously unknown subgenus belong to the subgenus *Asiconops*: *C. frontosus* Kröber, 1916; *C. indicus* Kröber, 1916; *C. maculiventris* Kröber, 1916; *C. nigrofasciatus* Kröber, 1916; and *C. punctifrons* Kröber 1916. Two new synonyms are introduced: *Conops vaginalis* Rondani, 1865 syn. nov. of *Conops truncatus* Loew, 1847 and *Siniconops fuscatus* Qiao & Chao, 1998 syn. nov. of *Physocephala sepulchralis* Brunetti, 1912.

Introduction

The recently published catalogue of Conopidae lists the depositories of primary type material based on published information (Stuke 2017). This present paper presents a revised catalogue of the type material of Conopidae deposited in the collection of the Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany (ZMHB).

Due to impressive historical and recent research in Diptera at the museum, several dipterists have added type material to the collection, including Hermann Loew (1807–1879; 10 species), Theodor Becker (1840–1928; 10 species); Anton Ferdinand Franz Karsch (1853–1936; 2 species), Oswald Duda (1869–1941; 1 species), Otto Kröber (1882–1969; 41 species and 2 lost species) and Jens-Hermann Stuke (1967; 9 species).

The Berlin collection is one of the most important for Conopidae worldwide, containing primary type material of some 73 species. Only the Natural History Museum (London; formerly the British Museum, Natural History) and the National Museum of Natural History (Smithsonian Institute) (Washington, DC) hold more type material.

Methods

The original labels are listed as citations. The labels are listed and numbered in the order found, commencing with the uppermost. Line breaks on labels are indicated by a slash (" / "), but if there are "/" signs on the labels themselves, these are included without spaces before and after. If text on labels could not be identified properly the line is marked by "[?]". The interpretation of cited locations is given in Table 1. The following acronyms are used for collections mentioned in the text:

MNHN Muséum National d'Histoire Naturelle (Paris, France)
NHML Natural History Museum (London, UK)
NMW Naturhistorisches Museum (Vienna, Austria)
SDEI Senckenberg Deutsches Entomologisches Institut (Müncheberg, Germany)
USNM Smithsonian Institution National Museum of Natural History; formerly, United States National Museum (Washington DC, USA)
ZMHB Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science (Berlin, Germany)
ZMUC University of Copenhagen, Zoological Museum (Copenhagen, Denmark)

Results

Abrachyglossum capitatum (Loew, 1847)

Conops capitatus Loew 1847: 2; type localities: "Vaterland: Es scheint nicht über das Alpengebiet hinauszugehen und kömmt auch im schlesischen Gebirge vor." – available, valid.

♀ syntype: (1) "Reinerz / 13/7 41"; (2) *"Brachyglossum ♀ / capitatum* Lw / O. Kröber det. 1912"; (3) "*Abrachyglossum / capitatum ♀ /* Stuke det. 2004".

♂ syntype: (1) "Riesengeb. / VII"; (2) *"capitatus / Loew*"; (3) *"Abrachyglossum / capitatum ♂ /* Stuke det. 2004".

♂ syntype: (1) "Altenbg. / 7/8"; (2) "Coll. / Gerst."; (3) *"Brachyglossum ♂ / capitatum* Lw / O. Kröber det. 1912"; (4) *"Abrachyglossum / capitatum ♂ /* Stuke det. 2004"".

Loew (1847) described only the female of *A. capitatum* but obviously had several specimens at hand because he gave a range for the distribution of the new species. In ZMHB there are only three specimens likely to have been collected before 1847, and which, therefore, should be accepted as syntypes.

Australoconops perbellus (Kröber, 1939)

Conops perbellum Kröber 1939b: 601–602; type locality: "W. Australien, Marloo Station, Wurarga" – available, valid.

♂ holotype: (1) "Type"; (2) "Typus"; (3) "W. Australien / Marloo Station / Wurarga 8.1935 / Gebr. Goerling S. G."; (4) *"Conops / perbellum / ♂* Kröb.".

Australoconops pseudocellifer (Kröber, 1939)

Conops pseudocellifer Kröber 1939b: 601; type locality: "Neuholland" – available, valid.

♀ holotype: (1) "Type"; (2) "5518"; (3) "Typus"; (4) *"Conops / pseudocellifer /* 1938 ♀ Krb"; (5) *"Conops ♀ / aurosa* Herm / O. Kröber det. 1914"; (6) *"aureorufa /* Macq. / Nov.Holl. Schultz".

Australoconops unicinctus (Kröber, 1939)

Conops unicinctus Kröber 1939b: 603–604; type localities: "S. W. Australien, Kalamunda", "Port Philipp" – available, valid.

♀ syntype: (1) "3039"; (2) "Typus"; (3) *"Conops / unicinctus /* n sp"; (4) *"pica / pica* et *aureorufa /* Macq. ? / Pt. Phil. Coulon".

Kröber (1939) described the material he used for the description of *A. unicinctus* as follows: "♂♀. ♀ als *pica* von mir beschrieben. Type: Berlin. ♂ von S. W. Australien, Kalamunda, 9.iii.–11.iii. Type: London" [♂♀. ♀ described as *pica* by me. Type: Berlin. ♂ from S. W. Australia, Kalamunda, 9.iii.-11.iii. Type: London]." Schneider (2010) and Stuke (2017) misinterpreted this statement and suggested only "Australien, Kalamunda" as the type locality. In fact Kröber (1916) also redescribed "*Conops picus* Mcq." [= *Australoconops picus* (Macquart, 1851)] and gave "Port Phillipp" as the location. Therefore "Port Phillipp" should be treated as a second locus typicus and the specimen described above regarded as the female syntype of *A. unicinctus*.

Brachyceraea brevicornis (Loew, 1847)

Conops brevicornis Loew 1847: 23; type locality: "Brusa im nördlichen Kleinasien" – available, valid.

♂ holotype: (1) "Brusa / 8/42 A. m"; (2) "Coll. / H. Loew"; (3) "Typus"; (4) *"Brachyceraea ♂ / brevicornis* LW" / O. Kröber det 1912".

Conops acuticornis Loew, 1847

Conops acuticornis Loew 1847: 8-9; type localities: "Das Alpengebiet; auch in Württemberg und Schlesien" – available, invalid: junior synonym of *Conops ceriaeformis* Meigen, 1824.

♂ syntypus: (1) "Märkl."; (2) "Coll. / H. Loew"; (3) "Typus"; (4) *"Conopilla ♂ / ceriaeformis* mg / O. Kröber det 1912"; (5) "Zool. Mus. / Berlin"; (6) *"Conops ♂ / ceriaeformis /* Stuke det. 2003".

♂ syntypus: (1) "Siles. / Sellind."; (2) "Coll. / H. Loew"; (3) "Paratypus"; (4) *"Conopilla ♂ / ceriaeformis* mg / O. Kröber det 1912"; (5) "Zool. Mus. / Berlin"; (6) *"Conops ♂ / ceriaeformis /* Stuke det. 2003".

♂ syntypus: (1) "cc. *C. signat* / v. Roser * / Stuttg."; (2) "Coll. / H. Loew"; (3) "Paratypus"; (4) *"Conopilla ♂ / ceriaeformis* mg / O. Kröber det 1912"; (5) "Zool. Mus. / Berlin"; (6) *"Conops ♂ / ceriaeformis /* Stuke det. 2003".

Conops atrimanus Kröber, 1939

Conops apicalis var. *atrimanus* Kröber 1939a: 379; type locality: "Uam, Kamerun" – available, invalid: available, invalid: junior synonym of *Conops ferruginosus* Kröber, 1915.

♀ holotype: (1) "S. O. Kamerun / Uam-Gebiet / G. Tessmann S. G. / bei Bossum [written perpendicularly] / 29.6.14 [written perpendicularly]"; (2) "*Conops apicalis* / var *atrimanus* Krb. / det. Kröber 1938".

Table 1. Historical locations on labels mentioned in the text and their modern interpretation.

Adeleide	Adelaide [Australia, South Australia]
Alai Geb.	Alay Mountains [Kyrgyzstan & Tajikistan]
Altenbg.	Altenburg [Germany, Thuringia]
Amboin.	Amboina [Indonesia, Maluku Islands]
Argentinien / Prov. Buenos Aires	Buenos Aires Province [Argentinia]
Asia minor / Taurus cilic.	Central Taurus Mountains [Turkey]
Assam	Assam [India]
Astrabad	Gorgan [Iran, Golestan Province]
Asuncion, / Paraguay	Asunción [Paraguay]
Asuncion, / Paraguy / Villa Morra	Villa Morra, neighborhood of Asunción [Paraguay]
Bampur	Bampur, town and river [Iran, Sistan and Baluchestan Province]
Basman	Bazman, town and mountain [Iran, Sistan and Baluchestan Province]
Berlin	Berlin [Germany]
Betschmanaland-Prot. / Kalahari / Severelela - Kooa	between "Severelela" and "Kooa" in the Kalahari Desert [Botswana]
Bozen	Bolzano [Italy, South Tyrol]
Brusa	Bursa [Turkey, Bursa Province]
Carolina	North- and South Carolina [USA]
Costa Rica / S. Jose	San José [Costa Rica]
Dalmat.	Dalmatia [Croatia]
Dech-i-Papid (=Дэх-и-Пабид)	Deh-e Pabid, village NW Eskelabad 28°37'N 60°47'E [Iran, Sistan and Baluchestan Province]
Dus-ab (=Дузъ-абъ)	Zahedan town [Iran, Sistan and Baluchestan Province]
Georgia	Georgia [USA]
Graecia	[Greece]
Hungria	[Hungaria]
Kala-i-bid (=Кала-и Бидъ)	Qal'eh-ye Bid, village, 28°39'N 60°22'E [Iran, Sistan and Baluchestan Province]
Kärnten / s. Mauthen	Mauthen [Austria, Carinthia]
Kirman (=Кирманъ, = Кирм.)	Kerman Province, in historical borders [Iran]
Kriviput	Krivi Put [Croatia]
Ku-i-Murgak (=Ку-и-Мургакъ)	Kuh-e Murgak mountain E of Bazman, 28°00'N 60°20'E [Iran, Sistan and Baluchestan Province]
Kyusyu / Mt. Kujyu / Oita Pref.	Mount Kujū [Japan, Kyushu Island]
Lindi, Ostafrika	Lindi [Tanzania, Lindi Region]
Mattogrosso	[Brasil, Mato Grosso]
Mersina	Mersin [Turkey, Province Mersin]
Morea mer., Tayget.	Taygetos Mountains [Greece, southern Peleponnes]
N-Argentinien / Salta 2500 m	Salta [Argentinia, Salta Province]
NE-Kreta, oberhalb / Chersónnissos	Chersónnissos [Greece, Crete]
Nimptsch / Schles.	Niemcza [Poland, Lower Silesian Province]
Nov.Holl.	Nova Hollandia [Australia]
NW.-D: Döttlingen / [Oldenburg]	Döttlingen [Germany, Lower Saxony]
Nyassa-See / Langenburg	Lumbila town at Lake Nyasa [Tanzania, Ludewa District]
Ober. Aeg	Upper Egypt [Egypt]
Ost-Afrika / Lindi	Lindi [Tanzania, Lindi Region]
Paraguay / San Bernardino	San Bernardino [Paraguay, Dep. Cordillera]
Pt. Phil.	Port Phillipp [Australia, Victoria]
Pungo Andongo	Pungo-Andongo [Angola, Province of Malanje]
Ragusa	Ragusa [Italy, Sicily]
Reinerz	Duszniki-Zdrój [Poland, Lower Silesian Province]
Riesengeb.	Riesengebirge = Krkonoše Mountains [Czech Republic & Poland]
San João / d. Rey	São João del Rei [Brazil, Southeast]
Sansibar / 6°S	Zanzibar at 6°S [Tanzania]
Sarepta	Sarepta = Volgograd [Russia, Volgograd Oblast]
Schwegyin	Shwegyin [Myanmar, Bago Region]
S.Cruz	Santa Cruz de Tenerife [Spain, Canary Islands]
Sikhim	Sikhim [India]
Siles.	Silesia [Poland & Czech Republic]
S. O. Kamerun / Uam-Gebiet	[Cameroon, North Region]
S. O. Kamerun / Uam-Gebiet / bei Bossum	Bossum [Cameroon, North Region]
Spoleto	Spoleto [Italy, Province Perugia]
Ssargad (=Саргад, = Саргадъ)	Sarhad, landscape (mountain plateau) between Zahedan and Iran Shar [Iran, Sistan and Baluchestan Province]
Stuttg.	Stuttgart [Germany]
Sutschan / Ussuri	Partisansk [Russia, Far East, Primorje]
Syrakus	Syracuse [Italy, Sicily]
Takao	Kaohsiung [Taiwan]
Togo / Bismarckburg	Bismarckburg, a former colonial station close to Yégué [Togo, Region Centrale, Pref. Sotouboua]
Toyenmongai bei / Tainan Formosa	central part of Tainan [Taiwan]
Triest	Trieste [Italy]
Tunisi / dint	[Tunisia]
Ungarn	[Hungary]
Usambara	Usambara Mountains [Tanzania]
W. Australien / Marloo Station / Wurarga	Marloo Station, Wurarga [Australia, Western Australia]
W. Sumatra / Bungus / Bucht Padang	Bungus Bay [Indonesia, Sumatra]
Wustung / b. Habelschwerdt	Stara Bystrzyca close Bystrzyca Kłodzka [Poland, Lower Silesian Province]

Conops bipunctatus Loew, 1852

Conops bipunctatus Loew 1852: 659; locus typicus not given – available, invalid: junior primary homonym of *Physocephala bipunctata* (Macquart, 1844), senior synonym of *Conops rondanii* Bezzi, 1901.

♀ holotype: (1) "3037"; (2) "Typus"; (3) "*Conops / (Smithiconops) / rondanii* / Stuke det. 2003".

Conops braunsii Kröber, 1915

Conops braunsii Kröber 1915a: 44; type locality: "Lindi, Ostafrika, Bothaville" – available, valid

♀ holotype: (1) "Ost-Afrika / Lindi / Fülleborn S."; (2) "Type"; (3) "*Conops ♀ / braunsii* Kröb. / O. Kröber det. 1914"; (4) "Zool. Mus. / Berlin".

Conops camaronensis Kröber, 1939

Conops camaronensis Kröber 1939a: 380; type locality: "Uam v." – available, valid.

♂ syntype: (1) "Type"; (2) "S. O. Kamerun / Uam-Gebiet / G. Tessmann S. G. / 29.6.14 [written perpendicularly]"; (3) "Typus"; (4) "*Conops camarunensis* [sic!] / Krb. / det. Kröber 1938".

♀ syntype: (1) "Type"; (2) "S. O. Kamerun / Uam-Gebiet / G. Tessmann S. G. / 29.6.14 [written perpendicularly] / bei Bossum [written perpendicularly]"; (3) "Typus"; (4) "*Conops camarunensis* [sic!] / Krb. / det. Kröber 1938".

Conops ferruginosus Kröber, 1915

Conops ferruginosus Kröber 1915a: 40; type locality: "Kap der guten Hoffnung" – available, valid.

♀ holotype: (1) "3036"; (2) "*Conops ♀ / ferruginosa* Kröb. / O. Kröber det. 1914"; (3) "Type"; (4) "Zool. Mus. / Berlin".

Conops frontosus Kröber, 1916

Conops frontosus Kröber 1916: 57; type locality: "Sikkim" – available, valid.

♂ holotype: (1) "Sikhim / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops ♂ / frontosus* Krb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

C. frontosus belongs in the subgenus *Asiconops*.

Conops indicus Kröber, 1916

Conops indicus Kröber 1916: 45; type locality: "Sikkim, Darjeeling" – available, valid.

♂ syntype: (1) "? Sikhim ? / Coll. Bingham"; (2) "*Conops ♂ / indicus* Krb. / O. Kröber det. 1914"; (3) "Zool. Mus. / Berlin".

♂ syntype: (1) "? Sikhim ? / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops ♂ / indicus* Krb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

♀ syntype: (1) "? Sikhim ? / Coll. Bingham"; (2) "*Conops ♀ / indicus* Kröb. / O. Kröber det. 1914"; (3) "Zool. Mus. / Berlin".

♀ syntype: (1) "? Sikhim ? / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops ♀ / indicus* Krb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

Bases on the information in the original description there should be 2 male and 5 female syntypes in the ZMHB. Therefore, 3 females are lost. *C. indicus* belongs in the subgenus *Asiconops*.

Conops insignis Loew, 1848

Conops insignis Loew 1848: 300–301; type locality: "Ragusa" – available, valid.

♂ holotype: (1) "Ragusa / Sturm"; (2) "Coll. / H. Loew"; (3) "Type"; (4) "*Conops ♂ / insignis* Lw. / O. Kröber det 1912"; (5) "Zool. Mus. / Berlin"; (6) "*Conops ♂ / insignis* / Stuke det. 2003".

Conops laetus Becker, 1922

Conops laeta Becker 1922: 200–201; type locality: "Sarepta, Süd-Russland" – available, invalid: junior synonym of *Conops insignis* Loew 1848.

♀ holotype: (1) "Sarepta / 30225"; (2) "Typus"; (3) "*Con. laeta* / Beck / det. Becker"; (4) "Zool. Mus. / Berlin"; (5) "*Conops ♀ / insignis* / Stuke det. 2003".

The specimen is almost completely destroyed.

Conops maculiventris Kröber, 1916

Conops maculiventris Kröber 1916: 50–51; type locality: "Sikkim; Birma, Carina Cheba" – available, valid.

♂ syntype: (1) "Sikhim / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops ♂ / maculiventris* Krb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

Based on the information in the original description there should be a male and a female syntype, but only the male syntype was found. *C. maculiventris* belongs in the subgenus *Asiconops*.

Conops minor Becker, 1922

Conops minor Becker 1922: 201–202; type localities: "Sarepta, Bozen, Ungarn, Griechenland" – available, invalid: junior primary homonym of *Physocephala minor* (Walker, 1852), junior synonym of *Conops flavifrons* Meigen, 1804.

♂ syntype: (1) "Bozen / 4.7.96 / Friese"; (2) "42201"; (3) "Zool. Mus. / Berlin"; (4) "*Conops / flavifrons ♂* / Stuke det. 2003"; (5) "Syntypus / *Conops minor* / Becker, 1922 / labelled by Stuke 2003".

♂ syntype (1) "Ungarn / 40873"; (2) "Zool. Mus. / Berlin"; (3) "*Conops / flavifrons ♂* / Stuke det. 2003"; (4) "Syntypus / *Conops minor* / Becker, 1922 / labelled by Stuke 2003".

♂ syntype: (1) "Graecia / 54367"; (2) "*minor* /Beck."; (3) "Zool. Mus. / Berlin"; (4) "*Conops / flavifrons ♀* / Stuke det. 2003"; (5) "Syntypus / *Conops minor* / Becker, 1922 / labelled by Stuke 2003".

Based on the original description there should be 7 female and 3 male syntypes. There is additional material in the collection which might represent further syntypes, but all of these additional specimens were identified by Kröber in 1912 as *C. flavifrons*, and it therefore seems improbable that Becker described from these specimens.

Conops nigrofasciatus Kröber, 1916

Conops nigrofasciatus Kröber 1916: 46–47; type locality: "Schwegyin bei Rangoon" – available, valid.

♀ holotype: (1) "Schwegyin / 11.97 / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops* ♀ / *nigrofasciatus* Krb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

C. nigrifrons belongs in the subgenus *Asiconops*.

Conops punctifrons Kröber, 1916

Conops punctifrons Kröber 1916: 52; type locality: "Sikkim" – available, valid.

♀ holotype: (1) "Sikhim / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops* ♀ / *punctifrons* Krb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

C. punctifrons belongs in the subgenus *Asiconops*.

Conops rugifrons Karsch, 1888

Conops rugifrons Karsch 1888: 381; type locality: "Usambara" – available, valid.

♂ holotype: (1) "Type"; (2) "Usambara / C. W. Schmidt / Febr - März 86"; (3) "*Conops* / *rugifrons* N.".

Conops sareptanus Becker, 1922

Conops sareptana Becker 1922: 202; type locality: "Sarepta"– available, invalid: junior synonym of *Conops silaceus* Wiedemann, 1824.

♀ holotypus: (1) "Sarepta / 30227"; (2) "Typus"; (3) "*sareptana* Beck."; (4) "Zool. Mus. / Berlin".

Contrary to the original description, the holotype is a female.

Conops stylatus Kröber, 1915

Conops stylatus Kröber 1915a: 56–57; type localities: "Belgischer Kongo; Kibimbi 2.II., Kilwa 19.I.", "Sansibar" – available, invalid: junior synonym of *Conops elegans* Meigen, 1804.

♂ syntype: (1) "7354"; (2) "Type"; (3) "*Conops* ♂ / *stylatus* Krb. / O. Kröber det. 1914"; (4) "Sansibar / 6°s. Hildebr."; (5) "*Conops* / *elegans* / Stuke det. 2003".

Conops vitellinus Loew, 1847

Conops vitellinus Loew 1847a: 4–5; type locality: "Gegend von Triest" – available, valid.

♂ holotype: (1) "Triest / 13/9 Zllr."; (2) "Coll. / H. Loew"; (3) "Typus"; (4) "*Conops* ♂ / *vitellinus* Lw. / O. Kröber det 1912"; (5) "Zool. Mus. / Berlin"; (6) "*Conops* ♂ / *vitellinus* / Stuke det. 2003".

Dalmannia confusa Becker, 1922

Dalmannia confusa: 294; type locality: "Kroatien, Kriviput" – available, invalid: junior synonym of *Dalmannia dorsalis* (Fabricius, 1794)

♂ holotype: (1) "Kriviput / 31.5.90"; (2) "Kroatien / 400/2."; (3) "Typus"; (4) "*D. confusa* / Beck. / det. Becker".

Deleskampomyia fasciata Kröber, 1940

Deleskampomyia fasciata Kröber 1940a: 71–72; type locality: "W. Australia, Marloo Stat., Wurarga" – available, valid.

♂ holotype: (1) "Type"; (2) "Typus"; (3) "W. Australien / Marloo Station / Wurgara 8.-9. 35 / A. Goerling S. G."; (4) "*Deleskampo- / myia fasciata* / ♂ Krb".

Leopoldius valvatus (Kröber, 1914)

Brachyglossum valvatum Kröber 1914: 186; type locality: "Sarepta" – available, valid.

♀ lectotype designated by Stuke et al. (2015): (1) "Sarepta Christoph"; (2) "nov. sp."; (3) "*Brachyglossum valvatum* Kröb. ♀ / O. Kröber det. 1912"; (4) "Zool. Mus. Berlin"; (5) "Lectotypus / *Brachyglossum valvatum* / Kröber, 1914 / des. Stuke & Clements 2015".

Myopa argentata Stuke, 2005

Myopa argentata Stuke 2005: 543–545; type locality: "Griechenland, Thessalia, Prov. Magnesia, Peninsula Pilio, Platanias 60 km SE Volos, Afilianes, 39°09'5"N, 23°17'0"E, 200 m" – available, valid

♂ holotype: (1) "Greece: Thessalia / Prov. Magnesia, Peninsula Pilio / Platanias (Πλατανιας) 60 km / SE Volos (Βολος), Afilianes / 39°09'5N, 023°17'0E / 15.IV.2003 200 m/ leg. C. Lange & J. Ziegler"; (2) "Holotypus / *Myopa argentata* / spec. nov. ♂ / Stuke det. 2003".

Myopa clausseni Stuke & Clements, 2008

Myopa clausseni Stuke & Clements 2008: 10–12; type locality: "Greece: NE-Crete, upper part of Chersónnissos, at 100–200m [35,34°N, 25,49°E]" – available, valid.

♀ holotype: (1) "NE-Kreta, oberhalb / Chersónnissos, / 100-200 m / leg. Claußen 18.4.1987"; (2) "*Myopa* ♀ / *polystigma* Rond. / det. Claußen 1988"; (3) "Holotypus / *Myopa clausseni* / spec. nov. ♀ / Stuke & Clements / det. 2004".

Myopa hirsuta Stuke & Clements, 2008

Myopa hirsuta Stuke & Clements 2008: 12–14; type locality: "Germany: Döttlingen (52,94°N, 8,38°E)" – available, valid.

♂ holotype: (1) "NW.-D: Döttlingen / [Oldenburg] 30.4.1978 / leg. Barkemeyer"; (2) "Holotypus / *Myopa hirsuta* / spec. nov. ♂ / Stuke & Clements / det. 2004".

Myopa maetai Stuke, 2003

Myopa maetai Stuke 2003: 413–417; type locality: "Japan; Kyusyu, Oita Pref., Mt. Kujyu" – available, valid.

♂ holotype: (1) "Kyusyu / Mt. Kujyu / Oita Pref. / 23–24.iv.1996 / Col. Y. Maeta"; (2) [Japanese text]; (3) "Holotypus / *Myopa maetai* / spec. nov. ♂ / Stuke det. 2002".

Myopa nigrifacies Becker, 1922

Myopa dorsalis Fbr. var. *nigrifacies* Becker 1922: 289; locus typicus not given – available, invalid: junior synonym of *Myopa dorsalis* Fabricius, 1794.

Holotype of unknown sex: (1) "Asia minor / Taurus cilic. / 1895. Holtz"; (2) "39487"; (3) "var. *nigrifacies*"; (4) "Zool. Mus. / Berlin".

Becker (1922) only described *M. nigrifacies* as one of his couplets in his key to *Myopa*, without any additional information concerning origin, sex, or number of specimens he had at hand. Kröber (1939a) subsequently identified and characterized the type specimen thus: "nur Thoraxrest mit beiden Flügeln vorhanden" ["only the thorax remaining, with both wings present"]. There are only four specimens of *M. dorsalis* from the Becker collection at ZMHB. Three of these can be excluded as type material of *M. nigrifacies* because they do not fit with the original description. The only remaining specimen is, in fact, the poor remnant described by Kröber, which has to be interpreted as the holotype of *M. nigrifacies*, with the sex not identified.

Myopa strandi Duda, 1940

Myopa polystigma var. *strandi* Duda 1940: 397–398; type localities: "Nimptsch", "Habelschwerdt (Mittelschlesien)" [Poland] – available, invalid: junior synonym of *Myopa vicaria* Walker, 1849.

♂ syntype: (1) "18 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♂ / Walker 1849 / det.: Flügel 2009".

♂ syntype: (1) "18 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♂ / Walker 1849 / det.: Flügel 2009".

♂ syntype: (1) "17 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* / D ♂ d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♂ / Walker 1849 / det.: Flügel 2009".

♂ syntype: (1) "20 4 12"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♂ / Walker 1849 / det.: Flügel 2009".

♂ syntype: (1) "20 4 12"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♂ / Walker 1849 / det.: Flügel 2009".

♂ syntype: (1) "20 4 12"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♀ [sic.] d. Duda"; (4) "Typus";

(5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♂ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "17 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♀ d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "20 4 12"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ [sic.] d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "18 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ [sic.] d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "18 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♀ d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "22 3 12"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ [sic.] d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "17 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ [sic.] d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "21 4 11"; (2) "Nimptsch / Schles. Duda"; (3) "*Strandi* D / ♂ [sic.] d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

♀ syntype: (1) "26 4 24"; (2) "Wustung / b. Habelschwerdt / I. Duda"; (3) "*Strandi* / D / ♂ [sic.] d. Duda"; (4) "Typus"; (5) "Zool. Mus. / Berlin"; (6) "*Myopa vicaria* ♀ / Walker 1849 / det.: Flügel 2009".

Myopotta horrida (Becker, 1922)

Myopa horrida Becker 1922: 290–291; type locality: "Griechenland, S. Morea, Taygetos" – available, invalid: junior synonym of *Myopotta rubripes* (Villeneuve, 1909).

♀ holotype: (1) "Morea mer., Tayget."; (2) "Holtz"; (3) "49312"; (4) "Typus"; (5) "*horrida* / Beck / det. Becker".

Physocephala assamensis Kröber, 1915

Physocephala assamensis Kröber 1915b: 121–122; type locality: "Assam" – available, valid.

♀ holotype: (1) "Assam"; (2) "Type"; (3) "Typus"; (4) "*Physocephala* ♀ / *assamensis* Krb. / O. Kröber det. 1914".

Physocephala aterrima Kröber, 1915

Physocephala aterrima Kröber 1915b: 122–123; type locality: "Sikkim" [India] – available, valid.

♂ syntype: (1) "Sikhim / Coll. Bingham"; (2) "*Physocephala* ♂ / *aterrima* Krb. / O. Kröber det. 1914".

♀ syntype: (1) "Sikhim / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Physocephala* ♀ / *aterrima* Krb. / O. Kröber det. 1914".

Kröber (1915b) stated in the original description that the type material was in his own collection.

Physocephala aureopygia Kröber, 1915

Physocephala aureopygia Kröber 1915b: 123–124; type locality: "Sikkim, Cap York" – available, valid.

♂ syntype: (1) "Sikhim / Coll. Bingham"; (2) "*Physocephala* / *aureopygia* Krb.".

♂ syntype: (1) "Sikhim / Coll. Bingham"; (2) "*Physocephala* ♂ / *aureopygia* Krb. / O. Kröber det. 1914".

♂ syntype: (1) "Sikhim / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Physocephala* ♂ / *aureopygia* Krb. / O. Kröber det. 1914".

♀ syntype: (1) "? Sikhim ? / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Physocephala* ♀ / *aureopygia* Krb. / O. Kröber det. 1914".

♀ syntype: (1) "Sikhim / E. Gutman, S. V."; (2) "*Physocephala* ♀ / *aureopygia* Krb. / O. Kröber det. 1914".

As with *P. aterima*, Kröber (1915b) stated in the original description that the type material was in his own collection.

Physocephala bicolor Kröber, 1915

Physocephala bicolor Kröber 1915b: 136–137; type locality: "Matto Grosso" – available, valid.

♂ holotype: (1) "Mattogrosso / Rohde."; (2) "Type"; (3) "*Physocephala* ♂ / *bicolor* Kröb. / O. Kröber det. 1914".

Physocephala bimarginipennis Karsch, 1887

Physocephala bimarginipennis Karsch 1887: 10; type locality: "Pungo-Andongo" – available, valid.

♀ holotype: (1) "Pungo Andongo / A. v. Homayer"; (2) "11031"; (3) "*Physocephala* / *bimarginipennis* / n. sp."; (4) "Holotypus".

Physocephala castanoptera (Loew, 1853)

Conops castanopterus Loew 1853: 33; type locality: "Savanah", "Carolina" – available, invalid: junior synonym of *Physocephala sagittaria* (Say, 1823).

1♀ syntype: (1) "Carolina, Germar"; (2) "Coll. / H. Loew"; (3) "Type"; (4) "*Conops* / *castanopterus*"; (5) "*Physocephala* ♀ / *sagittaria* Say / O. Kröber det 1913".

Stuke (2017) wrongly listed this species as a nomen dubium when in fact it is a junior synonym of *P. saggitaria*, as first suggested by Kröber (1915c).

Physocephala curticornis Kröber, 1915

Physocephala curticornis Kröber 1915d: 54–55; type locality: "Ungarn", "Ungarn: Cinkota" – available, invalid: junior synonym of *Physocephala vittata* (Fabricius, 1794).

♀ syntype: (1) "Hungria"; (2) "antennis / brevi ♂ / tur"; (3) "Type"; (4) "*Physocephala* ♀ / *curticornis* Kröb. / O. Kröber det. 1912".

The syntype reported here has no abdomen and the sex can therefore only be inferred from Kröber's identification label. The specimen was previously overlooked in the study reported by Stuke (2016) although the synonymy was assumed. The short antennae for which the species was described are a morphological aberration.

Physocephala fraterna (Loew, 1847)

Conops fraternus Loew 1847a: 18–19; type locality: "Kleinasien, Griechenland, Dalmatien und ganz Italien, von Zeller by Syrakus, Rom und in der Gegend von Spoleto gefangen" – available, invalid: junior synonym of *Physocephala vittata* (Fabricius, 1794).

♂ syntype: (1) "Dalmat."; (2) "[?] abd. segm. 5"; (3) "*Physocephala* ♂ / *fraterna* Lw. / O. Kröber det. 1912"; (4) "? Typus".

♂ syntype: (1) "Syrakus / 17/6. Zllr."; (2) "*Physocephala* ♂ / *fraterna* Lw. / O. Kröber det. 1912"; (3) "? Typus".

♂ syntype: (1) "Syrakus / 4/5. Zllr."; (2) "var. aurat. / fronteni / gra"; (3) "*Physocephala* ♂ / *fraterna* Lw. / O. Kröber det. 1912"; (4) "? Typus".

♂ syntype: (1) "Syrakus / 4/5. Zllr."; (2) "var. aurat. / fronteni / gra"; (3) "*Physocephala* ♂ / *fraterna* Lw. / O. Kröber det. 1912"; (4) "? Typus".

♀ syntype: (1) "Rom / 26/8. Zllr."; (2) "*Physocephala* ♀ / *fraterna* Lw. / O. Kröber det. 1912"; (4) "? Typus".

♀ syntype: (1) "Syrakus / 20/4. Zllr."; (2) "*Physocephala* ♀ / *fraterna* Lw. / O. Kröber det. 1912"; (3) "? Typus".

♀ syntype: (1) "Spoleto / 4/9. Zllr."; (2) "*Physocephala* ♀ / *fraterna* Lw. / O. Kröber det. 1912"; (3) "? Typus".

♀ syntype: (1) [no text, labelled only with a light blue triangle meaning the material was collected from Asia Minor by Loew 1841–42]; (2) "*Physocephala* ♀ / *fraterna* Lw. / O. Kröber det. 1912".

♂ syntype: (1) [no text, labelled only with a light blue triangle meaning the material was collected from Asia Minor by Loew 1841–42]; (2) "*Physocephala* ♂ / *fraterna* Lw. / O. Kröber det. 1912".

♀ syntype: (1) [no text, labelled only with a light blue square with a black triangle, meaning the material was collected from Rhodes by Loew in 1842]; (2) "*Physocephala* ♀ / *fraterna* Lw. / O. Kröber det. 1912".

♂ syntype: (1) "Astrabad / Christoph"; (2) "*Physocephala* ♂ / *fraterna* Lw. / O. Kröber det. 1912".

Physocephala furax Becker, 1913

Physocephala furax Becker 1913a: 612–613; type locality: "Pers.-Beludshistan, zwischen Dus-abad und Kalai-bid, Ssargad, Kirman" – available, invalid: junior synonym of *Physocephala antiqua* (Wiedemann, 1830).

♂ lectotype designated by Stuke (2015): (1) "Дузъ-абъ–Кала / -и Бидъ. Саргадъ / *Кирманъ* 15/23.VI98"; (2) "Эксп. В. Персію / 1898 / *Зарудный*"; (3) "Typus"; (4) "*Physocephala / furax* Beck / det. Becker"; (5) "Lectotypus / *Physocephala furax* / Becker & Stein, 1915 / des. Stuke, 2015".

Physocephala maculigera Kröber, 1915

Physocephala truncata Lw. var. *maculigera* Kröber 1915d: 71; type localities: "Oberägypten, Tunis, Sinai, Syrien, Algir, Biskra", "Tunis, Oberägypten, Syrien, Algier, Constantine, Biskra" – available, invalid: junior synonym of *Physocephala vittata* (Fabricius, 1794).

♂ syntype: (1) "*Physocephala* ♂ / *maculigera* Kröb. / O. Kröber det. 1912"; (2) "*Physocephala* / *maculigera* ♂ / Stuke det. 2004".

♂ syntype: (1) "Tunisi / dint 1882 / G. e L. Doria"; (2) "113."; (4) "*Physocephala* ♂ / *maculigera* Kröb. / O. Kröber det. 1912"; (5) "*Physocephala* / *maculigera* ♂ / Stuke det. 2004"; (6) "? Typus".

♂ syntype: (1) "Ober. Aeg."; (2) "Variet. ae- / gyptia-ca"; (3) "*Physocephala* ♀ / *maculigera* Kröb. / O. Kröber det. 1912"; (4) "*Physocephala* / *maculigera* ♀ / Stuke det. 2004"; (5) "? Typus".

♀ syntype: (1) "*Physocephala* ♀ / *maculigera* Kröb. / O. Kröber det. 1912"; (2) "*Physocephala* / *maculigera* ♀ / Stuke det. 2004".

♀ syntype: (1) "*Physocephala* ♀ / *maculigera* Kröb. / O. Kröber det. 1912"; (2) "*Physocephala* / *maculigera* ♀ / Stuke det. 2004".

♀ syntype: (1) "Ober. Aeg."; (2) "*Physocephala* ♀ / *maculigera* Kröb. / O. Kröber det. 1912"; (3) "*Physocephala* / *maculigera* ♀ / Stuke det. 2004"; (4) "? Typus".

♀ syntype: (1) "Ober. Aeg."; (2) "*Physocephala* ♀ / *maculigera* Kröb. / O. Kröber det. 1912"; (3) "*Physocephala* / *maculigera* ♀ / Stuke det. 2004"; (4) "? Typus".

♀ syntype: (1) "Tunisi / dint 1881 / G. e L. Doria"; (2) "113."; (4) "*Physocephala* ♀ / *maculigera* Kröb. / O. Kröber det. 1912"; (5) "*Physocephala* / *maculigera* ♀ / Stuke det. 2004"; (6) "? Typus".

Physocephala persica Becker, 1913

Physocephala persica Becker 1913a: 609–610 + pl. xiv; type localities: "Pers.-Beludshistan, Kirman, aus der Umgegend von Bampur und Basman, sowie zwischen Ku-i-Murgak und Dech-i-Papid, 21.VII.–18.VIII.1898; ferner aus der Umgebung von Kunscha, 6.V.1901)" – available, invalid: junior synonym of *Physocephala pusilla* (Meigen, 1804).

♂ syntype: (1) "Ку-и-Мургакъ / Дэх-и-Пабид Сар- / гад *Кирм*. 14/18 VIII98"; (2) "Эксп. В. Персію / 1898 / *Зарудный*"; (3) "Typus"; (4) "*Physocephala* / *persica* Beck / det. Becker".

From the original description there should be four syntypes. The sex was not given in the original description.

Physocephala rubicunda Kröber, 1915

Physocephala rubicunda Kröber 1915c: 94; type locality: "Südafrika" – available, invalid: junior synonym of *Physocephala maculipes* (Bigot, 1887).

♂ holotype: (1) "3055"; (2) "Type"; (3) "*Physocephala* ♂ / *rubicunda* Krb. / O. Kröber det. 1914".

Physocephala rufithorax Kröber, 1915

Physocephala rufithorax Kröber 1915b: 138–139; type localities: "Paraguay-Asuncion, Villa Morra, 29. XL, Brasil-Sta. Catharina; Peru-Madre de Dios." – available, valid.

♀ holotype: (1) "Type"; (2) "Asuncion, / Paraguy / Villa Morra / 29.11.1905 / J. O. Anisits [written perpendicularly]"; (3) "*Physocephala* ♀ / *rufithorax* Kröb / O. Kröber det. 1914".

Physocephala schmideggeri Stuke, 2017

Physocephala schmideggeri Stuke 2017: 613–619; type locality: "United Arab Emirates / Wadi Wurayah 25,40 N / 46,28 E" – available, valid.

♂ holotype: (1) "United Arab Emirates / Wadi Wurayah 25,40 N / 46,28 E lg. Schmid-Egger / 11.-19. III.2009 uae8"; (2) "Holotypus / *Physocephala* / *schmideggeri* / spec. nov. ♂ / des. Stuke 2014".

Physocephala sumatrensis Kröber, 1915

Physocephala sumatrensis Kröber 1915b: 119–120; type locality: "Sumatra, Padang Bungus-Bucht" – available, valid.

♂ holotypus: (1) "W. Sumatra 1.-6 / XII.08 Bungus / Bucht Padang / Schoede S. G."; (2) "Type"; (3) "Typus"; (4) "*Physocephala* ♂ / *sumatrensis* Krb. / O. Kröber det. 1914".

Physocephala truncata (Loew, 1847)

Conops truncatus Loew 1847: 21; type locality: "Sicilien; von Zeller zweimal im Juni bei Syrakus gefangen" – available, valid.

♂ syntypus: (1) "Syrakus / 17/6 Zllr."; (2) "*Physocephala* ♂ / *truncata* Lw / O. Kröber det. 1912"; (3) "*Physocephala* / *truncata* ♂ / Stuke det. 2004"; (4) "? Typus".

♂ syntypus: (1) "Syrakus / 17/6 Zllr."; (2) "*Physocephala* ♂ / *truncata* Lw / O. Kröber det. 1912"; (3) "*Physocephala* / *truncata* ♂ / Stuke det. 2004"; (4) "? Typus".

These two syntypes have been previously overlooked. Unfortunately, they have been misinterpreted and are not a colour morph of *P. vittata* as proposed by Stuke (2016) but are in fact conspecific with *Physocephala vaginalis* (Rondani, 1865). This synonymy was overlooked because whilst the female of *P. vaginalis* is easily identified due to its long theca, it is very difficult to recognise the male. Only by using the key of Stuke (2016) can males of *P. vittata* and *P. vaginalis* be acurately separated. *Conops vaginalis* Rondani 1865 is therefore placed as junior synonym of *Conops truncatus* Loew 1847 (**syn. nov.**).

Physocephala unicolor Kröber, 1915

Physocephala unicolor Kröber 1915b: 145; type locality: "Paraguay, San Bernardino" – available, valid.

♂ holotypus: (1) "Paraguay / San Bernardino / K. Fiebrig S. V. / 18.IV. [written perpendicularly]"; (2) "*Hyptis vestita* / Infloreszens"; (3) "Type"; (4) "*Physocephala* ♀ [sic] / *unicolor* Krb. / O. Kröber det. 1914"; "Zool. Mus. / Berlin". The abdomen is broken off and glued on a piece of paper which is pinned separately, bearing the lable: "abd. of type / *Physocephala* / *unicolor* Krb.".

Physocephala vespiformis Kröber, 1915

Physocephala vespiformis Kröber 1915b: 135–136; type localities: "Paraguay Asuncion, San João; Surinam, Juanjui-Amazonas." – available, invalid: junior synonym of *Physocephala aurifrons* (Walker, 1849).

♀ syntype: (1) "Type"; (2) "Asuncion, / Paraguay / 1906 / J. D. Anisits [written perpendicularly]"; (3) "*Physocephala* ♀ / *vespiformis* Kröb. / O. Kröber det. 1914"; (4) "Zool. Mus. / Berlin".

♀ syntype: (1) "3011"; (2) "*Physocephala* ♀ / *vespiformis* Kröb. / O. Kröber det. 1914"; (3) "Cotype".

♀ syntype: (1) "San João / d. Rey. / Sello."; (2) "Cotype"; (3) "*Physocephala* ♀ / *vespiformis* Kröb. / O. Kröber det. 1914".

Kröber (1915b) stated in the original description that the "Type" is in ZMHB and identified an unknown number of females from different locations. The three syntypes listed here conform with the stated loci typici and therefore all of these specimens should be treated a syntypes.

Physoconops (*Pachyconops*) *gracilior* (Kröber, 1915)

Conops gracilior Kröber 1915e: 150–151; type locality: "Paraguay, San Bernardino" – available, valid.

♂ syntype: (1) "Paraguay / San Bernardino / K. Fiebrig S. V. / 3.iv. [written perpendicularly]"; (2) "Type"; (3) "*Conops* ♂ / *gracilior* Kröb. / O. Kröber det. 1914".

♂ syntype: (1) "Paraguay / San Bernardino / K. Fiebrig S. V. / 11.iv. [written perpendicularly]"; (2) "*Hyptis vestita* / Infloreszens"; (3) "*Conops* ♂ / *gracilior* Kröb. / O. Kröber det. 1914".

♂ syntype: (1) "Paraguay / San Bernardino / K. Fiebrig S. V. / I. [written perpendicularly]"; (2) "*Conops* ♂ / *gracilior* Kröb. / O. Kröber det. 1914".

♀ syntype: (1) "Paraguay / San Bernardino / K. Fiebrig S. V. / 7.iv. [written perpendicularly]"; (2) "Type"; (3) "*Conops* ♀ / *gracilior* Kröb. / O. Kröber det. 1914".

Physoconops longistylus (Kröber, 1915)

Conops longistylus Kröber 1915e: 149–150; type locality: "S. João del Rey - Brasilien" – available, valid.

♀ syntype: (1) "3022"; (2) "S. João d. Rey. / Sello"; (3) "*Conops* ♀ / *longistylus* Kröb. / O. Kröber det. 1914".

Physoconops perbellum Kröber, 1939

Physoconops perbellum Kröber 1939c: 467–468; type locality: "Argentinien, Buenos Aires" – available, invalid: junior synonym of *Physoconops hermanni* (Kröber, 1915).

♂ holotype: (1) "Type"; (2) "Argentinien / Prov. Buenos Aires / 1.4.10 [written perpendicularly]"; (3) [illegible text]; (4) "Typus"; (5) "*Physoconops* / *perbellum* / n. sp.".

Physoconops striatifrons (Kröber, 1915)

Conops striatifrons Kröber 1915e: 132; type localities: "Georgia, Texas (?)", "Lincoln Nebraska" VIII., Georgia" – available, invalid: junior synonym of *Physoconops nigrimanus* (Bigot, 1887).

1 ♂ syntype: (1) "Georgia / Morrison"; (2) "7864"; (3) "Type"; (4) "*Conops* ♂ / *striatifrons* Krb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

Kröber (1915e) did not state the exact number of syntypes he used for the description, but it is likely that he had only the female mentioned above plus another female which was in his collection and which was almost certainly destroyed during World War II.

Physoconops varipes (Kröber, 1915)

Conops angustus var. *varipes* Kröber 1915e: 153–154; type locality: "Paraguay, San Bernardino" – available, valid.

♂ holotypus: (1) "Paraguay / San Bernardino / K. Fiebrig S. V. / 11.XII. [written perpendicularly]"; (2) "*Conops angustus* / Kröb. var. ♂ / O. Kröber det. 1914".

Pleurocerina nigrifacies (Kröber, 1940)

Paraconops nigrifacies Kröber 1940a: 66; type locality: "W. Australien, Marloo Stat., Wurarga" – available, valid.

♂ holotype: (1) "Type"; (2) "Typus"; (3) "W. Australien / Marloo Station / Wurarga 8.-9. 35 / A. Goerling S. G."; (4) "*Paraconops* / *nigrifacies* / ♂ Kröb".

Pleurocerinella bartaki Stuke, 2009

Pleurocerinella bartaki Stuke 2009: 212-215; type locality: "Botswana: Betschmanaland Prot. / Kalahari / Severelela - Kooa" – available, valid.

♂ holotype: (1) "Betschmanaland-Prot. / Kalahari / Severelela - Kooa / XI.04 / L. Schultze S."; (2) "*Pleurocerinella* / *dioctriaeformis* Brun."; (3) "Zool. Mus. / Berlin"; (4) "Holotypus / *Pleurocerinella* / *bartaki* / Stuke det. 2009".

Pseudophysocephala caenoneura Kröber, 1939

Pseudophysocephala caenoneura Kröber 1939a: 385; type locality: "Nyassa See, Langenberg [sic!]" – available, valid.

♀ holotype: (1) "Type"; (2) "Nyassa-See / Langenburg / 26.VII.-8.VIII. 98 / Fülleborn S."; (3) "Typus"; (4) "*Pseudophysocephala / stylata* Kb. / det. Kröber 1938"; (5) "Zool. Mus. / Berlin".

Pseudophysocephala constricta (Kröber, 1915)

Physocephala constricta Kröber 1915c: 85-86; type locality: "Cap." – available, valid

♀ lectotype designated by Camras (2001): (1) "3053"; (2) "Type"; (3) "*Physocephala* ♀ / *constricta* Krb. / O. Kröber det. 1914".

Camras (2001) referred to the specimen listed here as a lectotype, stating: "The female of *constricta* is designated as the holotype as important characters are in that sex." This comment is interpreted as a lectotype designation by Stuke (2017).

Pseudophysocephala fenestralis Kröber, 1939

Pseudophysocephala fenestralis Kröber 1939a: 386-387; type localities: "Cape Prov., George", "Nyassasee, Langenburg" – available, valid.

♂ syntype: (1) "Type"; (2) "Nyassa-See / Langenburg / 14.V.1899/ Fülleborn S."; (3) "Typus"; (4) "*Pseudophysocephala / fenestralis* Krb. /det. Kröber 1938".

Pseudophysocephala nitida (Kröber, 1915)

Conops nitidus Kröber 1915a: 54–55; type locality: "Togo, Bismarcksburg" – available, valid.

♂ holotype: (1) "Togo / Bismarckburg / 2.–18.vi.93 / L. Conradt S."; (2) "*Conops* ♂ / *nitidus* Kröb/ O. Kröber det. 1914"; (3) "Cotype"; (4) "Zool. Mus. Berlin"; (5) "*Pseudophysocephala / nitidus* / Kröber / det. Camras, 2000".

In addition to the male holotype there is also a female specimen in the collection at ZMHB bearing the same lables as the holotype. In the original description only the male sex was described and it was not stated whether or not there was more than one specimen available at the time. Kröber (1915) did, however, mention elsewhere in the same paper that in several cases he had more than one specimen of a sex at hand. On this basis we currently assume that the male specimen in the ZMHB is the holotype. On the other hand, Camras (2001) reported three syntypes, comprising the specimens from the Berlin collection together with another male deposited at USNM.

Pseudophysocephala stylata Kröber, 1939

Pseudophysocephala stylata Kröber 1939a: 385–386; type locality: "Langenberg [sic!]" – available, invalid: junior synonym of *Pseudophysocephala caenoneura* Kröber, 1939.

♂ holotype: (1) "Type"; (2) "Nyassa-See / Langenburg / 1.-26.VII.98 / Fülleborn S."; (3) "Typus"; (4) "*Pseudophysocephala / stylata* Krb."; (5) "Zool. Mus. / Berlin"; (6) "*Pseudophysocephala / caenoneura* Kröber / det. Camras 1999".

Sicus alpinus Stuke, 2002

Sicus alpinus Stuke 2002: 246–251; type locality: "Austria, Kärnten, in the south of Mauthen" – available, valid.

♀ holotype: (1) "Kärnten / s. Mauthen / 13.-16.7.1939 / Zwick"; (2) "Holotypus / *Sicus alpinus* spec. / nov. ♀ / Stuke det. 2002".

Sicus nigricans Kröber, 1939

Sicus ferrugineus L. var. *nigricans* Kröber 1939a: 370; type locality: "Sutschan, Ussuri" – available, invalid: junior synonym of *Sicus nishitapensis* (Matsumura, 1916).

♂ holotype: (1) "Sutschan / Ussuri"; (2) "*Sicus / nigricans* Kröb."; (3) "Holotypus"; (4) "*Sicus nishitapensis* ♂ / Stuke det. 2003".

Siniconops curtirostris (Kröber, 1916)

Conops curtirostris Kröber 1916: 52–53 [as "*Conops celebensis* Mej."]; type locality: "Sikkim"; available, invalid: junior synonym of *Siniconops sepulchralis* (Brunetti, 1912).

5♂♂ syntypes: (1) "Sikhim / Coll. Bingham"; (2) "*Conops* ♂ / *curtirostris* Kröb. / O. Kröber det. 1914"; (3) "Zool. Mus. / Berlin".

♂ syntypes: (1) "? Sikhim ? / Coll. Bingham"; (2) "*Conops* ♂ / *curtirostris* Kröb. / O. Kröber det. 1914"; (3) "Zool. Mus. / Berlin".

♂ syntype: (1) "Sikhim / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops* ♂ / *curtirostris* Kröb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

♀ syntype: (1) "Sikhim / Coll. Bingham"; (2) "*Conops* ♀ / *curtirostris* Kröb. / O. Kröber det. 1914"; (3) "Zool. Mus. / Berlin".

♀ syntype: (1) "Sikhim / Coll. Bingham"; (2) "Type"; (3) "Typus"; (4) "*Conops* ♀ / *curtirostris* Kröb. / O. Kröber det. 1914"; (5) "Zool. Mus. / Berlin".

This material was overlooked by Stuke (2018) in his review of the genus *Siniconops*. According to the original description Kröber examined 8 males and 3 female specimens of this species. Presumably Kröber kept one pair, which was destroyed with his collection, and only these 7 males and 2 females remain. There are also a further 2 males and 1 female with the same collecting labels but lacking Kröber´s identification label. These specimens were probably not examined by Kröber, however, and are very unlikely to be syntypes.

This long series of this species was not previously known and indicates some variation concerning the yellow marking on the hind margins of tergites 2–4 (varying from no yellow hind margins to distinctly yellow hind margins), the colouration of the legs (from light brown to almost completely black) and the colouration of the claws (from having a distinct brown base with a black tip to being completely black). *Siniconops fuscatus* Qiao & Chao, 1998 falls within the variation of this species. There is no

difference in the shape of the theca between the female syntypes of *S. curtirostris* and the female specimens of *S. fuscatus* reported by Stuke (2018). Therefore, these two species should be treated as conspecific, and *Siniconops fuscatus* Qiao & Chao, 1998 placed as junior synonym of *Physocephala sepulchralis* Brunetti 1912 (**syn. nov.**), along with *S. curtirostris*.

Siniconops nigripes (Kröber, 1913)

Conops nigripes Kröber 1913: 278–279; type localities: "Taihorinsho XI. und Sokutsu IX.", "Toyenmongei bei Tanan (Formosa)", "Kosempo", "Tapani und Koshun" – available, valid.

♂ syntype: (1) "Toyenmongai bei / Tainan Formosa / Rolle V.1910"; (2) "*Conops / nigripes* Kröb. / O. Kröber det. 1912"; (3) "Zool. Mus. / Berlin".

♂ syntype: (1) "Toyenmongai bei / Tainan Formosa / Rolle V.1910"; (2) "*Conops / nigripes* Kröb. / O. Kröber det. 1912"; (3) "Zool. Mus. / Berlin".

Zodion asiaticum Becker, 1922

Zodion asiaticum Becker 1922: 283; type locality: "Alai Gebirge, S.-Sibirien" – available, invalid: junior synonym of *Zodion cinereum* (Fabricius, 1794).

♂ holotype: (1) "Alai Geb. / VII.1903"; (2) "508/6."; (3) "Typus"; (4) "*asiaticum* / Beck. / det. Becker"; (5) "Zool. Mus. / Berlin".

Zodion caesium Becker, 1908

Zodion caesium Becker 1908: 90–91; type locality: "St. Cruz" – available, valid.

♂ holotype: (1) "S. Cruz / 47401"; (2) "Type"; (3) "*caesium* / Beck. / det. Becker"; (4) "*Zodion / caesium* / Type Beck. 1908 / Dr. Theod. Becker det.".

Zodion grisescens Kröber, 1939

Zodion grisescens Kröber 1939d: 537; type locality: "N. Argentinien, Salta" – available, invalid: junior synonym of *Zodion aureopygium* Kröber, 1915.

♂ holotype: (1) "Type"; (2) "N-Argentinien / Salta 2500 m / [illegible text] / J. Steinbach S.V. / III-IV 1905" [written perpendicularly]; (3) "Typus"; (4) "*Zodion / grisescens* / ♂ n. sp. Krb".

Zodion hauseri Stuke, 2014

Zodion hauseri Stuke 2014: 240–243; type locality: "Kazakhstan 29.–31.V.2001 / Charyn Valley W Chundza / 650 m 43°37'N, 79°21'E" – available, valid.

♂ holotype: (1) "Kazakhstan 29.-31.V.2001 / Charyn valey W Chundza / 650m 43°37'N, 79°21'E / leg. M. Hauser"; (2) "Holotypus / *Zodion hauseri* / spec. nov. ♂ / des. Stuke 2014".

Zodion malayensis Stuke, 2004

Zodion malayensis Stuke 2004: 187–188; type locality: "Malaysia, Pahang / 30 km, NE Raub, IV.-V., ET / 3°56N, 101°38E – available, valid.

♀ holotype: (1) "Malaysia, Pahang / 30 km, NE Raub, –300m / Lata Lembik, IV.-V., ET / 3°56'N, 101°38'E, 2002 / E. Jendenk + O. Šauša leg."; (2) "Holotypus / *Zodion malayensis* /spec. nov. ♀ / Stuke det. 2004".

Zodion pulchrum Loew, 1868

Zodion pulchrum Loew 1868: 384–385; locus typicus not given – available, invalid: junior synonym of *Zodion erythrurum* Rondani, 1865.

♂ holotype: (1) "Mersina / Lederer"; (2) "coll. / H. Loew"; (3) "Typus"; *Zodion / pulchrum / Loew*".

"Mersina in Cilien" is the historical name of Mersin on the Mediterranean coast of Turkey, and not in Italy as wrongly stated by Stuke (2017).

Specimens in ZMHB not justifiably assigned as type material

Conops rufifrons Doleschall, 1857

Conops rufifrons Doleschall 1857: 412–413; type locality: "Amboina". – available, valid.

Kröber (1916) mentioned 2 male and 3 female types in the ZMHB. Of these, the following material was found in the collection: 1♀ with (1) "*Conops* ♀ / *rufifrons* Dol. / O. Kröber det. 1914"; (2) "Zool. Mus. / Berlin"; 1 ♂ with (1) "3035"; (2) "*Conops* ♂ / *rufifrons* Dol. / O. Kröber det. 1914"; (3) "*rufifrons* / Dolesch.* / Amboin. Felder."; (4) "Zool. Mus. / Berlin". There was no information in the original description concerning the number or sex of the types. Horn et al. (1990) stated that the material collected in Java by Doleschall is in the Museum of Vienna. Therefore, there is doubt as to the actual depository of the type material; this requires further investigation.

Conops satanicus Bigot, 1887

Conops satanicus Bigot 1887a: 43; type locality: "Australie" – available, valid.

A ♀ specimen is present in ZMHB with the lables: (1) "Type"; (2) "5517"; (3) "Adeleide / Schumb."; "Typus"; (5) "*Conops* T7 / *satanicus* Big.". The holotype of *C. satanicus* is in NHML (Schneider 2010), so the Berlin specimen cannot be type material.

Myopa fasciata Meigen, 1804

Myopa fasciata Meigen 1804: 286; incomplete information about the *locus typicus* ["Sie ist nicht selten" and "Eine Abänderung aus Frankreich"] – available, valid.

Three specimens are currently assigned as type material: 1♂, 2♀: (1) "Berlin / Erichson S."; (2) "Type" [rotes Etikett]; (3) "*Myopa* / *fasciata* / Stuke det. 2002". The male and female syntypes are all in MNHN (Stuke 2017)

and there is no reason to believe the specimens in the ZMHB might be additional type specimens.

Physocephala amoena – invalid collection name

As far as we are aware there is no conopid known by this name in the published literature (Stuke 2017) and therefore it is interpreted as a collection name only. The female specimen of *Physocephala pusilla* (Meigen, 1804) in the collection which is labelled "Typus" under this name is therefore not a type specimen.

Physocephala annulata Kröber, 1913

Physocephala annulata Kröber 1913: 281; type locality: "Anping /. VII., Takao" [Taiwan] – available, invalid: junior synonym of *Physocephala limbipennis* de Meijere, 1910.

Two males deposited in the ZMHB have labels that fit with the locus typicus: (1) "Takao / 1.9.07"; (2) "Type"; (3) "Physocephala / annulata Kröb. / O. Kröber det. 1912"; one of these specimens also has a fourth lable: (4) "*Physocephala / annulata* /Kröb.". From the original description an unknown number of male and female syntypes should be in the collection "Deutsches Ent. Museum". In fact there are 4 male syntypes in the SDEI (Rohlfien and Ewald 1975), and therefore the material of ZMHB cannot be interpreted as type material.

Physoconops excisus (Wiedemann, 1830)

Conops excisa Wiedemann 1830b: 234; type locality: "Savannah"; HT ♂ [ZMUC, Parson 1948] – available, valid.

The male holotype of *P. excisus* is deposited in ZMUC (Parson 1948), and there is no reason to believe that one of two specimens in ZMHB from Loew's collection might be type material. ♂: (1) "3018"; (2) "Conops ♂ / excisus Lw / O. Kröber det. 1913"; ♀: (1) "3018"; (2) "Conops ♀ / excisus Lw / O. Kröber det. 1913".

Pseudophysocephala platycephala (Loew, 1853)

Conops platycephalus Loew 1853: 35; *locus typicus* not given – available, valid.

There is one specimen in the ZMHB which is labelled as a type as follows: (1) "3054"; (2) "Type"; (3) "*Physocephala ♂ / platycephala* Lw. / O. Kröber det. 1914"; (3) "Zool. Mus. / Berlin"; (4) "Allotype ♂ / *Physocephala / Platycephala* / (Loew) / det. Kröber, 1915". This specimen belongs to *P. platycephala* and was mentioned by Camras (2001) as "other type from the Berlin Museum". This specimen is not mentioned in the original description and is therefore not type material. The female holotype of *P. platycephala* is deposited in ZMUC (Camras 2001).

Zodion pictum Schiner, 1868

Zodion pictum Schiner 1868b: 370; type locality: "Columbien" – available, valid.

A male labelled (1) "Cotype"; (2) "Paratypus"; (3) "Costa Rica / S. Jose / 5. 25. / H. Schmidt"; (4) [blank blue label]; (5) "*Zodion / pictum* / Wd" is not type material because the locality data on the label does not fit with the original description. The holotype is deposited in the NMW (Kröber 1915e).

Type material lost from the ZMHB

Kröber (1939a) reported some Conopidae types which he could not find in the Berlin collection where he had expected them to be: *Conops pugioniformis* (Becker, 1913), *Conops ruficornis* Becker, 1913, *Physocephala detecta* Becker, 1913, *Physocephala laeta* Becker, 1913, *Physocephala punctithorax* Becker, 1913, and *Physocephala zarudnyi* Becker, 1913. All of these species were collected by N. Zarudny, and the material was sent back to Saint Petersburg after description. This material is now deposited in the collection of the Russian Academy of Sciences, Zoological Institute, Saint Petersburg (Narchuk and Ovtshinnikova pers. comm. in an email dated January 2019). There are only two species of which type material appears to have been lost from the ZMHB collection.

Physoconops fenestratus (Kröber, 1915)

Conops fenestratus Kröber 1915e: 134–135; type locality: "Lincoln, Nebraska" – available, invalid: junior synonym of *Physoconops brachyrhynchus*.

Kröber (1915) described the female and male of *P. fenestratus* but referred only to a female "Type" which was deposited in the "Kgl. zool. Mus. Berlin.". Therefore the male specimen should be interpreted as a paratype and the female specimen as a holotype. Only one female specimen was found in the collection: (1) "7703"; (2) "Dallas, / Texas Boll"; (3) "*Conops ♀ / fenestratus* Krb. / O. Kröber det. 1914"; (4) "Zool. Mus. / Berlin". This specimen does not appear to be the male holotype due to wrong collecting site data. The type material of *P. fenestratus* seems therefore to be lost.

Sicus indicus Kröber, 1940

Sicus indicus F. Kröber 1940b: 244; type locality: "Himalaya" – available, valid: not recognized (nomen dubium).

Based on information in the original description, the male holotype of *S. indicus* should be in the ZMHB collection but could not be found there.

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The Rubens morph of *Formica exsecta* Nylander, 1846 and its separation from *Formica fennica* Seifert, 2000 (Hymenoptera, Formicidae)

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Abstract

A study of numeric morphology-based alpha-taxonomy (NUMOBAT) considering the species *Formica exsecta* Nylander, 1846 and *F. fennica* Seifert, 2000 was performed in 166 nest samples with 485 worker individuals originating from 117 localities of the Palaearctic west of 59°E. The presence of intraspecific pilosity dimorphism is shown for *F. exsecta*. The setae-reduced phenotype, termed the Rubens morph, shows a frequency of about 25%, and the more abundant setae-rich phenotype, termed the Normal morph, one of 75%. The frequency of nests containing workers of both phenotypes is 15.5% in 58 samples from Denmark, Sweden, and Finland. Applying the DIMORPH test of Seifert (2016) on this territory, it is demonstrated that the association of Rubens and Normal phenotypes within the same nest cannot be interpreted as parabiosis of independent species ($p=0.017$) or as temporary ($p=0.0004$) and permanent ($p=0.0001$) socially parasitic association, whereas genetically mediated intraspecific dimorphism is most likely ($p=0.659$, all p data according to Fisher's exact test). The Rubens morph of *F. exsecta* is phenotypically most similar to *F. fennica* but is safely separable by four different forms of exploratory data analyses using nest centroids (NC) as input data: NC-Ward, NC-part. hclust, NC-part.kmeans, and NC-NMDS-k-means. Data on zoogeography and the narrow climate niche indicate that *F. fennica* is unlikely to occur in Norway.

Introduction

The distributional range of *Formica exsecta* Nylander, 1846 covers the Palaearctic from Iberia to Kamchatka, includes the submeridional, temperate and boreal zones in the horizontal scale, and extends from the planar to the subalpine zone in the vertical scale (Seifert 2000, 2018, Seifert and Schultz 2007). Strong pilosity and color variation has led in the past to the description of various other taxa close to *F. exsecta*: *F. exsecta rubens* Forel, 1874, *F. exsecta exsectopressilabris* Forel, 1874, *F. exsecta etrusca* Emery, 1909, *F. dalcqi* Bondroit, 1918, *F. exsecta sudetica* Scholz, 1924, *F. kontuniemii* Betrem, 1954, *F. nemoralis* Dlussky, 1964, and *F. mesasiatica* Dlussky, 1965. Whereas the species status of *F. mesasiatica* was recognized by Seifert (2000), albeit with some caution,

he synonymized the seven other taxa with *F. exsecta*. This assessment is in line with the current state of information after my examination of over 1100 samples of the subgenus *Coptoformica* from the whole Palaearctic, and with 800 of these samples being investigated by Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT).

Seifert (2018) stated the presence of a pilosity dimorphism in *F. exsecta*. He distinguished a setae-reduced Rubens morph and a setae-rich Normal morph and reported that the Rubens morph is very similar to *Formica fennica* Seifert, 2000. *Formica fennica* has a narrow habitat spectrum and is known so far from only four sites in southern Finland and two sites in the Caucasus whereas *F. exsecta* shows the widest habitat spectrum, largest total abundance and biggest geographical range of any *Coptoformica* species. In a study from Finland,

using microsatellite data, Hakala et al. (2018) found no genetic differences between two subjectively established morphological clusters. Within their material, they classified 38 samples as *Formica exsecta* and 33 samples as *F.* "*fennica*". The failing separation by microsatellite data in the samples of Hakala et al. is easily explained by the fact that >90% of their *F.* "*fennica*" samples actually belonged to the Rubens morph of *F. exsecta*. Using the DIMORPH test of Seifert (2016), the first aim of this paper is to demonstrate that the Rubens and Normal morph of *F. exsecta* do not represent different species. Using NC-clustering methods (Seifert et al. 2013, Csősz and Fisher 2015), the second aim is to show that the Rubens morph is reliably separable and heterospecific from *F. fennica*. Prompted by the paper of Hakala et al. (2018), I perform here another attempt to convince morphology-based alpha-taxonomists to abandon idiosyncratic approaches and to adopt reproducible numeric character description and evaluation when aiming to investigate the real structure of biodiversity.

Material and methods

To have an improved separation between the *Formica exsecta* morphs and between the Rubens morph of *F. exsecta* from *F. fennica*, the materials of this study were restricted to the Palaearctic west of 59°E, that is, west of the Ural Mountains. NUMOBAT data were recorded in 166 nest samples and 485 worker individuals, the majority of which is deposited in the collection of Senckenberg Museum of Natural History Görlitz. This material listed below in the following sequence and format: site, date in the yyyy.mm.dd format, field sample number "field No" which is found on the mounted specimens [latitude and longitude in decimal format, meters above sea level]. The accuracy of coordinates is proportional to the number of decimal points and "xx" in the sampling date sequence mean missing data. In some samples without any direct or derived information of date, the assumed period is given and the collector is named if known.

Formica exsecta Nylander, 1846

A total of 152 nest samples with 431 workers were investigated.

Austria: Brunau, 2001.09.xx [47.23, 10.85, 700]; Fernpass, 1994.07.04, no. 20 [47.40, 10.90, 1420]; Gilfert, Lafaster-Alm, 1995.10.22 [47.26, 11.76, 1758]; Großglockner, Franz-Josephs-Höhe, 1968.xx.xx [47.075, 12.751, 2369]; Großglockner, Glocknerhaus, 1994.06.20 [47.070, 12.769, 2200]; Gschnitz, Sandertal, 1995.09.24 [47.00, 11.40, 1700]; Gschnitz, Schatthang, 1995.09.24 [47.00, 11.40, 1900]; Gschnitz, Blockfeld, 1995.09.24 [47.00, 11.40, 1900]; Kitzbühel, Bischof, 1994.08.22 [47.405, 12.512, 2000]; Kleiner Gamsstein, 1995.10.22 [47.733, 14.467, 1100]; National Park Kalkalpen, 2011.08.05 [47.750, 14.438, 990]; Pottenbrunn-3 km SSW, 1994.05.12, no. 043 [48.215, 15.718, 330]; Rofan,

1994.07.07, no. g23 [47.45, 11.78, 2000]; Seetaler Alp, Zirbitzkogel, 1971.09.04 [47.06, 14.55 2000]; Spitz-15 km W, Jauerling, 1990.07.05 [48.353, 15.332, 700]; Vikartal, 1995.10.08 [47.20, 11.45, 1500]. **Bulgaria**: Rhodopes: "Betova" [site not identifiable], 1985.07.03 [42?, 24.5?, 1300]; Rhodopes: Pamporovo, 1975.07.20 [41.61, 24.67, 1400]; Rila: Borovec, 1977.08.01 [42.26, 23.61, 1300]; Rila: Borovec, 1988.06.16 [42.26, 23.61, 1900]. **Denmark**: Jutland, Rye, 1986.08.xx [56.08, 9.73, 77]. **Finland**: Broända, 1996.07.07, no. 27, no. 130 [60.11, 24.27, 30]; Jyväskylä, Kypäramäki, 1998.06.01 [62.24, 25.70, 140]; Järajärvi-S, 2002.07.23 no. 039 [69.641, 29.046, 102]; Järajärvi-S, 2002.07.23 no. 040 [69.641, 29.045, 101]; Järajärvi-S, 2002.07.23 no. 041 [69.642, 29.045, 101]; Järajärvi-S, 2002.07.23 no. 042, no. 044 [69.642, 29.046, 100]; Kiannanniemi, 2002.07.19, no. 018 [65.165, 29.105, 207]; Kiiminki-26 km ENE, 1996.07.15, no. 146 [65.208, 26.325, 120]; Käylä-2 km NE, 1996.07.17, no. 147 [66.320, 29.170, 250]; Käylä-3 km E, no. 113, no. 159 [66.310, 29.203, 250]; Köyliö, 1999.06.25 [61.117, 22.300, 70]; Puhos-6.5 km WNW, 1996.07.13, no. 114 [62.107, 29.793, 97]; Renko-13 km WSW, 1996.07.11, no. 19 [60.836, 24.067, 136]; Sodankylä-26 km NNE, 1996.07.18, no. 55 [67.64, 26.74, 205]; Sodankylä-33 km N, 2002.07.21, no. 029, no. 031 [67.707, 26.749, 208]; Tammela-9 km ENE, 1996.07.11 [60.83, 23.93, 120]; Tronsböle-0.2 km NE, Oby, 2015.05.07, no. A, no. B [59.940, 23.198, 20]; Utajärvi-2 km NE, no. 120 [64.728, 24.426, 80]. **France**: Mt. Canigou, pre 1918, type *F. dalcqi* [42.51, 2.45, 2000]; Mt. Canigou, pre 1930 (leg. Weiss) [42.51, 2.45, 2200]; Refuge des Besines, 1998.09.17, no. 016 [42.604, 1.868, 2100]. **Germany**: Althüttendorf, 1985.05.07 [52.96, 13.80, 71]; Canthnitz-0.7 km E, 1997.08.23, no. 220 [53.376, 13.394, 103]; Dabelow, 1982.06.01 [53.248, 13.198, 64]; Dallgow-S, 1996.08.03 [52.52, 13.06, 41]; Eberswalde, 1987.06.12 [52.83, 13.79, 31]; Eberswalde-2.4 km E, 1997.08.21 [52.82, 13.85, 66]; Eberswalde-5 km N, 1995.07.10 [52.89, 13.88, 38]; Eberswalde-Buchholz, 1985.05.07 [52.88, 13.76, 70]; Eberswalde-Finow, 1987.04.12 [52.84, 13.73, 35]; Federsee: Wildes Ried, 1990.09.xx [48.045, 9.648, 583]; Federsee: Wildes Ried, 1991.05.xx [48.045, 9.648, 583]; Geesow, 1987.08.03 [53.239, 14.388, 25]; Meseberg, 1982.08.30 [52.95, 13.10, 50]; Müritzhof, 1988.07.27 [53.45, 12.74, 70]; Carwitz, NSG Hauptmannsberg, 2000.04.22, no. 014, no. 016, no. 017, no. 019, no. 024 [53.31, 13.455, 115]; Neulöwenberg 1982.06.xx [52.90, 13.19, 67]; Oberhersdorf-2 km ENE, 1991.09.04 [50.180, 6.542, 580]; Ödenwaldstetten, 1991.05.19, no. 19 [48.35, 9.39, 750]. **Italy**: Abetone, pre. 1920 [44.143, 10.666, 1400]; Abetone, Seletta, 1960.07.15 [44.132, 10.644, 1700]; Apennino Modenese: Le Pozze, 1941.07.26, [44, 11, 1000, guess]; Bosco di Corniglio, 1985.08. xx [44.44, 10.04, 880]; Corvara: Colfosco, 1993.08.22 [45.56, 11.86, 1900]; Monte Cimone, Lago Ninfa, 1959. xx.xx, no. 55–57 [44.21, 10.72, 1500]; Praccia, 1890.07. xx, type *F. etrusca* [44.061, 10.911, 750]; Pejo-6 km N, Stelvio NP, 2004.06.16, no. 18 [46.411, 10.688, 2400];

Toscanian Alps: Giulia (leg. Wolf) pre 1945 [44,10,1000, guess]. **Netherlands**: Bergen, 1994.09.13 [52.670, 4.677, 11]. **Norway**: Alta-9.5 km S, 2015.07.10, no. 1, no. 2 [69.911, 23.081, 90]; Gjoktbukmyra, 2016.07.11, no. 4 [69.147, 29.207, 64]; Hedmark: Dalholen, 1993.06.28 [62.191, 9.746, 820]; Klingenberg, 2015.08.20, no. 6 [61.017, 11.855, 493]; Klingenberg-E, 2012.07.13, no. 93 [61.001, 12.060, 460]; Klingenberg-Ulva, 2012.07.13, no. 92 [61.001, 12.059, 462]; Osen: Drageid: Seter-4.8 km E, 2012.04.29 [64.392, 10.589, 45]; Osen: Drageid, 2015.08.24, no. 1–3 [64.392, 10.589, 55]; Osen: Drageid, 2016.08.23, no. 3 [64.391, 10.590, 59]; Oyermoen, 2012.06.27, no. 71 [60.248, 12.442, 300]; Tysil: Torberget, 2015.08.21, no. 4, no. 5 [61.105, 12.019, 528]; Tysil: Torberget, 2016.07.23, no. 1, no. 2 [61.105, 12.019, 528]. **Russia**: Kormovische, 2001.xx.xx, no. U79 [56.83, 57.95, 250]; Svenigorod, 1985.08.xx, no. 623 [55.70, 36.72, 150]; Voronesh Zapovednik, 1962.08.29, no. 221, type *F. nemoralis* [51.809, 39.446, 130]. **Slovenia**: Loibl Pass-5 km S, 1994.07.11, no. g10, no. 12 [46.404, 14.277, 700]. **Spain**: Camprodon-10 km NW, 1994.07.13 [42.401, 2.304, 1600]; Sierra de Guadarrama, 2009.10.16 [40.823, -3.960, 1824]. **Sweden**: Aaland, 1998.xx.xx, no. S60 [60.23, 19.95, 20]; Abisko, 1951.07.xx [68.50, 18.66, 500]; Andrarum, 1992.06.09, no. g4, no. g17 [55.708, 13.966, 115]; Ange-WSW, 2002.08.03, no. 029–032 [62.422, 15.000, 269]; Arvidsjaur-Aljeplog, 2002.07.29, no. 013, no. 014 [65.926, 18.311, 464]; Attonträsk-4 km SW, 1996.07.29, no. 109, no. 125 [64.401, 18.004, 471]; Attoträsk-6 km NE, 1996.07.28, no. 49, no. 76, no. 137, no. 141 [64.461, 18.153, 430]; Degeberga- 6 km SSW, 1992.06.09, no. g89 [55.784, 14.045, 125]; Falkenberg, 2000.xx.xx [56.92, 12.49, 32]; Kalix, 2000.xx.xx, no. S96, no. S100, no. S101 [65.84, 23.10, 7]; Orsa-45 km N, 2002.08.04, no. 036, no. 037 [61.407, 14.819, 480], Orsa-45 km N, 2002.08.04, no. 039 [61.409, 14.821, 476]; Storuman, 2002.07.31, no. 018 [64.924, 17.034, 422]; Storuman, 2002.07.31, no. 019 [64.923, 17.033, 423]; Sweg, 2002.08.04, no. 034 [62.140, 13.984, 378]; Upland: Hallnäs, 1998.xx.xx, no. S75 [60.53, 17.87, 10]; Öland: Böda, 1992.06.14 [57.250, 17.06, 9]; Öland: Borgholm Slott, 2000.10.08, no. 008–010 [56.870, 16.640, 60]; Östernoret-3 km SW, 1996.07.29, no. 71, no. 126 [64.071, 17.290, 320]. **Switzerland**: Alp La Schera, 1998.07.26, no. 51 [47.648, 10.194, 2080]; Valle Fermaur: Apples, pre 1874, type *F. rubens* [46.550, 6.433, 622]; La Punt-3.7 km NW, no. 58, no. 106 [46.588, 9.900, 2150]; S-Scharl-0.5 km S, 1998.07.27, no. 184 [46.713, 10.336, 1900]; S-Scharl-0.8 km S, 1998.07.27, no. 243 [46.710, 10.334, 2100]; S-Scharl-0.9 km S, 1998.07.27, no. 182 [46.709, 10.333, 2215]; S-Scharl-2.6 km SSE, 1998.07.27, no. 146 [46.697, 10.350, 2140]; S-Scharl-2.6 km SSE, 1998.07.27, no. 247 [46.697, 10.347, 2175]; Stabelchod, 1998.07.28, no. 81 [46.661, 10.241, 1940]; Stabelchod, 1998.07.28, no. 174 [46.665, 10.243, 1990]; Stabelchod- 1 km W, 1998.07.28, no. 172 [46.662, 10.224, 1880]; Ticino: Piora, 1981.07.22 [46.544, 8.686, 1930]. **Turkey**: Gerede, 1976.02.27 [40.810, 32.192, 1600].

Formica fennica Seifert, 2000

A total of 14 nest samples with 54 workers were investigated.

Azerbaijan: Ilisu, 2006.06.03, no. 24 [41.457, 47.063, 1706]. **Finland**: Iisalmi Kotikylä, 1998.07 [63.450, 27.167, 100]; Iisalmi Kotikylä, 2009.07.24 [63.450, 27.167, 100]; Ilomantsi, Maukkula, pre 1996 (leg. Saaristo) [62.62, 30.84, 170]; Luhanpää-1.42 km NE, 1999.07.07, no. 273 [61.058, 25.050, 130]; Luhanpää-1.42 km NE, 2001.07.22, no. 1, no. 2 [61.058, 25.050, 130]; Puhos-6.5 km WNW, 1996.07.13, no. 86, no. 105, no. 119 (type *F. fennica*) [62.108, 29.800, 100]; Puhos-6.5 km WNW, 2002.07.19, no. 013–015 [62.108, 29.800, 100]. **Georgia**: Schenako, 1985.08.01 [42.732, 45.662, 1600].

Stereomicroscopic equipment and measurement procedures were as given in Seifert (2019).

NUMOBAT data were recorded in the primary characters CS, CL, CW, ClySet, ClyPub, EyeHL, F2L, F3L, nCox, nHTfl, nMet, nOce, OceD, SL, sqPDG, sqPDO, TERG, and T3f; the recording rules are explained in Seifert (2018: 399–407). It is repeated and emphasized here that the performance of species delimitation in *Coptoformica* is strongly dependent from identification of basal remains of broken-off setae by high-resolution microscopy. The standardized characters were used in the analyses as variable of absolute body size (CS), as shape variables (CL/CW, SL/CS, OceD/CS, F2L/CS, F3L/CS, F2L/F3L), as variables describing seta conditions (ClySet, ClyPub, EyeHL, nCox, nHTfl, nMet, nOce, OceD, TERG, T3f) and as variables describing pubescence conditions (ClyPub, sqPDG, sqPDO).

Hypotheses on phenotype dimorphism within the *F. exsecta* sample were formed by a Two-Step Cluster Analysis (TSCA). The TSCA was run with automatic determination of the number of clusters using the SPSS 15.0 software package. The first step of analysis is construction of a Cluster Features (CF) tree which provides a capsule summary of the data file. The second step is grouping the leaf nodes of the CF tree using an agglomerative clustering algorithm which produces a range of solutions which are then compared using Schwarz's Bayesian Criterion to determine the "best" number of clusters. The hypothesis provided by the TSCA was checked and corrected by a single run of a linear discriminant analysis (LDA). LDA, Principal Component analysis (PCA), ANOVA and X^2 tests were run with the SPSS 15.0 software package. The DIMORPH test was performed according to Seifert (2016).

Nest samples of *F. exsecta* containing only worker individuals of the setae-reduced Rubens morph are under increased risk of being confused with *F. fennica*. In order to demonstrate a clear species separation, these samples were run together with those of *F. fennica* in different forms of exporatory data analyses using nest centroids as input data (NC clustering; Seifert et al. 2013). These were firstly hierarchical NC-Ward clustering, secondly and thirdly the hierarchical method NC-part.hclust and the iterative

vector-quantization method NC-part.kmeans (the latter two methods are implemented in partitioning algorithms based on recursive thresholding, Csősz and Fisher 2015), and nonmetric multidimensional scaling combined with iterative vector-quantization NC-NMDS-k-means (Seifert et al. 2013). Checking samples with controversial classifications was done by an interaction of NC clustering and a controlling linear discriminant analysis (LDA) in which these samples were run as wild-cards following the rationale described in Seifert et al. (2013). The final classification ("final species hypothesis") was established by the LDA in an iterative procedure and there remained no undecided cases even if their posterior probabilities were close to 0.5.

Standard air temperature (TAS) in °C of sampling sites 2 m above ground can be used as a rough approximation of the thermal niche component (Steiner et al. 2010, Seifert et al. 2014). Following Seifert and Pannier (2007), TAS was calculated as mean air temperature from 1 May to 31 August of the nearest three meteoro-logical stations of the years 1961 to 1990 provided by Klimaabteilung der Zentralanstalt für Meteorologie und Geodynamik (1996). Values were corrected for an altitudinal temperature decrease of 0.661 °C per 100 m: TAS=-0.694*LAT+0.078*LON-0.00661*ALT+52.20.

Results and discussion

Existence of pilosity and pubescence dimorphism in *Formica exsecta*

The analysis of phenotype variance was restricted to the characters CS, CL/CW, SL/CS, ClySet, ClyPub, nOce, OceD/CS, EyeHL, sqPDO, sqPDG, TERG, nCox, nHTFl, and nMet because the full set of characters was not available for all Western Palaearctic samples. Yet, three of the four excluded characters (F2L/CS, F3L/CS, and F2L/F3L) did not contribute to morph separation (Table 1). Within 431 worker individuals investigated,

Table 1. Morphometrics of worker individuals of *Formica fennica* and the two pilosity morphs of *F. exsecta*. Data are given as arithmetic mean ± standard deviation [lower extreme, upper extreme]; *n* = number of individuals. The columns with data of an univariate ANOVA test (*F* values, significance levels *p*, and degrees of freedom *df2*) are placed between the columns of the compared entities. *F* values of most discriminative characters are given in heavy type.

	F. exsecta Normal morph (*n*=288)	ANOVA *F, p df2*	*F. exsecta* Rubens morph (*n*=143)	ANOVA *F, p df2*	*F. fennica* (*n*=54)
CS [μm]	1390 ± 81 [1143,1586]	1.66, 0.198 429	1397± 83 [1145,1608]	**65.03**, 0.000 195	1287 ± 93 [1050,1468]
CL/CW	1.045 ± 0.023 [0.983,1.119]	15.50, 0.000 429	1.054 ± 0.020 [1.009,1.105]	18.52, 0.000 195	1.068 ± 0.021 [1.019,1.118]
SL/CS	1.028 ± 0.022 [0.966,1.085]	9.91, 0.002 429	1.020 ± 0.023 [0.965,1.071]	0.09, 0.762 195	1.022 ± 0.026 [0.962,1.084]
EyeHL	27.2 ± 6.9 [0.0,60.3]	0.89, 0.347 429	26.5 ± 8.0 [16.1,44.8]	5.17, 0.024 195	23.9 ± 2.3 [20.7,27.0]
TERG	1.03 ± 0.16 [1.0,2.0]	**227.18**, 0.000 429	1.92 ± 0.98 [1.00,4.00]	**117.02**, 0.000 195	3.48 ±0.64 [3.0,6.0]
nCOX	9.63 ± 2.99 [2.5,18.5]	**399.87**, 0.000 429	4.00 ± 2.26 [0.5,13.0]	**97.07**, 0.000 195	0.89 ±0.88 [0.0,3.0]
nHTFL	9.45 ± 1.89 [5.1,15.5]	69.28, 0.000 429	7.93± 1.65 [3.8,13.1]	6.69, 0.010 195	7.22 ±1.93 [4.2,13.9]
nMET	2.26 ± 2.15 [0.0,10.0]	**100.89**, 0.000 429	0.37 ± 0.75 [0.0,3.7]	13.09, 0.000 195	0.00 ± 0.00 [0,0.0]
sqPDO	5.38 ± 0.98 [3.21,8.91]	**79.53**, 0.000 429	6.43 ± 1.44 [3.74,13.40]	2.51, 0.115 195	6.77 ± 1.04 [4.52,9.92]
sqPDG	6.87 ± 1.20 [3.93,9.84]	12.64, 0.000 429	7.31 ± 1.36 [4.33,10.73]	2.35, 0.127 195	7.61 ± 0.56 [6.58,8.71]
ClySet	4.09 ± 0.56 [2.0,5.0]	**1206.1**, 0.000 429	2.17 ± 0.48 [1.0,3.0]	32.46, 0.000 195	1.72 ± 0.53 [1.0,3.0]
ClyPub	3.13 ± 1.04 [0.8,6.5]	0.70,0.404 429	3.01 ± 1.25 [0.5,6.5]	26.23, 0.000 195	2.07 ± 0.82 [0.5,4.3]
nOce	2.16 ± 0.56 [0.7,6.0]	**95.59**, 0.000 429	1.57 ± 0.65 [0.0,4.0]	**195.10**, 0.000 195	0.24 ± 0.42 [0.0,1.7]
OCED /CS	0.188 ± 0.010 [0.155,0.210]	0.00, 0.97 429	0.188 ± 0.011 [0.161,0.217]	20.27, 0.000 195	0.180 ± 0.010 [0.156,0.198]
T3f	0.97 ± 0.15 [0.00,1.00]	34.46, 0.000 301	0.77 ± 0.41 [0.00,1.00]	**144.19**, 0.000 182	0.06 ± 0.22 [0.00,1.00]
FL2/FL3	0.987 ± 0.040 [0.896,1.077]	3.03, 0.084 142	0.979 ± 0.040 [0.885,1.085]	20.60, 0.000 144	1.004 ± 0.033 [0.938,1.094]
FL2/CS	13.57 ±0.59 [12.43,14.77]	4.57, 0.034 142	13.37 ±0.53 [12.08,14.63]	0.30, 0.586 144	13.31 ±0.68 [11.98,15.21]

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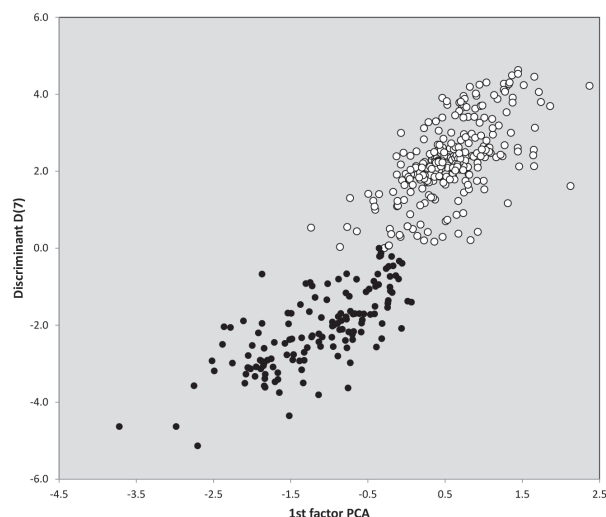
Figure 1. Discriminant value D(7) and 1st factor of a principal component analysis. Data of 288 workers of the Normal morph (white dots) and 143 workers of the Rubens morph (black dots) of *Formica exsecta*.

the Two-Step Cluster Analysis (TSCA) distinguished only two clusters: the Normal morph and the Rubens morph. The final morph hypothesis was established by a single run of an LDA which confirmed 96.3% of the TSCA classifications. Based on this hypothesis, a stepwise character-reduced LDA was run which extracted a discriminant function of seven characters with

$$D(7) = 5.098*SL/CS + 1.609*ClySet-0.044*EyeHL-0.191*sqPDO-0.45*TERG + 0.100*nCox+0.064*nMet-7.9705.$$

Individuals with D(7) <0 were classified as Rubens morph and those with larger values as Normal morph. This discriminant classified 94.9% of the 431 specimens with posterior probabilities > 0.90 (the recognition threshold used in the DIMORPH test, see below). Figure 1 presents a bivariate plot of D(7) and the first factor of a PCA considering these seven characters. Table 1 shows that the morphs are strongest separated by clypeal setae conditions (ClySet). The composition of the type samples is given in Table 2. Only Rubens morph workers were observed within the type series of *F. rubens* Forel, 1874 and *F. etrusca* Emery, 1909. Eight workers of the type serie of *F. nemoralis* Dlussky, 1964 belonged to Rubens but one worker to Normal whereas all three investigated type specimens of *F. dalcqi* Bondroit, 1918 belonged to Normal.

Evidence for conspecificity of the Normal and Rubens morph

Within 152 nest samples from the Palaearctic west of 59°E, 104 samples contained only the Normal morph, 28 only the Rubens morph and 20 a mixture of both the Normal and Rubens morph. This figure of 13.2% of mixed nests already indicates heterospecificity to be most unlike-

Table 2. Morph composition in type series of taxa synonymized with *Formica exsecta* Nylander, 1846. D(7) is the discriminant value considering seven phenotypic characters, p(Norm) and p(Rube) are the posterior probability for the Normal and Rubens morph. Data indicating the Normal morph are shaded in grey.

Taxon; site; specimen no.	D(7)	p(Norm)	p(Rube)
F. exsecta rubens Forel, 1874; Apples; no. 1	-1.692	0.0004	0.9996
F. exsecta rubens Forel, 1874; Apples; no. 2	-2.582	0.0000	1.0000
F. exsecta rubens Forel, 1874; Apples; no. 3	-0.665	0.0364	0.9636
F. exsecta rubens Forel, 1874; Apples; no. 4	-2.769	0.0000	1.0000
F. exsecta etrusca Emery, 1909; Praccia; no. 1	-2.396	0.0000	1.0000
F. exsecta etrusca Emery, 1909; Praccia; no. 2	-2.107	0.0001	0.9999
F. exsecta etrusca Emery, 1909; Praccia; no. 3	-1.862	0.0002	0.9998
F. exsecta etrusca Emery, 1909; Praccia; no. 4	-1.945	0.0001	0.9999
F. exsecta etrusca Emery, 1909; Praccia; no. 5	-0.3925	0.1114	0.8886
F. dalcqi Bondroit, 1918; Mount Canigou; no. 1	2.256	0.9999	0.0001
F. dalcqi Bondroit, 1918; Mount Canigou; no. 2	0.568	0.8954	0.1046
F. dalcqi Bondroit, 1918; Mount Canigou; no. 3	3.414	1.0000	0.0000
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 1	-3.134	0.0000	1.0000
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 2	-2.601	0.0000	1.0000
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 3	-2.939	0.0000	1.0000
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 4	-2.874	0.0000	1.0000
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 5	-2.554	0.0000	1.0000
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 6	-1.684	0.0004	0.9996
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 7	1.082	0.9880	0.0120
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 8	-3.087	0.0000	1.0000
F. nemoralis Dlussky, 1964; Voronesh Zapovednik; no. 9	-2.023	0.0001	0.9999

ly. Yet, checking the alternatives intraspecific dimorphism versus heterospecificity by the DIMORPH test is problematic considering the huge geographic area and heterogenous sampling philosophies of different collectors. Among the conditions allowing to run the DIMORPH test are panmictic behaviour and random sampling, i.e., no preference to collect certain phenotypes (Seifert 2016). Both conditions are not really fulfilled in the whole data set. As a matter of fact, *F. exsecta* samples with reduced setae conditions (suspicious during field sampling or during laboratory sorting to possibly represent *F. bruni* Kutter, 1967, *F. fennica*, or *F. suecica* Adlerz, 1902) were more frequently collected (and analyzed) than the much more frequent hairy samples. This distorts the estimates of allele frequencies in favour of the Rubens morph.

The only coherent geographic area with random, unbiased sampling and evaluation of *F. exsecta* samples in-

cluded Finland, Sweden, and northern Denmark, largely based on the collecting activity of the Senckenberg Museum of Natural History Görlitz. Selecting this area makes also sense because the geographic reference is then well comparable with that in the study of Hakala et al. (2018).

The DIMORPH test was run for this area with the following basic data and parameters. Among 58 nest samples, 42 samples contained only the Normal morph, seven samples only the Rubens morph, and nine samples a mixture of both morphs. These data are based on a recognition threshold of $p > 0.90$ in the LDA considering seven characters. Of the 157 individuals in the data set, 74.5% belonged to the Normal morph and 25.5% to the Rubens morph. Supposing a dominant-recessive inheritance and the Hardy-Weinberg model of population genetics, this would result in a frequency of the recessive 'allele' of 0.505 if Rubens is recessive and of 0.863 if Normal is recessive. Using these parameters, the DIMORPH test was run for both assumptions with 500 repeats each and the data were averaged. The clear results are presented in Table 3. Applying Fisher's exact test, observed and predicticted morph distributions differed with $p = 0.017$ for the scenario of parabiosis

Table 3. DIMORPH test comparing 58 observed within-nest phenotype compositions with four prediction models. Agreement of observation and predictions was tested by Fisher's exact test (p) and the Chi-squared test (X^2, p).

within-nest phenotype composition	observed	parabiosis	prediction heterospecificity temporary social parasitism	permanent social parasitism	prediction intraspecific dimorphism
only Rubens	7	8.20	2.08	0.00	8.41
Rubens + Normal	9	0.58	0.09	1.16	12.20
only Normal	42	49.22	55.84	56.84	37.39
Fisher's p		0.017	0.0004	0.0001	0.659
X^2, p		8.07, 0.018	13.4, 0.001	15.28, 0.0001	0.88, 0.547
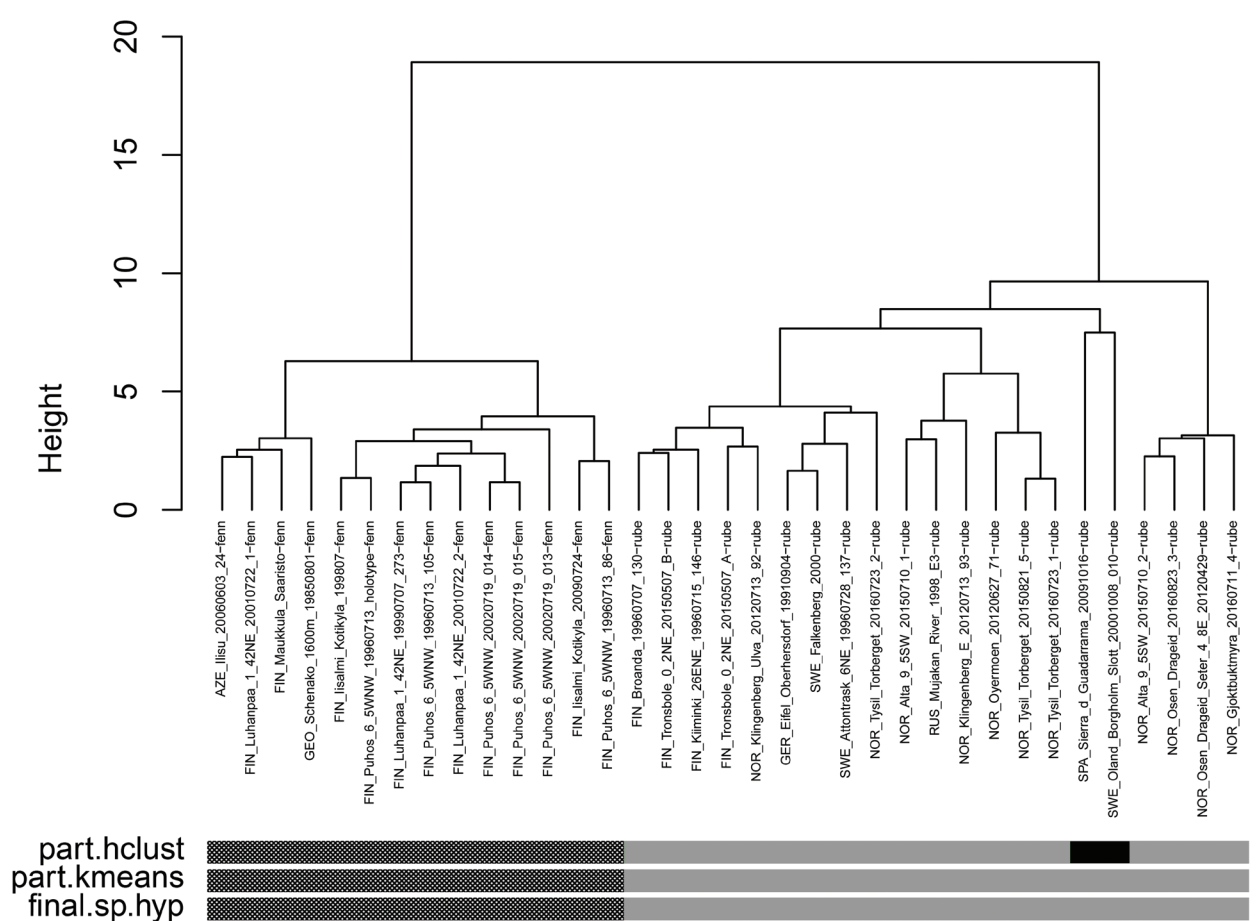
Figure 2. Three exploratory and a hypothesis-driven data analysis using nest centroids (NC) as input data. Evaluated were 21 nest samples of *Formica exsecta* containing only Rubens morph workers (grey bars right) and 14 nest samples of *F. fennica* (textured grey bars left). The classifications of NC-Ward and NC-part.kmeans coincide completey whereas NC-part.hclust is also in general agreement but exposes two outlier samples (black bar).

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of independent species, with p=0.0004 for the scenario of temporary social parasitism and with p=0.0001 for the scenario of permanent social parasitism. In contrast, no significant difference was found between the observed distribution and the prediction for intraspecific dimorphism (Fisher's test p=0.659, X^2 test p=0.547).

The separation of the Rubens morph from *Formica fennica*

Nest samples of *Formica exsecta* containing only worker individuals of the Rubens morph are at increased risk of being confused with *F. fennica*. Only these critical samples, but this time originating from the whole of the Western Palaearctic and having T3f data available, were included in the following analyses. These were 21 nest samples of the Rubens morph with 82 workers and 14 samples of *F. fennica* with 54 workers.

In first analytic step all 18 NUMOBAT characters were used unselectively as input and for the exploratory data analyses NC-Ward, NC-part.hclust, and NC-NMDS-k-means. After running samples with classifications disagreeing between the different methods as wild cards, NC-Ward clustering and NC-part.hclust both showed a classification error of 0% with the latter exposing two samples as outliers (=5.7%), whereas NC-NMDS-k-means showed an error of 5.7%. NC-part.kmeans was not able to confirm the existence of two clusters for the complete unselected character set.

Accepting the former hypotheses, the character set was reduced by a stepwise LDA to the eight characters CS, CL/CW, ClySet, nOce, sqPDG, nCox, T3f, and F2L/F3L. Under this setting, all four NC-clustering algorithms achieved a classification error of 0% with NC-part.hclust exposing two samples (5.7%) as outliers (Fig. 2). On the individual level, the classification error of the LDA was 2.9% in 136 workers. The sample from Norway, Osen: Drageid: Seter-4.8 km E, 2012.04.29 [64.392N, 10.589E, 45 m] is determined under this setting with a sample mean of p = 0.9032 as Rubens morph if the three available specimens are run as wild-cards. A wild-card run considering all 18 characters results in a determination with p=0.9916. This should be emphasized as, based on a much weaker data basis available in the year 2012, I had erroneously determined this sample as *F. fennica* (published by Suvák 2013).

Data on zoogeography and climate niche do also not support the presence of *F. fennica* in Norway. Since *F. fennica* apparently does not spread north to the boreal zone and does not elevate to the subalpine zone (Seifert 2018), the high Skandinavian Fjäll should represent a strong distributional barrier for postglacial immigration from the east. The much narrower climate niche of *F. fennica* is explicitly indicated by the mean air temperature TAS of the sites from 1 May to 31 August. TAS is 11.98 ± 3.28 [4.75, 18.44] °C for 111 sites of *F. exsecta* and 13.78 ± 0.90 [12.72, 15.09] °C for the six known sites of *F. fennica*. Immigration to Norway, if at all, appears only possible via Skåne (Sweden) and along the Oslo Fjord.

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About *Notiophilus* Duméril, 1806 (Coleoptera, Carabidae): Species delineation and phylogeny using DNA barcodes

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http://zoobank.org/C63A90C7-9612-4DC1-AB8B-8E87BA515B38

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Abstract

The genus *Notiophilus* Duméril, 1806 is a distinctive taxon of small, diurnal and morphologically similar beetles exhibiting large eyes and widened second elytral intervals. In this study we analysed the effectiveness of DNA barcodes to discriminate 67 specimens that represent 8 species of *Notiophilus* from Central Europe. Interspecific K2P distances below 2.2% were found for *N. biguttatus* (Fabricius, 1779) and *N. quadripunctatus* Dejean, 1826, whereas intraspecific distances with values > 2.2% were revealed for *N. rufipes* Curtis, 1829. An additional phylogenetic analysis of all available species revealed a close relationship of *N. directus* Casey, 1920, *N. semistriatus* Say, 1823, *N. simulator* Fall, 1906 and *N. sylvaticus* Dejean, 1831, possibly indicating a radiation of these species in North America. Low support values of most other nodes, however, do not allow additional phylogenetic conclusions.

Introduction

The Carabidae or ground beetles are a huge cosmopolitan family with an estimated number of more than 40,000 species worldwide (Lindroth 1985, Lorenz 2005). As part of its subfamily Nebriinae, the tribe Notiophilini Motschulsky 1850 is a relatively small taxon that includes only one genus: *Notiophilus* Duméril, 1806. Nevertheless, this genus is one of the more distinctive genera of Carabidae. With a body length of less than 7 mm, species of *Notiophilus* are small carabids that can be easily recognised by the enormous eyes and furrowed frons, their extremely uniform general habitus with narrow, parallel-sided elytra, as well as by the characteristic dilated second elytral interval ("Spiegelfeld") that can be

broad as the 3rd plus 4th interval or broader (Fig. 1) (e.g. Lindroth 1961–1969). Many species exhibit wing dimorphism with macropterous (long-winged) and brachypterous (short-winged) morphs (Lindroth 1986, Chapman et al. 2005). Typically, beetles of this genus are diurnal, sun-loving insects and very rapid in their movements. They are visual carabids, preying upon mites, springtails and other small arthropods (e.g. Anderson 1972, Bauer 1981, Ernsting and Mulder 1981, Ernsting et al. 1992). To date, 57 species have been described from the Palearctic, Oriental, Nearctic and Neotropical regions (Barševskis 2011, Bousquet 2012, Löbl and Löbl 2017). For Europe, 14 species are recorded (Barševskis 2007), whereas 9 are known from Germany and Central Europe (Müller-Motzfeld 2006, Trautner et al. 2014). Thanks to the thorough
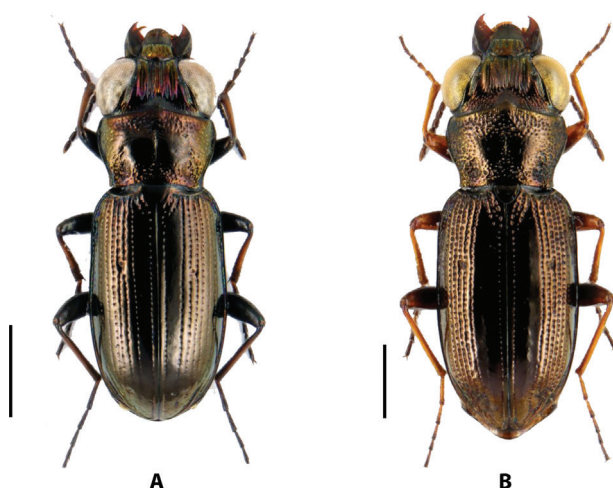
Figure 1. Two representative species of the genus *Notiophilus* amongst those analysed in this study: A: *Notiophilus germinyi* Fauvel in Grenier, 1863 and B: *Notiophilus rufipes* Curtis, 1829. Note the characteristic different size of the second elytral intervals ("Spiegelfeld") for both beetle species. Scale bars = 1 mm. Source of photos: http://www.eurocarabidae.de/ (access date: 2019–01–15).

studies of Arvīds Barševskis (Latvia), our knowledge about the biogeography and taxonomy of this genus has increased significantly in recent years (e.g. Barševskis 2001, 2007, 2009, 2011, 2012). Based on the fact that the largest diversity of species and the highest number of endemics are found in Asia, the central part of this continent is hypothesised as the centre of origin of *Notiophilus*, followed by a subsequent colonisation of Europe, North Africa and North America (Barševskis 2007). In terms of the phylogeny of this genus, however, no analysis has been performed to date.

As noted, species of *Notiophilus* are remarkably similar in habitus and display a considerable individual variation, making identification difficult (e.g. Lindroth 1961–1969, Hannig 2005, Heijermann and Aukema 2014). Consequently, molecular methods may represent another useful alternative for correct specimen identification. Recently, the analysis of DNA sequence data, in particular the use of an approx. 660 base pair (bp) fragment of the mitochondrial cytochrome *c* oxidase subunit 1 (COI), has been proposed as the marker of choice, as a so-called "DNA barcode", for specimen identification (Hebert et al. 2003a, Hebert et al. 2003b). DNA barcoding relies on the assumption that the observed interspecific genetic variation exceeds the intraspecific variation to such a proportion that a clear gap exists. As a consequence, unidentified individuals can be assigned correctly to their species (Hebert et al. 2003a, Hebert et al. 2003b). Not surprisingly, DNA barcoding has been criticised from its beginning, for example for the inappropriate use of neighbour-joining trees for analysis or the application of fixed distance thresholds (Will and Rubinoff 2004, Goldstein and DeSalle 2010, Collins and Cruickshank 2013). Nevertheless, nu-

merous studies clearly demonstrate the usefulness of DNA barcoding, in particular for insects (e.g. Hausmann et al. 2011, Park et al. 2011, Morinière et al. 2014, Schmidt et al. 2015, Havemann et al. 2018). Thus, the compilation of comprehensive and representative DNA barcode libraries represents an essential step for subsequent studies, for example, biodiversity assessment studies via metabarcoding based on modern high-throughput sequencing technologies (e.g. Yu et al. 2012, Cristescu 2014, Brandon-Mong et al. 2015, Porter and Hajibabaei 2018). Despite the high number of described species, however, the number of studies that tested the efficiency of DNA barcodes for species identification of ground beetles is still low (Greenstone et al. 2005, Maddison 2008, Raupach et al. 2010, Woodcock et al. 2013, Pentinsaari et al. 2014, Hendrich et al. 2015, Raupach et al. 2016, Raupach et al. 2018).

As part of our efforts in building a comprehensive DNA barcode library of ground beetles of Germany, we analysed the quality of DNA barcodes to discriminate Central European species of the carabid genus *Notiophilus*. Furthermore, we reconstructed the phylogeny of this small but charismatic carabid genus for the first time, with a focus on the zoogeographic distribution of the analysed species.

Material and methods

Sampling of specimens

All analysed ground beetles were collected between 2005 and 2017 using various classical sampling methods (i.e. hand collecting, pitfall traps) and stored in ethanol (96%). The analysed specimens were identified by two of the authors (KH, MJR) using the key provided in Müller-Motzfeld (2006). In total, 35 new barcodes were generated. For our analysis, we also included 32 DNA barcodes of a previous study (Hendrich et al. 2015). As a result, the complete dataset consisted of 67 DNA barcodes. Most beetles were collected in Germany ($n = 61$, 91%), but for comparison, some specimens were also included from Austria ($n = 3$, 4%), Belgium ($n = 2$, 3%) and Slovenia ($n = 1$, 2%). Our analysis covers eight of the nine species recorded from Germany (88.9%): *Notiophilus aestuans* Dejean, 1826, *N. aquaticus* (Linnaeus, 1758), *N. biguttatus* (Fabricius, 1779), *N. germinyi* Fauvel in Grenier, 1863, *N. palustris* (Duftschmid, 1812), *N. quadripunctatus* Dejean, 1826, *N. rufipes* Curtis, 1829 and *N. substriatus* Waterhouse, 1833. Only specimens of the rare species *N. laticollis* Chaudoir, 1850 were missing (see Trautner et al. 2014). The number of analysed specimens per species ranged from a minimum of 3 (*N. quadripunctatus*) to a maximum of 16 (*N. biguttatus*).

DNA barcode amplification, sequencing and data depository

Laboratory operations were carried out, following standardised protocols for COI amplification and sequencing

(Ivanova et al. 2006, deWaard et al. 2008), at the Canadian Center for DNA Barcoding (CCDB), University of Guelph, the molecular labs of the Zoologisches Forschungsmuseum Alexander Koenig in Bonn and/or the working group Systematics and Evolutionary Biology at the Carl von Ossietzky University Oldenburg, Germany. Representative photos from each studied beetle were taken before molecular work was performed. One or two legs of one body side were removed for the subsequent DNA extraction which was performed using NucleoSpin Tissue Kit (Macherey-Nagel, Düren, Germany), following the extraction protocol.

Detailed information about used primers, PCR amplification, and sequencing protocols can be found in a previous publication (see Raupach et al. 2016). All purified PCR products were cycle-sequenced and sequenced in both directions at a contract sequencing facility (GATC, Konstanz, Germany), using the same primers as used in PCR. Double stranded sequences were assembled and checked for mitochondrial pseudogenes (numts) by analysing the presence of stop codons, frameshifts, as well as double peaks in chromatograms with the Geneious version 8.1.9 programme package (Biomatters, Auckland, New Zealand) (Kearse et al. 2012). Routinely, BLAST searches (nBLAST, search set: others, programme selection: megablast) were performed to confirm the identity of all new sequences as ground beetle barcodes, based on already published sequences (high identity values, very low E-values).

Comprehensive voucher information, taxonomic classifications, photos, DNA barcode sequences, primer pairs used and trace files (including their quality) are publicly accessible through the public dataset "DS-BANOT" (Dataset ID: dx.doi.org/10.5883/DS-BANOT) on the Barcode of Life Data Systems (BOLD; www.boldsystems.org) (Ratnasingham and Hebert 2007). All new barcode data have been deposited in GenBank (accession numbers: MK567377-MK567411).

DNA Barcode analysis: Species identification

The analysis tools of the BOLD workbench were employed to calculate the nucleotide composition of the sequences and distributions of Kimura-2-parameter distances (K2P; Kimura 1980) within and between species (align sequences: BOLD aligner; ambiguous base/gap handling: pairwise deletion). All barcode sequences became subject of the Barcode Index Number (BIN) analysis system, implemented in BOLD that clusters DNA barcodes in order to produce operational taxonomic units that typically closely correspond to species (Ratnasingham and Hebert 2013). A threshold of 2.2% was applied for a rough differentiation between intraspecific and interspecific distances based on Ratnasingham and Hebert (2013). These BIN assignments on BOLD are constantly updated as new sequences are added, splitting and/or merging individual BINs in light of new data (Ratnasingham and Hebert 2013).

In addition, all sequences were aligned using MUSCLE (Edgar 2004) and analysed using a neighbour-joining cluster analysis (NJ; Saitou and Nei 1987) based on K2P distances with MEGA X (Kumar et al. 2018) in order to visualise the DNA barcode divergences and species cluster. As outgroup taxa we used three barcode sequences of *Nebria brevicollis* (Fabricius, 1792) (accession numbers: KM451780, KM452043, KM452651). Non-parametric bootstrap support values were obtained by re-sampling and analysing 1,000 replicates (Felsenstein 1985) implemented in MEGA X. For species pairs with interspecific distances < 2.2%, maximum parsimony networks were constructed with TCS 1.21, based on default settings (Clement et al. 2000) as part of the software package PopART v.1.7 (Leigh and Bryant 2015) after an alignment using MUSCLE (Edgar 2004). Such networks allow the identification of possible haplotype sharing between species as a consequence of recent speciation or on-going hybridisation processes.

DNA Barcode analysis: Phylogenetic applicability

As part of our phylogenetic study, we used one representative sequence per analysed species, namely a sequence of the most abundant haplotype. Furthermore, we added sequences of all additional species available at BOLD with a length of at least 500 base pairs (bp), following the same procedure if more than one sequence was given: *Notiophilus aeneus* (Herbst, 1806), *N. borealis* Harris, 1869, *N. directus* Casey, 1920, *N. reitteri* Spaeth, 1900, *N. semistriatus* Say, 1823, *N. simulator* Fall, 1906 and *N. sylvaticus* Dejean, 1831. Five CO1 sequence of the genus *Nebria* Latreille, 1802 (*N. brevicollis* (Fabricius, 1792) (KM451780), *N. frigida* R.F. Sahlberg, 1844 (KU875532), *N. metallica* Fischer von Waldheim, 1822 (KU875541), *N. nivalis* Paykull, 1790 (KU875543) and *N. salina* Fairmaire & Laboulbène, 1854 (KM444378)) were used as outgroup taxa. In total, this dataset consisted of 20 sequences. All sequences were aligned using MUSCLE with default settings (Edgar 2004).

The accuracy of phylogenetic reconstructions depends on various factors, e.g. sequence quality, the correct identification of homologous sites, the absence of heterotachy or, in particular, substitution saturation (Xia 2009). In the extreme case that sequences have experienced full substitution saturation, the given similarity between the sequences will depend entirely on the similarity in nucleotide frequencies and often do not reflect their phylogenetic relationships (e.g. Steel et al. 1993, Xia et al. 2003). As a consequence, fast evolving protein coding genes, such as COI, cannot be used for phylogenetic analysis that focus on deep and old branches (e.g. Wetzer 2002, Goetze 2003, Maddison et al. 2014), but can be useful for the study of more recent phylogenetic events on species level (e.g. Klopfstein et al. 2010, Matzen da Silva et al. 2011, Dai et al. 2012). Therefore, DAMBE 7.0.28 (Xia 2018) was used to check if the COI dataset of *Notiophilus* was subject to saturation following the Xia approach (Xia 2009). Saturation plots were made using the number of transitions and transversions plotted against patristic distances (*p*-distances).

Phylogenetic relationships were analysed under the maximum likelihood criterion using IQ-TREE 1.6.8 (Nguyen et al. 2015). The best model nucleotide substitution was determined based on the Bayesian Information Criterion (BIC) with Modelfinder (Kalyaanamoorthy et al. 2017). In order to assess nodal support, 10,000 ultrafast bootstrap replicates (Hoang et al. 2018) and 10,000 replicates of a SH-aLRT test (Guindon et al. 2010) were performed. Ultrafast bootstrapping (UFBoot) has been demonstrated to be largely unbiased compared to standard or alternative bootstrapping, whereas SH-aLRT values have been shown to be as conservative as standard non-parametric bootstrap values (Minh et al. 2013). Typically, nodes with support values of UFBoot ≥ 95 and SH-aLRT ≥ 90 were considered as very robust and values ≥ 80% as robust (Minh et al. 2013, Hoang et al. 2018). Following Barševskis (2007), we added biogeographic information for each analysed species.

Results

DNA Barcode analysis: Species identification

Overall, 67 DNA barcode sequences were analysed for eight of the nine species of the genus *Notiophilus* from Germany. Fragment lengths of the analysed DNA barcode fragments ranged from 549 to 658 bp. As is typically known for arthropods, a high AT-content was found for the DNA barcode region: the mean sequence compositions were A = 28%, C = 16.3%, G = 17.3% and T = 38.4%. Intraspecific K2P distances within a genus ranged from zero to a maximum of 3.62% (*N. rufipes*), whereas interspecific distances within the analysed genus had values between 0.62 and 10.22% (Table 1). The lowest interspecific distances of distinct barcode clusters were found for *N. biguttatus* and *N. quadripunctatus* with values ranging from 0.49% to 0.82% (Table 1). As a result, both species became subject to the same BIN (AAO0964). In contrast to this, maximum intraspecific pairwise distances > 2.2%

were found for *N. rufipes* (3.62%), resulting in two BINs (AAX5571, AAC7024) for this species (Table 1). Unique BINs were identified for the remaining five species (63%).

The NJ analyses, based on K2P distances, revealed non-overlapping clusters with bootstrap support values of 100% for six species (75%). Nodal support values below 85% were found for *N. biguttatus* and *N. quadripunctatus* (Fig. 2). A detailed topology is presented in the supporting information (Suppl. material 1). Our statistical maximum parsimony analysis indicated closely related haplotypes for the studied specimen of *N. biguttatus* (*n* = 16) and *N. quadripunctatus* (*n* = 3) (Fig. 3). We identified three different haplotypes with one dominant haplotype (h1) for *N. biguttatus* (Fig. 3), whereas only one haplotype (h1*) was found for all analysed beetles of *N. quadripunctatus* (*n* = 3). However, this haplotype is separated from haplotype h1 and h2 of *N. biguttatus* only by five additional mutational steps (Fig. 3). Two distinct monophyletic lineages, in combination with high distances, were found for *N. rufipes* (Figs 2, 4, Table 1).

### DNA Barcode analysis: Phylogenetic applicability

The test of substitution saturation revealed that the observed index of substitution saturation (*Iss*: 0.22) for the alignment was significantly lower than the corresponding critical index substitution saturation (*Iss.c* (symmetrical tree): 0.74; *Iss.c* (asymmetrical tree): 0.54), indicating that there was no or little saturation in the dataset (Suppl. material 2).

Modelfinder revealed the GTR+F+R3 model as the optimal nucleotide substitution model for our dataset with the following rate parameters: nucleotide frequencies A: 0.29, C: 0.16, G: 0.17, T: 0.38; substitution rates RAC: 0.01, RAG: 40.39, RAT: 21.52, RCG: 1.45, RCT: 98.02, RGT: 1; model of rate heterogeneity: FreeRate with 3 categories: category 1 with a relative rate = 0.06 and a proportion of 0.69, category 2 with a relative rate = 2.02 and a proportion of 0.27 and category 3 with a relative rate = 12.74 and a proportion of 0.03).

Table 1. Molecular distances based on the Kimura 2-parameter model of the analysed specimens and species of the genus *Notiophilus*. Divergence values were calculated for all studied sequences, using the Nearest Neighbour Summary implemented in the Barcode Gap Analysis tool provided by the Barcode of Life Data System (BOLD). Align sequencing option: BOLD aligner (amino acid based HMM), ambiguous base/gap handling: pairwise deletion. ISD = intraspecific distance. BINs are based on the barcode analysis from 18–11–2018. Species with maximum intraspecific distances > 2.2% and species pairs with interspecific distances < 2.2% are marked in bold.

| Species	*n*	Mean ISD	Max ISD	BIN	Nearest Species	Distance to NN
Notiophilus aestuans Dejean, 1826	4	0.24	0.48	ACB8850	*N. aquaticus*	7.04
Notiophilus aquaticus (Linnaeus, 1758)	10	0.58	1.12	AAY5028	*N. aestuans*	7.04
***Notiophilus biguttatus* (Fabricius, 1779)**	**16**	**0.22**	**0.77**	**AAO0964**	***N. quadripunctatus***	**0.62**
Notiophilus germinyi Fauvel in Grenier, 1863	5	0.43	0.92	AAY5659	*N. rufipes*	10.22
Notiophilus palustris (Duftschmid, 1812)	10	0.26	1.11	AAX5556	*N. aquaticus*	9.17
***Notiophilus quadripunctatus* Dejean, 1826**	**3**	**0**	**0**	**AAO0964**	***N. biguttatus***	**0.62**
***Notiophilus rufipes* Curtis, 1829**	**8**	**1.55**	**3.62**	**AAX5571, AAC7024**	***N. palustris***	**9.24**
Notiophilus substriatus Waterhouse, 1833	11	0.08	0.31	ACC3407	*N. aquaticus*	7.73
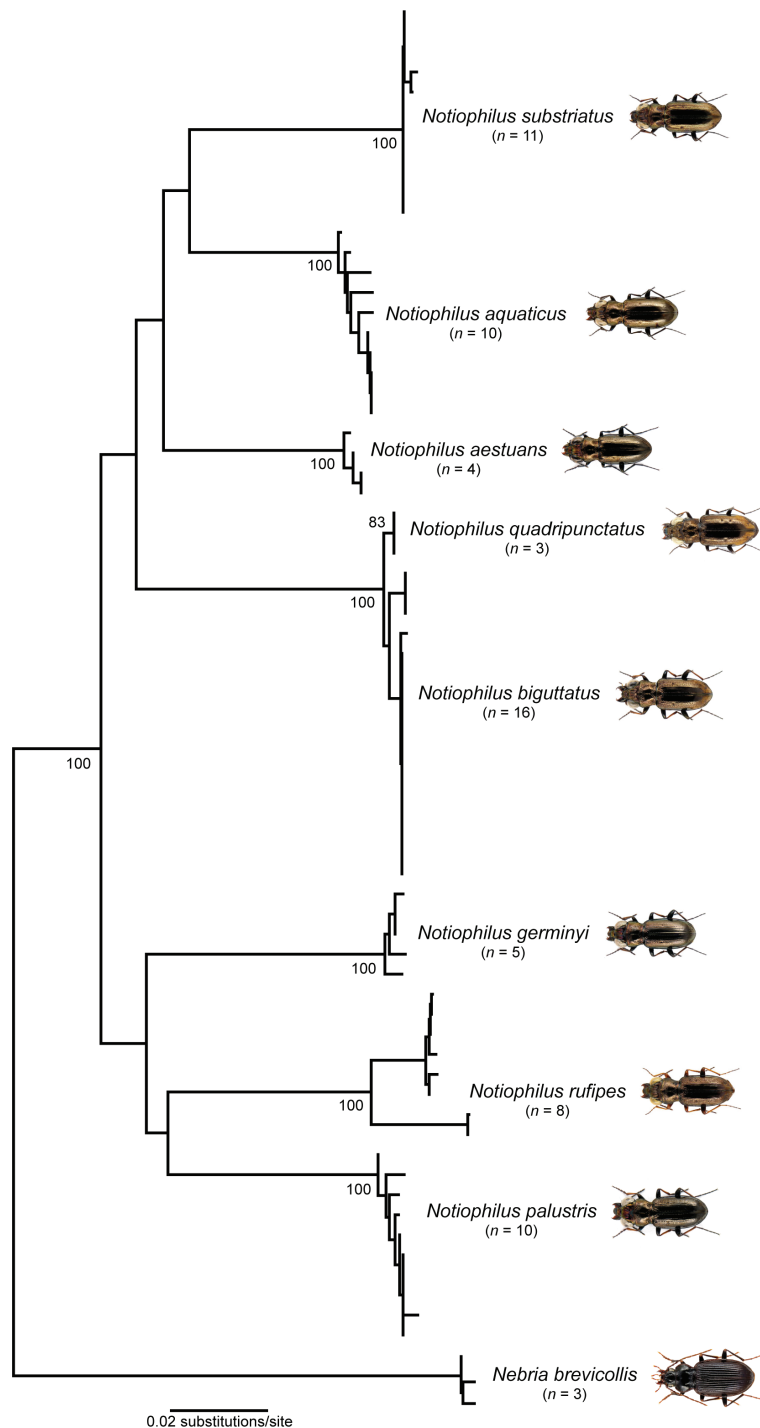
Figure 2. Neighbour joining (NJ) topology of the analysed ground beetle species of *Notiophilus,* based on Kimura 2-parameter distances. Numbers next to nodes represent non-parametric bootstrap values > 90% (1,000 replicates). Source of photos: http://www.eurocarabidae.de/ (access date: 2019–01–15).

The results of the phylogenetic analysis are visualised in Figure 5. High nodal support > 90% was found for five nodes only, whereas medium support (SH-aLRT: 80–90%; UFBoot: 80–90%) was revealed for two nodes. All other nodes had support values < 80%, indicating low support. High nodal support values revealed that *N. aeneus* represents the sister taxon to all other analysed *Notiophilus* species. All other taxa are part of two clades: one clade included *N. biguttatus* and *N. quadripunctatus* (100%/100%); all other species were found in a second clade with medium support (87.4%/85%). Furthermore, high nodal support was found for a clade with *N. directus*, *N. semistriatus*, *N. simulator* and *N. sylvaticus* (97.5%/95%) and a clade with *N. germinyi*, *N. rufipes* and *N. palustris* (99.1%/97%).

Notiophilus biguttatus (Fabricius, 1779)
(*n* = 16)

Notiophilus quadripunctatus Dejean, 1826
(*n* = 3)
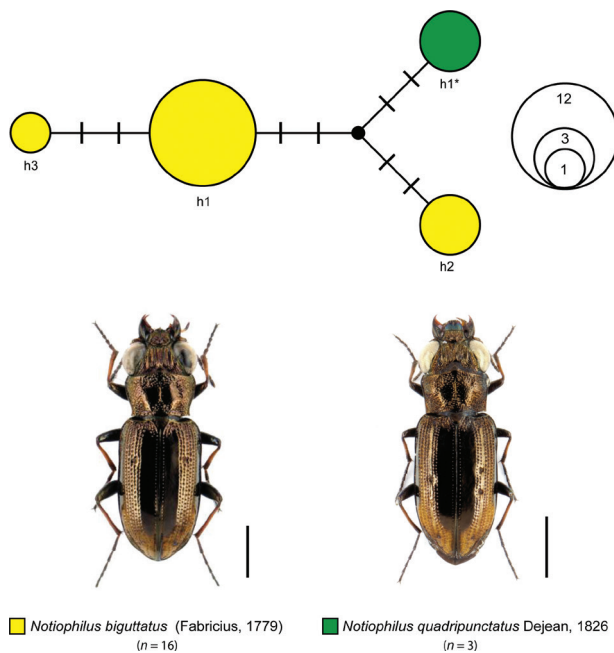
Figure 3. Maximum statistical parsimony network of *Notiophilus biguttatus* (Fabricius, 1779) and *Notiophilus quadripunctatus* Dejean, 1828. Parameters used included default settings for connection steps, gaps being treated as fifth state. Each line represents a single mutational change, whereas small black dots indicate missing haplotypes. The numbers of analysed specimens (*n*) are listed and the diameter of the circles is proportional to the number of specimens for each haplotypes (see given open half circles with numbers). Scale bars = 1 mm. Source of photos: http://www.eurocarabidae.de/ (access date: 2019–01–15).
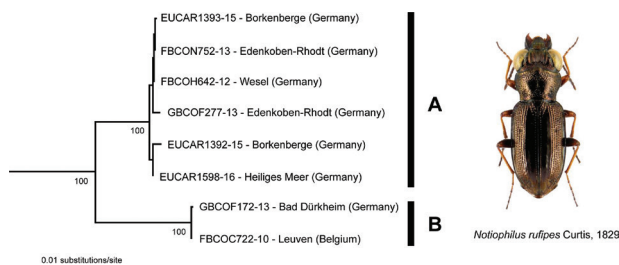
Figure 4. Subtree of the neighbour joining topology, based on Kimura 2-parameter distances of all analysed specimens of *Notiophilus rufipes* Curtis, 1829. Branches with specimen ID-number from BOLD, species names and sample localities. Numbers next to internal nodes are non-parametric bootstrap values (in %). Source of photo: http://www.eurocarabidae.de/ (access date: 2019–01–15).

Discussion

For many decades, ground beetles have been used regularly as indicators of biodiversity and habitat quality (e.g. Goulet 2003, Koivula 2011, Kotze et al. 2011, Li et al. 2017). Consequently, their correct identification rep-

resents a pivotal component for ecological studies and conservation planning. Our species delineation analysis demonstrated that most (*n* = 7, 87.5%) of the analysed species of *Notiophilus* from Germany and Central Europe can be successfully identified by using DNA barcode sequence data and the BIN approach. This result correlates with previous barcoding studies of ground beetles (Raupach et al. 2010, Raupach et al. 2011, Pentinsaari et al. 2014, Hendrich et al. 2015, Raupach et al. 2018). Nevertheless, our analysis revealed low interspecific distances, as well as high intraspecific variability that are worthy of discussion.

Low interspecific distances were found for *N. biguttatus* and *N. quadripunctatus* (0.62%) (Fig. 3). Based on their very similar morphology, a close relationship has been previously hypothesised (e.g. Hemmann and Trautner 2002). Both species can appear sympatric. However, only comprehensive analysis of i) more specimens sampled from various localities, ii) other faster evolving, in particular nuclear markers as microsatellites or RAD-Seqs, and iii) comprehensive morphological and morphometric studies will help to clarify if two closely related but distinct species exist or hybridisation still takes place.

In contrast to this, maximum intraspecific pairwise distances with values between 1.5 and 3.6% were found between two distinct monophyletic lineages of *N. rufipes* (Fig. 4). The collection sites of both lineages A (*n* = 6) and B (*n* = 2) revealed no specific geographical pattern (Fig. 4). We also found no differences in their male genitalic characters. Based on the low number of studied specimens and the mitochondrial marker used, we are currently unable to identify factors that generate the observed variability. Examples of such factors may include: i) phylogeographic events as reported for other carabids (e.g. Zhang et al. 2006, Faille et al. 2015, Weng et al. 2016), ii) the presence of the maternally inherited endosymbionts such as *Wolbachia* (e.g. Roehrdanz and Levitan 2007, Duron et al. 2008, Werren et al. 2008, Gerth et al. 2011), or iii) the existence of cryptic species (e.g. Faille et al. 2013, Liebherr 2015, Sproul and Maddison 2017). Additional specimens from different locations have to be carefully analysed using morphological and molecular data to answer these results.

Despite the fact that only few nodes had high support values, the phylogenetic analysis revealed some important results: i) *N. aeneus* represents the sister taxon to all other analysed *N.* species, ii) all other taxa are part of two clades: one clade includes *N. biguttatus* and *N. quadripunctatus* with maximum support (100%/100%); all other species are found in a second clade with medium support (87.4%/85%), iii) high nodal support is shown for a clade with the closely related species of *N. directus*, *N. semistriatus*, *N. simulator* and *N. sylvaticus* and iv) high nodal support is revealed for clade with *N. germinyi*, *N. rufipes* and *N. palustris* (Fig. 5). The close relationship of *N. directus*, *N. semistriatus*, *N. simulator* and *N. sylvaticus* and the low distance values between these species (1.8 to 6.4%) give evidence for a possible

Figure 5. Maximum likelihood phylogeny inferred in IQ-TREE, based on the CO1 barcode fragment for the genus *Notiophilus*. The model of nucleotide substitution used was selected with Modelfinder as part of the IQ-TREE work package. The tree was rooted with five *Nebria* species as outgroup. Nodal support was calculated with SH-aLRT (above) and UFBoot (below) values. Black dots indicate very robust nodes with very high values (SH-aLRT ≥ 90%, UFBoot ≥ 95%), grey dots indicate moderately robust nodes (SH-aLRT ≥ 80%, UFBoot ≥ 80%) and white dots indicate weak nodes (SH-aLRT < 80%, UFBoot < 80%) (see Material and Methods for details). Continent silhouettes indicate the biogeographic distribution of the analysed taxa (from left to right: Africa, Europe, Asia and North America).

radiation of these four species in North America (Fig. 5). If Asia represents the real hypothetical centre of origin of *Notiophilus* (Barševskis 2007), North America has been colonised at least two times. Interestingly, both species that were documented for Africa, are closely related. The low support values of most nodes, however, do not allow additional suggestions concerning the colonisation patterns of other regions by this genus.

Conclusions

The assessment of biodiversity using molecular tools represents an essential aspect of modern biological sciences. In this context, our dataset represents another step in building a comprehensive DNA barcoding library for carabids in Germany and Central Europe. Furthermore, a first phylogenetic analysis of this genus is presented. Although the present dataset included sequences of only 15 of the 57 known species of *Notiophilus* and, in particular, endemic species from Central Asia are missing, our analysis reveals some important insights into the phylogeny of this genus, including a well-supported clade of *N. directus*, *N. semistriatus*, *N. simulator* and *N. sylvaticus* that gives some evidence for a possible radiation of these species in North America, as well as a close relationship of *N. germinyi*, *N. palustris* and *N. rufipes*.

Acknowledgements

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Contribution to the knowledge of male and female eremochaetid flies in the late Cretaceous amber of Burma (Diptera, Brachycera, Eremochaetidae)

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Abstract

A new and a previously known species of the genus *Zhenia* Q. Zhang, 2016 (Eremochaetidae) are illustrated and described based on two males and a female in amber: *Zhenia burmensis* **sp. nov.** and *Z. xiai* Q. Zhang, 2016. The male *Z. xiai* is the first male of this species recorded. The relationships of Archisargoidea (including Eremochaetidae, *Zhenia*) are reassessed based on male genitalia. The superfamily is more likely related to the Stratiomyomorpha than to the Muscomorpha (including Nemestrinoidea). The components and structures of the ovipositor are re-illustrated. The results of our comparative study demonstrate that the ovipositor of *Zhenia* is similar in shape and detail to that of *Rhagoletis pomonella* (Walsh, 1867) (Tephritidae). This study concludes that the ovipositor of *Zhenia* is most likely formed from abdominal eighth and ninth segments instead of the cerci, as a previous study found.

Introduction

The Eremochaetidae is an important family of primitive, extinct flies of the lower Brachycera (Diptera) which ranged from the Late Jurassic through to the earliest Late Cretaceous (Oxfordian-Cenomanian) in Laurasia. The family includes 17 species subdivided into nine genera within two subfamilies (Ussatchov 1968; Kovalev 1986, 1989; Evenhuis 1994; Ren and Guo 1995; Mostovski 1996; Ren 1998; Zhang 2014; Zhang et al. 2014; Zhang et al. 2016). *Zhenia xiai* Q. Zhang et al., 2016 is the only eremochaetid species recovered from Late Cretaceous amber. All other eremochaetid flies are fossil impressions in shales and occur from the Late Jurassic to the Early Cretaceous. Thus, *Zhenia xiai* is the first eremochaetid tridimensionally preserved fly and the youngest spe-

cies in the geological age. Recently, several specimens of male and female *Zhenia* Q. Zhang et al., 2016 were discovered from the same locality and horizon: the Upper Cretaceous of Myanmar amber in Hukawng Valley, Kachin Province, Myanmar.

The excellent preservation of these specimens allows a detailed description and review of some taxonomic characters, especially the male terminalia, which are a key source of characters used to distinguish species of *Zhenia* and, furthermore, critical to the phylogenetic placement of the Archisargoidea. A new species, *Zhenia burmensis* sp. nov., is illustrated and described based on a male and a female specimen. *Zhenia xiai* was described based on three female flies (Zhang et al. 2016). Shortly after, Grimaldi and Barden (2016) redescribed and reviewed this species on the basis of another female fly from the same locality.

They argued that the ovipositor of *Zhenia* is formed from cerci instead of abdominal eighth and ninth segments and that the Archisargoidea (including Eremochaetidae and *Zhenia*) is closely related to the Nemestrinoidea or the Muscomorpha. On the basis of an almost complete male fly, an additional description of this species is reported here, and the systematic placement of *Zhenia* (including Eremochaetidae, Archisargoidea) is reappraised based on the characters of male genitalia. It is more likely related to the Stratiomyomorpha than to the Muscomorpha (including Nemestrinoidea). Meanwhile, the components and structures of the female ovipositor are re-illustrated and re-interpreted. Through a comparative study, we believe that, like the apple maggot fly (Tephritidae), the ovipositor of *Zhenia* is formed from the abdominal eighth and ninth segments, and the cerci (if present) form the tip of the piercing aculeus.

Materials and methods

The line drawings were produced with the aid of a camera lucida, the digital photomicrographs were taken using a stereomicroscope (Zeiss Stereo Discovery V 16), and the confocal microscopic photographs of the male terminalia were taken using a confocal scanning laser microscopy (CLSM Zeiss LSM710 with 10× objectives and a laser at 488 nm).

Wing venation terminology follows Wootton and Ennos (1989) and Shcherbakov et al. (1995). The cell traditionally named the anal cell is, in fact, considered here to be the cubital cell. The material is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Taxonomy

Order Diptera Linnaeus, 1758
Suborder Brachycera Zetterstedt, 1842
Superfamily Archisargoidea Rohdendorf, 1962
Family Eremochaetidae Ussatchov, 1968
Subfamily Eremomukhinae Mostovski, 1996

Genus *Zhenia* Q. Zhang et al., 2016

Type species. *Zhenia xiai* Q. Zhang et al., 2016.

Emended diagnosis. Closely similar to *Eremomukha* Mostovski, 1996, but smaller (body <10 mm long); cell r1 narrowly open, or closed at or just before wing margin; R4+5 simple or with a very shallow fork; M1 arising distad to end of discal cell; claw vestigial or absent; pulvillus and empodium extremely developed; male genitalia with aedeagus long, subcylindrical, gonocoxite stout, gonostylus without spine, cercus short, one-segmented, positioned behind hypoproct(?); female with ovipositor of piercing type, including swollen abdominal eighth segment, elongated, tapering eighth sternite with cloacal

opening at middle of ovipositor, aculeus (fused ninth segment +cerci?) strongly sclerotized.

Remarks. Until now, the subfamily Eremomukhinae has included eight species belonging to two genera: *Eremomukha* (*Eremocreta*) *addita* Mostovski, 1996, *Eremomukha* (*Eremocreta*) *posita* Mostovski, 1996, *Eremomukha* (*Eremocreta*) *sorosi* Mostovski, 1996, *Eremomukha* (*Eremomukha*) *angusta* J. Zhang, 2014, *Eremomukha* (*Eremomukha*) *tsokutukha* Mostovski, 1996, *Eremomukha* (*Eremomukha*) *insidiosa* Mostovski, 1996, *Eremomukha* (*Eremomukha*) *tenuissima* J. Zhang, 2014, and *Zhenia xiai*. Recently, new *Zhenia* specimens have been recovered from the Late Cretaceous amber of Myanmar. Among them, one new female and two new male flies of the genus *Zhenia* were identified. Based on these new findings, an emended diagnosis of this genus is proposed. *Zhenia* demonstrates close similarities in body structure and wing venation to *Eremomukha*, an Early Cretaceous eremochaited genus from Mongolia and China, but *Zhenia* differs mainly from *Eremomukha* by the characterized M1, which arises distad to end of discal cell. In contrast, *Eremomukha* has M1 arising directly from the anterior margin of the discal cell.

Zhenia xiai Q. Zhang et al., 2016
Figures 1, 2, 3b, 8C

Diagnosis. Male flies with antennal pedicel subcylindrical; Rs deviating from R clearly distal to M fork; R2+3 meeting R1 just at C (i.e. cell r1 sessile); R4+5 simple; section C between R4+5 and M1 longer than section C between M1 and M2; M1 slightly arched upwards medially, ending behind apex of wing; M3 arched downwards medially; haltere with boot-like knob; abdominal second segment longest; basitarsus of hindleg as long as, or shorter than, tarsomeres II–V combined; genitalia with gonocoxite conical, gonostylus sickle-like, aedeagus relatively short, not reaching hind margin of gonocoxite.

Description. Male. Body and legs brown (Fig. 1A, C), covered with dense short hairs (Fig. 1D). Head large, subovate. Eyes large, holoptic, occupying almost whole head (Figs 1A, C, 2A). Antenna thin and short; scape very small, spherical; pedicel elongated, subcylindrical, slightly wider apically than basally; flagellum ovate-oblong, narrower and shorter than pedicel; arista long, slightly longer than scape, pedicel and flagellum combined (Figs 1B, 2A). Mouthparts with only boot-like labellum visible (Fig. 2A).

Thorax stout, thicker and longer than head. Scutum distinctly convex; scutellum rather small, triangular. Wing narrow and long, 3.2 times longer than wide, apex of wing round (Figs 1A, 2A). Costal vein terminating at the wing apex; vein Sc short, ending nearly at level of end of distal cell; R1 long, straight; Rs deviating from R clearly distal to M fork, section of Rs stem nearly as long as section bR4 + 5; R2 + 3 almost straight, fused with R1 just at anterior margin of wing; cell r1 narrow

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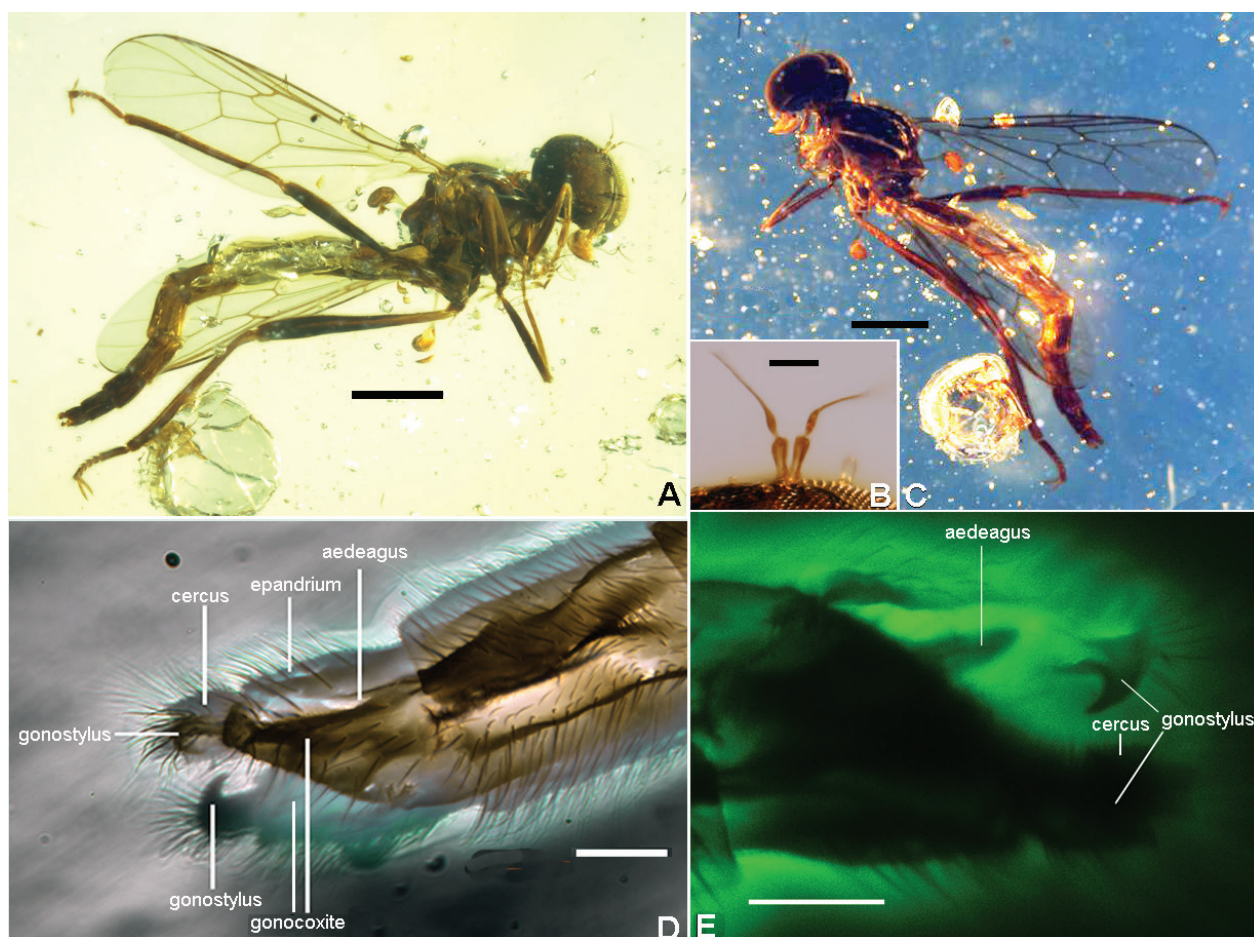
Figure 1. *Zhenia xiai* Q. Zhang et al., 2016. Photomicrographs (**A–C**) and Confocal microscopic photographs (**D, E**), topotype NIGP170824, male **A** habitus (right lateral view) **B** habitus (left lateral view) **C** antennae **D** male genitalia (right lateral view) **E** male genitalia (left lateral view). Scale bars: 1 mm (**A, C**); 0.1 mm (**B, D, E**).

and long, fusiform, with no petiole; section of R4 + 5 + M1 separating from anterior margin of cell d nearly at its end, forked distinctly distad to level of the apex of the discal cell, about 10 times longer than section bM2; M1 slightly arched medially, terminating clearly behind wing apex. M2 more or less arched downwards apically; M3 clearly arched downwards apically, M4 absent; cell d hexagonal, nearly 2.7 times longer than wide; m-m long, straight; bM3 short; m-cu long, nearly three times longer than bM3; cell br obviously longer than, but nearly as wide as, cell bm; cell cu (traditionally anal cell) closed with short petiole (Figs 1A, 2A). Haltere thin and long, knob relatively large, boot-like (Fig. 2A). Forelegs and midlegs relatively thin and short but with pulvillus and empodium extremely elongated, which are very closely similar in length and in shape to those of hindleg; hindlegs relatively stout and long; coxa stout, obtuse-triangular; femur clavate, nearly as long as half of abdominal length; tibia subcylindrical, slightly shorter and obviously narrower than femur; tarsus very short, nearly one-third of length of tibia, basitarsus shorter than, or nearly as long as, tarsomeres II–V combined, ratio of tarsomeres 1.0:0.24:0.21:0.33:0.55, empodium

similar in length and shape to pulvillus, narrowly phylliform in lateral view, less than one-half of length of tarsus (Fig. 2A, C).

Abdomen thin and long, subcylindrical, nearly two times longer than head and thorax combined; eight segments visible; first very short, second longest, remainder gradually reduced in length terminally; ratio of segments 1.0:2.2:2.1:1.5:1.5:1.0:0.9:0.8; ninth segment forming male genitalia, nearly as long as eighth (Figs 1A, B, 2A). Genitalia covered with thin and long hairs; gonocoxite stout and long, subconical, basally thicker than apically; gonostylus with dense hairs on outer margin but glabrous on inner margin, relatively small, sickle-like, sharp apically, strongly curved inwards; aedeagus (phallus) relatively short, not reaching hind margin of gonocoxite, simple (not forked apically), rounded apically (Figs 1D, E, 2B).

Dimensions. Topotype NIGP170824, body length ca 7.8 mm; head length 1.0 mm; thorax length 1.5 mm; wing length 4.4 mm, width 1.4 mm; hindleg length 5.9 mm (coxa 0.5 mm, trochanter 0.2 mm, femur 2.3 mm, tibia 2.1 mm, tarsus 0.8 mm); abdomen length 5.3 mm.

Distribution. Myanmar amber, Late Cretaceous (Cenomanian); Hukawng Valley, Kachin Province, Myanmar.
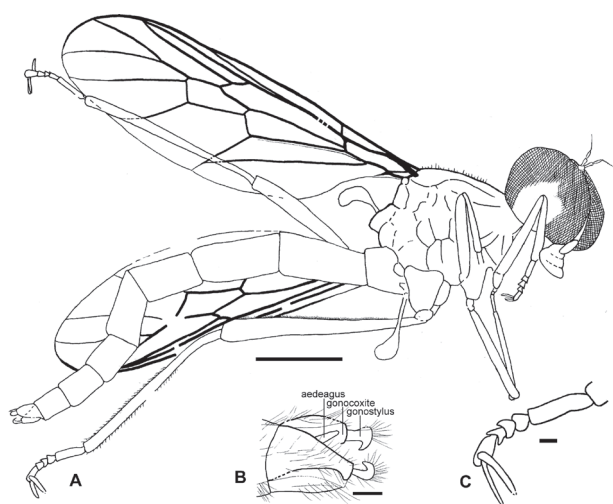
Figure 2. *Zhenia xiai* Q. Zhang et al., 2016. Line drawings, topotype NIGP170824 **A** habitus (right lateral view) **B** male genitalia (left lateral view) **C** tarsus of hindleg. Scale bar 1 mm (**A**); 0.1 mm (**B, C**).

Figure 3. Difference and similarity between two sets of ovipositors. Photomicrographs (lateral view), **A** *Zhenia xiai* Q. Zhang et al., 2016 (after Grimaldi and Barden 2016, AMNH BuSD-2) **B** *Zhenia xiai* Q. Zhang et al., 2016 (after Q. Zhang et al. 2016, holotype BA02-15001). Scale bars: 0.1 mm (**A, B**).

Remarks. *Zhenia xiai* was erected based on three female flies from Myanmar amber: the holotype BA02-15001 and two paratypes NIGP163430 and BA02-15003 (Q. Zhang et al. 2016). The new male specimen from the 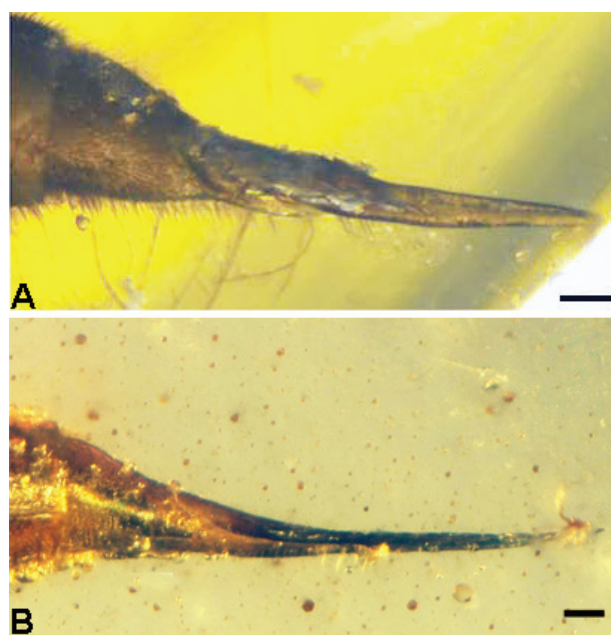same locality demonstrates many close similarities in body structures and wing venation to those of *Z. xiai* and is assigned to this species. The following characters are shared by the male and females: antennal pedicel elongate, subcylindrical, wider apically than basally; the second abdominal segment longest; basitarsus of hindleg shorter than (or nearly as long as) tarsomeres II–V combined; in wing venation, Rs deviating from R clearly distal to M fork; section C between R4+5 and M1 longer than section C between M1 and M2; M1 arched upwards medially, ending behind apex of wing; M3 arched downwards medially (vs *Z. burmensis* sp. nov. described below). The male differs from those females in that: cell r1 is sessile (vs with short petiole in female); and R4+5 is simple (vs forked apically in female). These differences might be sexually dimorphic or individual variation.

Grimaldi and Barden (2016) described another female fly (AMNH BuSD-2) from the same locality that was assigned to *Z. xiai*. Indeed, it demonstrates close similarities in body structures and wing venation to those of *Z. xiai* but differs from the holotype of (BA02-15001) and the paratype (NIGP163430) of this species in that: antennal pedicel is conical, basally clearly thicker than apically (vs subcylindrical, apically thicker than basally); body is covered with dark brown markings dorsally on thorax and on abdominal tergites and sternites (vs no dark brown markings dorsally on thorax and on abdominal tergites and sternites except for the paratype BA02-15003); and the abdominal second to sixth segments are almost equal in length, with the third longest (vs the second longest); ovipositor is fringed with dense hairs ventrally (vs almost glabrous), and relatively shorter and stouter than that of the holotype (Fig. 3). Grimaldi and Barden's (2016) specimen is very closely similar to the female *Z. burmensis* sp. nov. (Figs 6E, 7C; see descriptions below). These differences indicate that this fly (AMNH BuSD-2) may not be a member of *Z. xiai* and is most likely related to *Z. burmensis* sp. nov. Owing to the same markings on abdominal tergites and sternites, and the almost equal abdominal second to sixth segments in length (Q. Zhang et al. 2016: 3, fig. 1C), the paratype (BA02-15003) may be closely related to the specimen AMNH BuSD-2 rather than to *Z. xiai* (BA02-15001 and NIGP163430). Unfortunately, it is a poorly preserved specimen, and many taxonomic characteristics are indistinct. Therefore, the placement of the female specimens BA02-15003 and AMNH BuSD-2 is debatable.

Zhenia burmensis sp. nov.

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Figures 4–7, 8D

Diagnosis. Rs deviating from R just at level of M fork; R2+3 meeting R1 before C (i.e. cell r1 closed with short petiole); R4+5 simple; section C between R4+5 and M1 slightly shorter than section C between M1 and M2; M1 straight, ending at apex of wing; M3 straight; haltere with globose knob; abdominal fourth segment longest; basitarsus of hindleg longer than tarsomeres II–V combined; male genitalia with subovate gonocoxite, straight and clavate gonostylus, aedeagus long, obviously reaching beyond hind margin of gonocoxite; female ovipositor relatively short and stout.
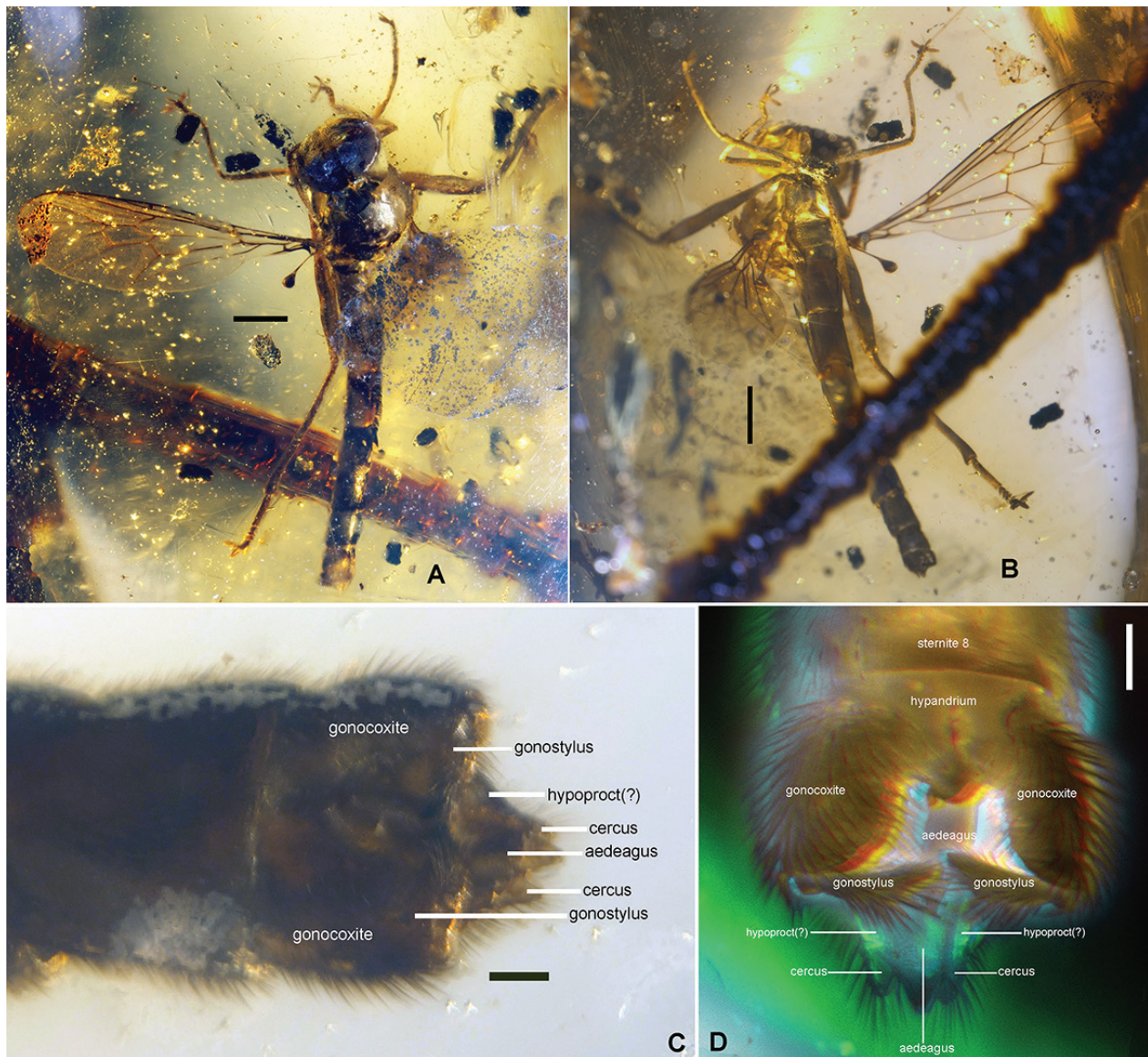
Figure 4. *Zhenia burmensis* sp. nov. Photomicrographs (**A–C**) and Confocal microscopic photograph (D), holotype NIGP170825, male **A** habitus (dorsal view) **B** habitus (ventral view) **C** male genitalia (ventral view) **D** male genitalia (ventral view). Scale bars: 1 mm (**A, B**); 0.1 mm (**C, D**).

Description. Male. Body and legs brown (Fig. 4A, B), covered with dense short hairs (Fig. 4C, D). Head large, subovate. Eyes large, holoptic, occupying almost the entire head (Figs 4A, 5A).

Thorax relatively small, nearly globose, almost as wide as but slightly longer than head. Scutellum rather shorter but relatively wide, over three times wider than long (Figs 4A, 5A). Wing narrow and long, 3.3 times longer than wide, apex of wing round (Fig. 5A). Costal vein terminating at the wing apex; vein Sc short, ending nearly at level of middle of distal cell; Rs deviating from R just at level of M fork, section of Rs stem nearly as long as section bR4 + 5; R2 + 3 slightly arched apically, running slightly convergent to R1, fused with R1 just before anterior margin of wing; cell r1 narrow and long, fusiform, with short petiole; section of R4 + 5 + M1 separating from anterior margin of cell d nearly at its end, forked distinctly distal to the level of the apex of the discal cell, about 1.5 times longer than section bM2; M1 straight, terminating nearly at wing apex. M2 and M3 almost straight; M4 absent; cell d hexagonal, nearly 2.7 times longer than wide; m-m long, straight; bM3 short; m-cu long, twice longer than bM3; cell br obviously longer than, but nearly as wide as, cell bm; cell cu (traditionally anal cell) closed with short petiole (Fig. 5A). Haltere thin and long, club relatively small, subglobose (Fig. 5A). Forelegs and midlegs relatively thin and short but with pulvillus and empodium extremely elongate, very similar in length and in shape to the hindleg; hindlegs relatively stout and long; femur clavate, less than half of abdominal length; tibia subcylindrical, longer and obviously narrower than femur; tarsus very short, less than one-half of length of
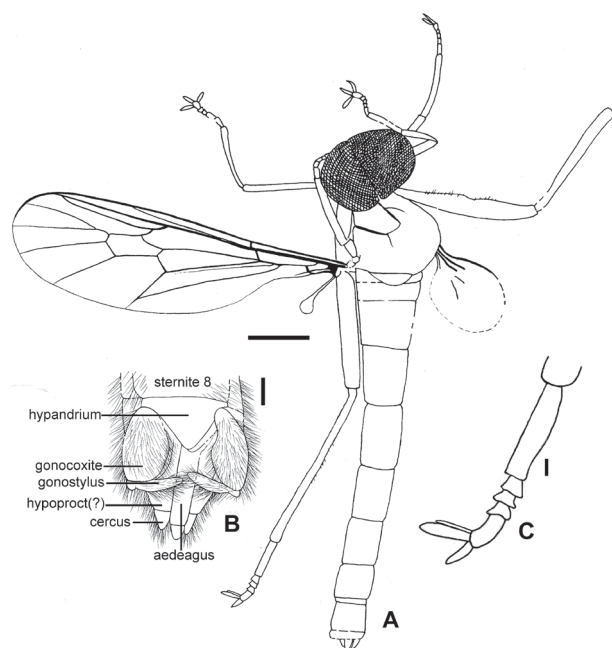
Figure 5. *Zhenia burmensis* sp. nov. Line drawings, holotype NIGP170825, **A** habitus (dorsal view) **B** male genitalia (ventral view) **C** tarsus of hindleg. Scale bar: 1mm (**A**); 0.1 mm (**B, C**).

tibia, basitarsus longer than tarsomeres II–V combined, ratio of tarsomeres 1.0:0.16:0.11:0.11:0.36, empodium longer than pulvillus, narrowly phylliform in lateral view, less than one-third of length of tarsus (Fig. 5C).

Abdomen thin and long, subcylindrical, nearly 2.4 times longer than head and thorax combined; eight segments visible; first very short, fourth longest, ratio of segments 1.0:2.9:3.6:4.0:3.1:2.9:2.1:1.7; ninth segment forming male genitalia, clearly shorter than eighth (Figs 4A, B, 5A). Genitalia covered with thin and long hairs; hypandrium large, triangular, 1.7 times wider than long, separated from epandrium, and articulated horizontally with gonocoxite; gonocoxite stout and long, subovate, distinctly narrowed basally; gonostylus relatively small, straight, clavate, slightly thickened medially, rounded apically, and articulated horizontally on gonocoxite; aedeagus (phallus) stout and long, cylindrical, distinctly extending beyond hind margin of gonocoxite, simple (not forked apically), rounded apically; cercus one-segmented, short and wide, subtriangular, slightly longer than wide, not reaching apex of aedeagus (Figs 4D, 5B).

Female. Body dark brown, legs brown (Fig. 6A). Head large, subovate; antennal first flagellomere conical, basally distinctly wider than apically; arista rather thin and long. Eyes large, occupying almost whole head in lateral view (Figs 6B, 7A, B).

Thorax relatively large, nearly globose, clearly longer than head. Scutellum rather shorter (Figs 6A, 7A). Wing narrow and long, 2.8 times longer than wide, apex of wing round (Fig. 7A). Costal vein terminating at the wing apex; vein Sc short, ending nearly at level of middle
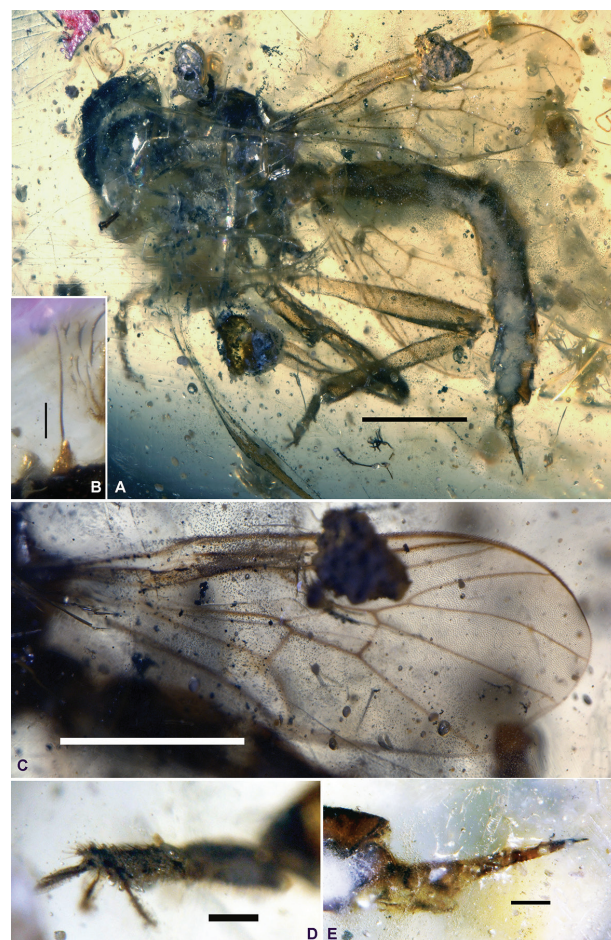

Figure 6. *Zhenia burmensis* sp. nov. Photomicrographs, paratype NIGP170826, female **A** habitus (lateral view) **B** antenna **C** wing **D** tarsus of hindleg **E** ovipositor (lateral view). Scale bars: 1mm (**A, C**); 0.1 mm (**B, D, E**).

of distal cell; Rs deviating from R just at level of M fork, section of Rs stem nearly as long as section bR4 + 5; R2 + 3 nearly straight, running slightly convergent to R1, but not coalesced with R1; cell r1 narrow and long, narrowly open apically; section of R4 + 5 + M1 separating from anterior margin of cell d nearly at its end, forked distinctly distad to level of d's end, about twice longer than section bM2; M1 smoothly arched, terminating nearly at wing apex. M2 and M3 almost straight; M4 absent; cell d hexagonal, nearly twice longer than wide; m-m long, straight; bM3 short; m-cu long, about three times longer than bM3; cell br obviously longer and wider than cell bm; cell cu (traditionally anal cell) closed nearly at hind margin (Fig. 7A). Hindlegs relatively stout and long; femur clavate, about half of abdominal length; tibia subcylindrical, slightly shorter and narrower than femur; tarsus very short, about one-third of length of tibia, basitarsus slightly longer than tarsomeres II–V combined, empodium and pulvillus narrowly phylliform, about one-third of length of tarsus (Figs 6D, 7A).

Abdomen thin and long, subcylindrical, nearly 1.8 times longer than head and thorax combined; eight seg-

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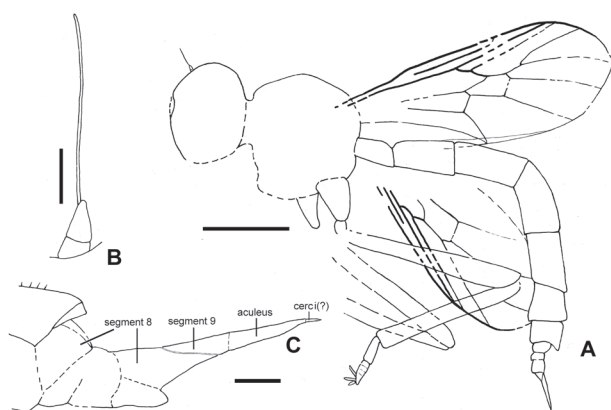
Figure 7. *Zhenia burmensis* sp. nov. Line drawings, paratype NIGP170826, female **A** habitus (lateral view) **B** antenna **C** ovipositor (lateral view). Scale bar: 1mm (**A**); 0.1 mm (**B, C**).

ments visible; first very short, third, and fourth longest, ratio of segments 1.0:1.6:1.8:1.8:1,5:1.0:0.5:0.9; ovipositor formed from modified eighth and ninth segments: eighth elongated, separated in two or three sections, its sternite only moderately (not extremely) elongate, ninth forming sclerotised aculeus, cerci (if present) located at apex of aculeus (Figs 6E, 7C, 8D).

**Dimensions.** Holotype (male) NIGP170825, body length ca 8.6 mm; head length 1.2 mm; thorax length 1.5 mm; wing length 5.5 mm, width 1.7 mm; hindleg length ca 6.8 mm (femur 2.4 mm, tibia 2.9 mm, tarsus 1.5 mm); abdomen length 6.3 mm. Paratype (female) NIGP170826, body length approximately 7.1 mm; head length 0.8 mm; thorax length 1.5 mm; wing length 3.2 mm, width 1.3 mm; hindleg length ca 4.4 mm (femur 2.0 mm, tibia 1.8 mm, tarsus 0.6 mm); abdomen length (excluding ovipositor) 4.0 mm, ovipositor length 0.8 mm.

Distribution. Myanmar amber, Late Cretaceous (Cenomanian); Hukawng Valley, Kachin Province, Myanmar.

Remarks. Based on the following characters, male *Z. burmensis* sp. nov. can be distinguished from male *Z, xiai*: knob of haltere is globose; third and fourth abdominal segments are longest; basitarsus of hindleg is longer than combined tarsomeres II–V; genitalia has ovate gonocoxite, straight and clavate gonostylus, and longer aedeagus, which obviously reaches beyond the hind margin of the gonocoxite.

On the other hand, the wing venation, ratio of abdominal segments and ratio of tarsi of hindleg of this female specimen resemble closely that of male *Z. burmensis* sp. nov., and, thus, it can be provisionally regarded as a member of *Z. burmensis* sp. nov. Female *Z. burmensis* sp. nov. can also be separated from female *Z. xiai* in that: the first flagellomere of the antenna becomes conical instead of subcylindrical; cell r1 runs open apically, R4+5 is simple (not forked apically); tarsus of hindleg is relatively short and stout; and ovipositor is relatively short and stout.

Nevertheless, owing to the clearly smaller size than that of male *Z. burmensis* sp. nov., the female described here may represent another, as yet, undescribed species.
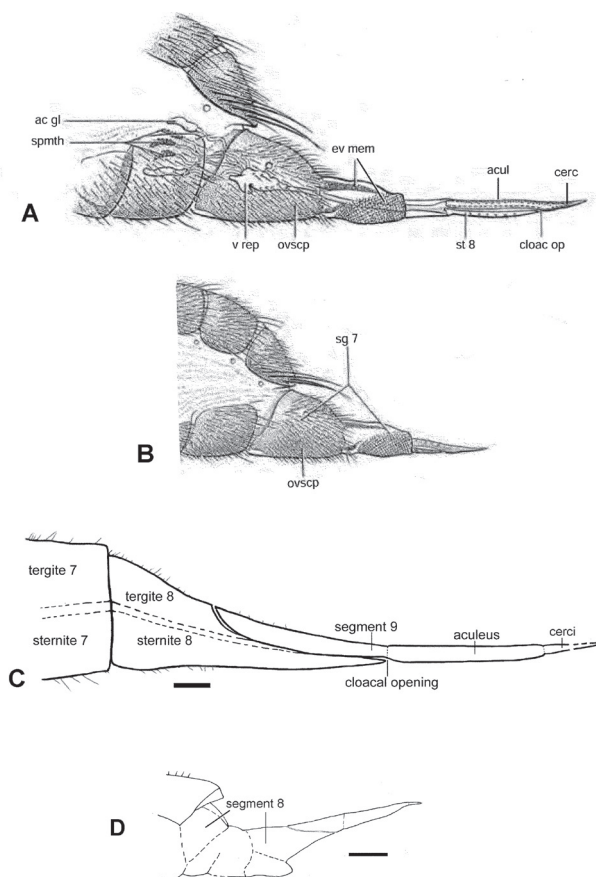
Figure 8. Difference and similarity between four sets of ovipositors. Line drawings (lateral view), **A** *Rhagoletis pomonella* (Walsh, 1867) (ovipositor extended, after Cumming and Wood 2009) **B** *Rhagoletis pomonella* (Walsh, 1867) (ovipositor not extended, after Norrbom 2010) **C** *Zhenia xiai* Q. Zhang et al., 2016 **D** *Zhenia burmensis* sp. nov. Scale bars: 1mm (**C, D**). **ac gl** – accessory gland; **acul** – aculeus; **cerc** – cercus; **cloac op** – cloacal opening; **ev mem** – eversible membrane; **ovscp** – oviscape; **sg** – segment; **spmth** – spermatheca; **st** – sternite; **tg** – tergite; **v rep** – ventral receptacle.

Discussion

Male terminalia in Diptera demonstrate the most extreme diversity and greatest variability in structure. This is especially significant when comparing the lower Diptera to cyclorrhaphans. In addition, male terminalia are a key morphological source of characters used to distinguish species in the vast majority of dipteran families (Sinclair et al. 2013). To date, however, only seven specimens of male eremochaetid flies have been discovered. All are impression fossils and were found in shales from the Callovian-Oxfordian Karabastau Formation in Kazakhstan (Ussatchov 1968), the Lower Cretaceous Gurvan-Eren Formation in Mongolia (Kovalev 1986), and the Lower Cretaceous Yixian Formation in China (Ren and Guo 1995; Zhang et al. 2014; Zhang 2014). Among them, the characteristics of the male genitalia have been described only in three species: *Eremomukha* (*Eremomukha*) an-

gusta, *E.* (*E.*) *tenuissima* and *Lepteremochaetus elegans* (Zhang 2014).

Here we describe male eremochaetid flies from amber for the first time. The male genitalia of *Zhenia* reveal that this genus is very similar to the Early Cretaceous genus *Eremomukha* (*Zhenia xiai* and *Z. burmensis* sp. nov. vs *Eremomukha* (*Eremomukha*) *angusta* and *E.* (*E.*) *tenuissima*). They share the extremely swollen gonocoxites, the relatively thin and short gonostyli, and the elongate, subcylindrical aedeagi that are indistinguishably fused to the parameral sheath. Additionally, they are also closely similar in their body structures and wing venation: very large head, small thorax, very thin and long abdomen, the long and straight R2+3, the narrow and elongated cell r1 which is closed with very short petiole or just at C, and the characterized R4+5, which is simple, or forked very shallowly. All these morphological similarities indicate that *Zhenia* is closely related to *Eremomukha*.

The placement of Archisargoidea (including Eremochaetidae) is currently disputed. It is assigned either within Stratiomyomorpha (Oberprieler and Yeates 2012) or (more probably) as an extinct sister group to the Muscomorpha (Grimaldi and Barden 2016). Fortunately, some male genitalic structures of *Zhenia* can be distinguished using confocal scanning laser microscopy: the aedeagus completely encircled by and indistinguishably fused with the parameral sheath reveals that, like the Archisargidae (Zhang 2017), the Eremochaetidae (including *Zhenia*) can be placed into the Stratiomyomorpha + Muscomorpha (sensu Woodley 1989; Sinclair et al. 1993, 2013; Cumming and Wood 2009). Furthermore, its gonostyli are directed medially and articulated, moving only in a horizontal plane in opposition to each other (Figs 1D, E, 4D, 5B). This arrangement undoubtedly represents the plesiomorphic condition in Stratiomyomorpha (as well as in Xylophagomorpha and Tanbanomorpha). In contrast, the gonostyli of Muscomorpha move obliquely or in a dorsoventral direction, which is considered a synapomorphic character (Sinclair et al. 2013). Thus, on the basis of the male genitalia of *Zhenia*, the Archisargoidea (including Eremochaetidae) is most likely related to Stratiomyomorpha and not to Muscomorpha. These flies belong to an extinct, primitive group within the lower Brachycera and lived in the Jurassic to the Cretaceous (ca 160–100 Ma).

As for the female *Zhenia*, we contend that the ovipositor is formed from the abdominal eighth and ninth segments, "eighth segment forming base of ovipositor, with its sternite clearly longer than tergite" (Zhang et al. 2016: 4). However, Grimaldi and Barden (2016: 1) argued that the ovipositor is "formed from modified cerci (not tergites 8 and 9 as originally reported)", albeit with the disclaimer (Grimaldi and Barden 2016: 18) that "the base of the oviscapt is bulbous and the sharp tips of the cerci (aculeus) point posteriad, which is seen in most archisargoid females whose terminalia are preserved (including *Zhenia*)". Due to having different explanations, we consider a further discussion of the ovipositor of *Zhenia* is required. The female terminalia include the genital and anal segments of the abdomen posterior to the preabdo-

men that are modified for oviposition and copulation. The segments involved vary depending on the group, but generally consist of the eighth to tenth segments (including proctiger) in lower Brachycera (i.e. orthorrhaphous Brachycera) (Cumming and Wood 2009). The eighth segment of *Zhenia* is beyond doubt the base of the ovipositor (Zhang et al. 2016: 4; Grimaldi and Barden 2016: 18). The base of aculeus of *Zhenia* arises directly from the hind margin of the eighth segment (Figs 3, 8C, D). This state is inconsistent with the conjecture previously proposed that the aculeus is formed from cerci (Grimaldi and Barden 2016). As a ground plan of Diptera, cerci are one of a pair of terminal appendages on either side of the anus derived from the proctiger, which is, in a strict sense, the anus-bearing region posterior to, or arising from, the tenth segment, but generally used for all associated structures behind the ninth segment (cerci) in male dipterans and in females of at least Cyclorrhapha (Cumming and Wood 2009). Thus, it is a reasonable deduction that the aculeus arises from the eighth segment and is formed from the ninth segment.

An aculeate ovipositor has evolved a number of times in Diptera. It occurs in various groups, including a few Tipulidae, Phoridae, Pipunculidae, some Conopidae, Tephritoidea, Cryptochaetidae and Tachinidae (Pritchard 1983; Feener and Brown 1997; Skevington and Dang 2002; Stireman 2006; Grimaldi et al. 2011; Zhang et al. 2016; Grimaldi and Barden 2016; Zhang 2017). In various groups, the ovipositor involves different segments and structures (Cumming and Wood 2009). Compared with these groups, the ovipositor of female *Z. xiai* and *Z. burmensis* sp. nov. demonstrates close similarities in shape and detail to of the ovipositor in female *Rhagoletis pomonella* (Walsh, 1867) (Tephritidae, Tephritoidea, Cyclorrhapha), the apple maggot fly. They share some similar characters (Fig. 8): the base of ovipositor is bulbous and formed respectively from either the eighth (in the two former species) or the seventh (in the latter species) segment; the following posterior one (the ninth and the eighth, respectively) forms the piercing part of the ovipositor, the aculeus; the cloacal opening is well developed, and positioned at the tip of the eighth sternite (in the two former species), or between the divided sclerites of the eighth sternite (in the latter species); and the cerci (if present) are, as the terminal part of aculeus, located at the tip of the ovipositor. It should be noted that in Tephritidae the aculeus consists of an elongate tergite and sternite and is formed from the eighth segment (Cumming and Wood 2009; Norrbom 2010). For this reason, we propose that the aculeus of *Zhenia* is formed most likely from the ninth segment (or ninth+tenth segments) instead of cerci as proposed by Grimaldi and Barden (2016). In addition, there is no indication of extinct or extant brachycerans with a piercing aculeus formed from an extremely elongate cercus. But, like those of female Archisargidae (Zhang 2017), the similarities of ovipositor in shape and structures of Eremochaetidae (including *Zhenia*) and Tephritidae are considered to be the result of convergent evolution, and do not represent evidence of close relationships.

Prior to this study, the genus *Zhenia* was regarded as including endoparasitoid flies having larvae that feeding on other arthropods (Zhang et al. 2016), and this conjecture was also accepted by other authors (Grimaldi and Barden 2016). However, given the characterized structures of the pretarsi (unsclerotized and phylloid pulvilli and empodia, as well as vestigial claws) and the location of the cloacal opening (distant from the tip of ovipositor), it is most likely that, like various Tephritoidea, *Zhenia* oviposits by piercing plants (e.g. fruits or rotten wood) instead of arthropod hosts. In particular, the pretarsi can only adhere to the surface of inactive hosts and cannot hold onto active hosts, such as arthropods.

Acknowledgements

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On Bulgarian sawflies, including a new species of *Empria* (Hymenoptera, Symphyta)

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http://zoobank.org/6A252079-0880-45A2-A920-3C0DFEAC79C5

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Abstract

Thirty-nine species of sawfly (Symphyta) are recorded for the first time in Bulgaria. Most of these were collected during early spring of 2018, in the south-east of the country (Burgas and Varna Provinces). *Empria aridicola* Macek & Prous, **sp. nov.** is described as new to science from specimens collected in several central, east and south European countries. Lectotypes are designated for *Poecilosoma parvula* Konow, 1892, *Empria pravei* Dovnar-Zapolskij, 1925 and *E. pseudoklugi* Dovnar-Zapolskij, 1929. *Empria pravei* and *Sciapteryx byzantina* Benson, 1968 are at present only known in Europe from the coastal zone of the Black Sea. The new Bulgarian records of *Hoplocampa cantoti* Chevin, 1986 and *Neomessa steuslofii* (Konow, 1892) represent large extensions in their recorded ranges, previously comprising respectively only northern France, and north-eastern Germany. Possible host plant associations are noted for several species, based on observations of adults.

Introduction

The first modern inventory of sawflies (Symphyta) recorded in Bulgaria was by Hellén (1967) who listed 107 species. After the publication of several subsequent works on the Bulgarian sawfly fauna, most significantly those by Vassilev (1978), Meitzner and Taeger (1982), and Taeger (1987), the number of recorded species rose to 346 definitely present, and two in need of confirmation, as collated in a survey of the European sawfly fauna (Taeger et al. 2006). However, published records of some species already recorded in Bulgaria were overlooked during the compilation of the latter work (Georgiev 1990; Stoyanov and Ljobomirov 2000; Georgiev et al. 2002, 2004), and

a small number of other species have been added since 2006 (Georgiev 2006; Blank et al. 2013; Doychev 2015). Nevertheless, the total number of species known in Bulgaria remains rather low considering the high diversity of habitats and climatic zones in the country. By comparison, Taeger et al. (2006) listed 469 species from Hungary and 486 from Romania.

In an effort to fill part of this knowledge gap, MP and AL collected in Bulgaria from 31 March to 14 April 2018. The dates were chosen with the intention of finding phenologically early species, sampling of which we suspected to have been previously relatively neglected in the country. We collected mainly in south-eastern Bulgaria, generally not far from the Black Sea, in the Burgas

and Varna provinces, except for some localities further inland, in Pazardzhik and Sliven provinces, which were visited during the journeys respectively from and to Sofia airport. The localities in Burgas Province, therefore, lie within the rather ill-defined Euxinian biogeographic province, which extends along the western Anatolian Black Sea coast, and northwards through the Thracian coastal areas of Turkey into Bulgaria north to about Ropotamo or Burgas (Browicz 1989). Although many organisms are considered to occur in Europe only within this zone (Fet and Popov 2007), no special effort has hitherto been made, as far as we are aware, to investigate its sawfly fauna. As a matter of convenience, records of two additional noteworthy species are included; these records are from other Bulgarian provinces and were based on specimens examined in the private collection of Matti Viitasaari (Helsinki) and the Swedish Museum of Natural History (Stockholm). We used the results of DNA sequencing to answer questions on the taxonomy and phylogeny of several rarely collected taxa.

Material and methods

Collections were made mainly by sweeping, using hand nets with handles extendable to about 2 m to reach into shrubs and the lower branches of trees. Unless otherwise stated, all specimens referred to are in the collection of the Senckenberg Deutsches Entomologisches Institut (Müncheberg) and were collected and determined by A. Liston and M. Prous. Accession numbers (DEI-GISHym[and five numerals]) are given for some vouchers which are figured, or for which genetic sequences were obtained and / or genitalia examination undertaken [with database-based images].

The newly obtained DNA sequences were sequenced as described previously (Prous 2012; Prous et al. 2017, 2019). Additional primers used for sequencing that are not mentioned in Prous (2012) and Prous et al. (2017, 2019) were as follows:

NaK_1250Fv2 ATGTGGTTYGAYAAYCARATHATI-
             GA
POL2_467F   ATHTGYGARGGNGGNGAYGARAT-
             GGA
POL2_1732R   GARAADATYTGYTTNCCNGTCCA
POL2_2569R   TGNACCATNACNGAYTCCATAG-
             CYTTDAT.

For most specimens, one mitochondrial and two nuclear genes were sequenced. The mitochondrial gene used is complete (1536 bp) or partial (1078–1119 bp) cytochrome c oxidase subunit I (COI). The two nuclear markers are fragments of sodium/potassium-transporting ATPase subunit alpha (NaK, 1654 bp) and DNA dependent RNA polymerase II subunit RPB1 (POL2, 2495–2717 bp). The NaK fragment does not include any introns, but POL2 has one short intron (86–99 bp) that was excluded from phylogenetic analyses. When excluding the intron in POL2,

the alignment of all genes was straightforward because of the lack of insertions or deletions in the studied specimens (length differences were only due to the extent the gene regions were amplified and sequenced). Some of the analysed sequences were published previously by Prous et al. (2011), Prous and Heidemaa (2012), Leppänen et al. (2012), Malm and Nyman (2015), and Schmidt et al. (2017). Additionally, a few of the COI sequences were obtained from BOLD (http://www.boldsystems.org/). The newly obtained DNA sequences have been submitted to NCBI GenBank (accessions MK561857– MK561967 and MK574673–MK574674). Phylogenetic analyses using maximum likelihood (ML) were done with IQ-TREE 1.5.6 (http://www.iqtree.org/) (Nguyen et al. 2015). By default, IQ-TREE runs ModelFinder (Kalyaanamoorthy et al. 2017) to find the best-fit substitution model and then reconstructs the tree using the model selected according to Bayesian information criterion (BIC). We complemented this default option with a SH-like approximate likelihood ratio (SH-aLRT) test (Guindon et al. 2010) and ultrafast bootstrap (Hoang et al. 2018) with 1000 replicates to estimate robustness of reconstructed splits.

Additional abbreviations used in the text are:

CMH   Collection of Mikk Heidemaa, Tartu, Estonia
MNHN   Muséum National d'Histoire Naturelle, Paris, France
MT   Malaise trap
NMPC   National Museum, Praha, Czech Republic
NNR   National Nature Reserve
NR   Nature Reserve
PLA   Protected Landscape Area
SDEI   Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
TUZ   Natural History Museum, University of Tartu, Tartu, Estonia;
USNM   National Museum of Natural History, Smithsonian Institution, Washington DC, USA
ZIN   Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia
ZSM   Zoologische Staatssammlung, München [= Munich], Germany

Results and species commentaries

Taxa are listed in alphabetical order. Species for which we know of no previously published record for Bulgaria are indicated by an asterisk [*].

Argidae

Sterictiphora geminata (Gmelin, 1790)*

Material. Varna: 1♂ (DEI-GISHym88789), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 03.04.2018.

Sterictiphora geminata has a wide Palaearctic distribution (Sundukov 2017), including North Africa (Lacourt 1986).

Sterictiphora longicornis Chevin, 1982*

Material. Burgas: 1♂, Mrezhichko 1 km W, 370 m, 42.860N, 27.397E, 07.04.2018. 1♂ (DEI-GISHym88832), Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 10.04.2018. 1♀, Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Varna: 1♂ (DEI-GISHym88750), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 03.04.2018. 1♂, locality as previous, 06.04.2018. 1♀,1♂, locality as previous, 08.04.2018. 1♂, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 05.04.2018. 2♀, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 08.04.2018. 1♂, locality as previous, 09.04.2018. 1♂, locality as previous, 11.04.2018. 1♂, Goren Chiflik 1 km SW, 40 m, 43.001N, 27.621E, 13.04.2018.

Although the hosts of other *Sterictiphora* species, as far as they are known, are all woody species of Rosaceae, *S. longicornis* was recorded by Macek (2012) as having been reared from *Carpinus betulus* L. All of the specimens which we collected in Bulgaria were netted within woodland dominated by *Carpinus*.

The previously recorded range of this species is mainly in Central Europe, with a single record from "Yugoslavia" (Taeger et al. 2006). The latter record is based on 1♂, Serbia, Beograd, Avala, 500 m, 26.03.2001, leg. Z. Nikolić, det. A. Taeger (Z. Nikolić Collection, University of Belgrade).

Diprionidae

Gilpinia frutetorum (Fabricius, 1793)*

Material. Varna: 1♀ (DEI-GISHym84162), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 03.04.2018.

Gilpinia frutetorum has a very extensive range in Europe, extending through Asia Minor to eastern Siberia, and by introduction in North America (Sundukov 2017).

Pamphiliidae

Pamphilius marginatus (Serville, 1823)*

Material. Burgas: 1♂, Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 10.04.2018. 1♀ (DEI-GISHym88850), Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Varna: 1♀, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 11.04.2018.

Only recorded in central and southern Europe, including various Balkan countries (Viitasaari 2002).

Tenthredinidae

Ardis pallipes (Serville, 1823)*

Material. Burgas: 1♂, Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 04.04.2018. 1♀, 1♂ (DEI-GISHym88780), Prosenik 1 km NW, 150 m, 42.805N, 27.436E, 07.04.2018.

Varna: 1♀, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 09.04.2018. 1♂, Goren Chiflik 1 km SW, 40 m, 43.001N, 27.621E, 13.04.2018.

Ardis pallipes has an extensive Holarctic distribution (Lacourt 1999), but is found in the Nearctic probably through introduction.

Empria aridicola Macek & Prous, sp. nov.*
http://zoobank.org/70BA4DE0-9FB8-465E-B78C-387D882944BF

Description of the holotype (variability in other specimens in parentheses).

Male (Figs 9–15).

Body length. 5.2 (5.1–6.0) mm.

Colour. Black; following parts white or pale brown: (anterior and posterior margins of tegula); posterior margin of pronotum; profemur apically; anterior of protibia and posterior slightly (posterior completely black); anterior of mesotibia; (base of metatibia slightly); large triangular membranous area on tergum 1; posterior margins of terga and sterna slightly; cenchri; and paired patches on posterior margins abdominal terga 2–4 (2–3).

Head. Clypeus tridentate, with rather inconspicuous median keel, and median tooth smaller than lateral teeth; head behind eyes in dorsal view parallel to subparallel with posterior halves converging toward the occipital carina; area between frontal crests in dorsal view reaching (slightly exceeding) the level of crests; malar space 1.2 (0.9–1.3) times as long as the frontal ocellar diameter; length of postocellar area 2.2 (1.8–2.7) times as long as the lateral ocellar diameter; postocellar area 2.2 (1.9–2.4) times as wide as long; flagellum 1.9 (1.8–2.3) times as long as breadth of head.

Thorax. Propleura not meeting in front; distance between cenchri slightly longer than (as long as) cenchrus width; wings smoky (hyaline), venation brown; vein 2A+3A of fore wing complete; vein m-cu in hind wing present; subbasal tooth of tarsal claw close to apical one and distinctly shorter.

Abdomen. Subgenital plate (sternum 9) without emargination. Penis valve with distinct spine subapically at dorsal margin of valviceps; valviceps slightly longer than (as long as) valvura; ventral margin of valviceps distinctly concave; dorsal margin of valviceps with few teeth and its basal and apical part bending similarly, forming nearly semicircle; valvar strut slightly curved.

Female (Figs 1–8).

Body length. 5.9–6.9 mm.

Colour. Black; following parts white or pale brown: anterior and posterior margins of tegula, or completely black; posterior margin of pronotum; profemur apically; protibia anteriorly and sometimes slightly posteriorly; mesotibia anteriorly; metatibia slightly basally or completely black; large triangular membranous area on tergum 1; posterior margins of terga and sterna slightly; cenchri; and paired patches on posterior margins abdominal terga 2–3 or 2–4.

Figures 1–8. *Empria aridicola* female paratypes, DEI-GISHym80378 (**1–5, 7, 8**) and DEI-GISHym15134 (**6**). **1** body dorsal **2** body lateral **3** head dorsal **4** head frontal **5** head and thorax lateral **6** saw **7, 8** tarsal claws.

Head. Clypeus tridentate, with rather inconspicuous median keel, and median tooth smaller than lateral teeth; head behind eyes in dorsal view parallel to subparallel with posterior halves converging toward the occipital carina; area between frontal crests in dorsal view reaching or slightly exceeding the level of crests; malar space 1.2–1.5 times as long as the frontal ocellar diameter; length of postocellar area 2.1–2.6 times as long as the lateral ocellar diameter; postocellar area 1.8–2.4 times as wide as long; flagellum 1.6–1.9 times as long as breadth of head.

Thorax. Propleura not meeting in front; distance between cenchri as long as or slightly longer than cenchrus width; wings hyaline or smoky, venation brown; vein 2A+3A of fore wing complete; vein m-cu in hind wing present; subbasal tooth of tarsal claw close to apical one and distinctly shorter.

Abdomen. Sawsheath simple, narrow in dorsal view and distinctly longer than cerci. Lancet with 14 or 15 serrulae, more or less triangular with microdenticles at anterior margin.

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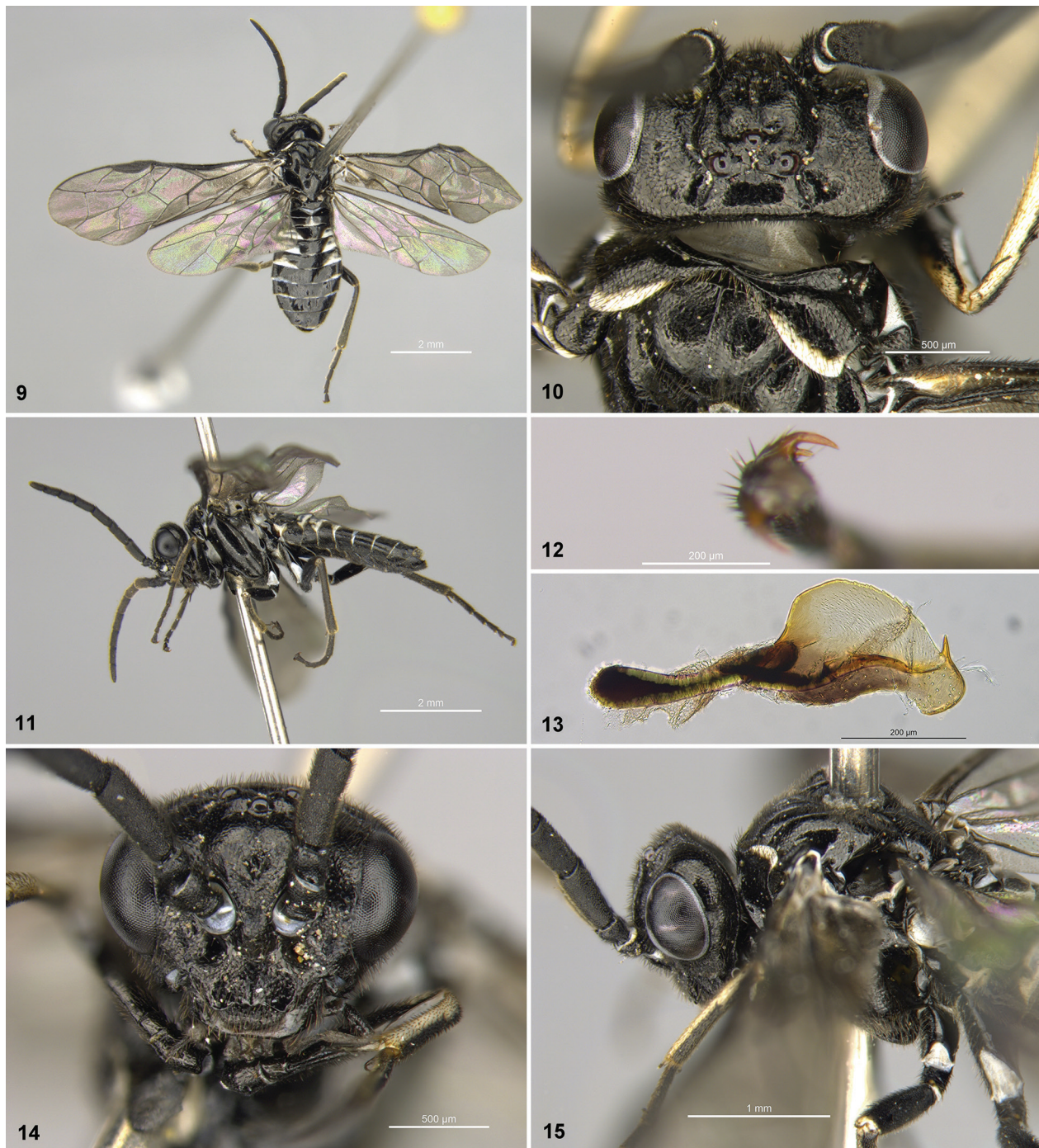
Figures 9–15. *Empria aridicola* male holotype, DEI-GISHym12004. **9** body dorsal **10** head dorsal **11** body lateral **12** tarsal claw **13** penis valve **14** head frontal **15** head and thorax lateral.

Holotype. 1♂, DEI-GISHym12004, Bulgaria, Varna, Goren Chiflik 1 km SW, 43.001N, 27.621E, 40 m, 13.4.2018, leg. A. Liston & M. Prous (SDEI).

Paratypes. BULGARIA: 3♂, Burgas, Indzhe Voivoda 3 km NE, 42.235N, 27.451E, 250 m, 12.4.2018, leg. A. Liston & M. Prous (SDEI); 2♂ (one with ID number DEI-GISHym88915), Varna, Tsonevo 5 km S, 42.982N, 27.451E, 100 m, 8.4.2018, leg. A. Liston & M. Prous (SDEI).

CZECH REPUBLIC: 2♀, 1♂, Bohemia or., Chlumec nad Cidlinou env., Báň NR, 24.04. –30.04.2001, MT, leg. B. Mocek (NMPC); 1♂, Bohemia cent., Milovice,

5.05.2006, swept, leg. J. Macek (NMPC); 1♀, Bohemia cent., Karlštejn NNR, 24.04.2011, swept, leg. J. Macek (NMPC); 1♂, Moravia mer., Bílé Karpaty PLA, Čertoryje NNR, 29.05.2005, MT, leg. J. Macek (NMPC); Moravia mer.: 3♀, Dolní Dunajovice, 10.04.2017, swept, leg. V. Kubáň (NMPC).

FRANCE: 1♀, MNHN_Empria_82, Picardie, Laigneville, 49.3N. 2.45E (MNHN); 1♂, MNHN_Empria_7, Ile-de-France, Lardy, 48.517N, 2.267E, 6.6.1913 (MNHN); 2♂, MNHN_Empria_72 and MNHN_Empria_73, Rhone-Alpes, Rochecolombe, 44.5N, 4.45E, 8.4.1951
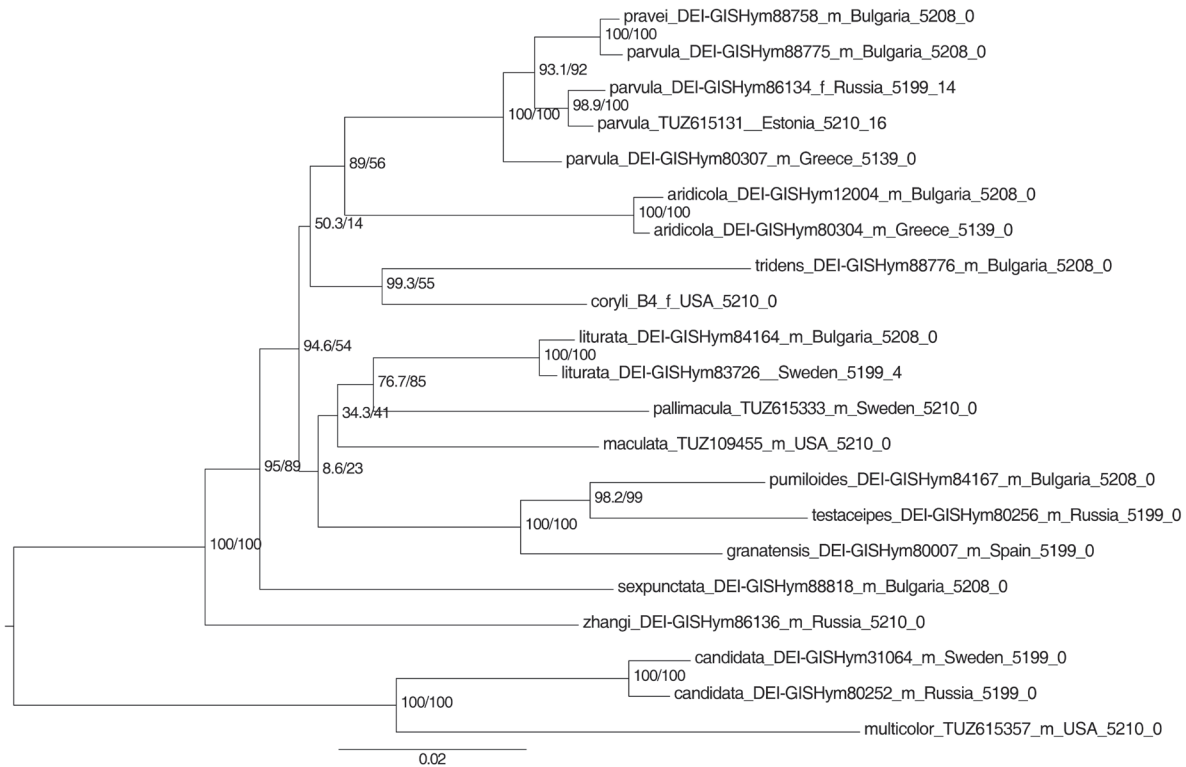
Figure 16. Maximum likelihood tree of *Empria* based on three genes. Best-fit model chosen according to Bayesian information criterion was GTR+R3. Numbers beside nodes show SH-aLRT support (%) / ultrafast bootstrap support (%) values. Support values for weakly supported branches (<90) are not shown. Letters "f" and "m" stand for "female" and "male". Numbers at the end of the tip labels refer to the length of the sequence and the number of ambiguous positions (e.g. polymorphisms). *Empria candidata* and *E. multicolor* were used to root the tree. The scale bar shows the number of estimated substitutions per nucleotide position.

(MNHN); 1♀, BC ZSM HYM 04606, Alsace, Mulhause, Westhalten, 47.967N, 7.267E, 327 m, 6.4.1999, leg. C. Schmid-Egger (ZSM).

GERMANY: 1♂, Brandenburg, Drehna, Weinberg, 51.767N, 13.8E, 13.5.1980, leg. J. Oehlke (SDEI); 1♂, Brandenburg, Kleiner Rummelsberg, Nordhang, 1.M, 52.917N, 14.017E, 27.4.1993–29.4.1993, leg. M. Sommer, Malaise trap (SDEI); 1♀, Thüringen, Lausnitz, FND Totenstein, Hecke, 50.733N, 11.678E, 28.4.2009, leg. F. Burger (SDEI); 1♂, Brandenburg, Mallnow, Oderhänge, NSG Adonishänge, 52.45N, 14.5E, 1.5.2013, leg. A.D. Liston (SDEI); 1♂, BC ZSM HYM 04610, Bayern, Auwald b. Breitenfurt, 49.137N, 11.447E, 390 m, 5.4.2009, leg. J. Hable (ZSM); 1♂, BC ZSM HYM 16743, Bayern, Magerrasen zw. Grossbissendorf und Hohenfels, 49.215N, 11.827E , 435 m, 2.5.2012, leg. J. Hable (ZSM); 1♀, BC ZSM HYM 11775, Bayern, Neumarkt, TK 6834, Qu. 4, S-exponierter Hang, Berching NW-Rand, Haarbe, 49.105N, 11.442E, 388 m, 10.4.2011, leg. J. Hable (ZSM); 1♂, BC ZSM HYM 11810, Bayern, Neumarkt, TK 6934, Qu. 2, Kreuzberg, noerdl. Ortsrand von Dietfurt, 49.04N, 11.586E, 453 m, 21.4.2011, leg. J. Hable (ZSM); 1♂, BC ZSM HYM 04613, Bayern, Zeil, 50.010N, 10.594E, 229 m, 7.7.1998, leg. K. Mandery (ZSM).

GREECE: 1♂, DEI-GISHym80304, Achaia, Ano Vlasia 4 km S, 37.97N, 21.894E , 1000 m, 24.4.2017, leg. SDEI Hym-group (SDEI); 1♀, DEI-GISHym80378, Achaia, Kalavryta Ski Center, 38.005N, 22.199E, 1700 m, 27.4.2017,

leg. SDEI Hym-group (SDEI); 2♀ (DEI-GISHym15134 and DEI-GISHym15131), 1♂ (DEI-GISHym15132), Ioánnina, Kónitsa E 1km, 40.043N, 20.767E, 870 m, 10.5.2007, leg. M. Wei (SDEI); 1♂, DEI-GISHym80396, Sterea Ellas, Lamia W 48 km, Timfristos SW 3 km, 38.91N, 21.93E, 1101 m, 11.5.2007, leg. A.D. Liston (SDEI); 1♀, Achaia, Pirgaki 2 km NNW, 38.178N, 22.084E , 750 m, 25.4.2017, leg. SDEI Hym-group (SDEI); 1♂, TUZ109463, Sterea Ellas, Timfristos Oros, East flank, 38.95N, 21.817E , 1700 m, 14.4.2008, leg. A.D. Liston (TUZ).

HUNGARY: 8♂, 1♀, Tokód, 16.04.2005, swept, leg. J. Macek; 1♀, Epöl, 16.04.2005, swept, leg. J. Macek (NMPC); 1♂, Pest, Veroce, 47.826N, 19.022E, 122 m, 1.5.2005–10.5.2005, leg. Z. Nyiro, Malaise trap (USNM).

RUSSIA: 1♀, I02-01a, Ulyanovsk Oblast, Radishchevsky, 8 km S Vjazovka ("Радищевский р-н 8 Ю с. Вязовка"), 2.5.2002, leg. A. Isajev (CMH).

SLOVAKIA: 1♀, Slovakia mer., Devínska Kobyla, 6.v.1982, swept, leg. J. Macek (NMPC).

Etymology. The species name, a noun, is formed from the Latin components *aridus* (dry) and the suffix *-cola* (inhabitor), and refers to its occurrence in dry places.

Genetic data. Based on mitochondrial and nuclear genes, the exact placement within *Empria* s. str. (i.e. excluding *E. candidata* and *E. multicolor*) is not well supported (Fig. 16). According to mitochondrial COI barcodes, all the specimens belong to the same BIN, the nearest neighbour being a BIN within the *E. immersa* group with a distance of 7.5%.

Host plants. Possibly *Rubus caesius* L. (*ex larva* rearing by JM), but likely other Rosaceae in addition because *R. caesius* seemed to be absent in places where the Bulgarian specimens were collected. From the larva illustrated in Figures 17 and 18 an adult female was reared, but the specimen was destroyed during an attempt to dissect the ovipositor (Czech Republic, Bohemia or., NR Báň u Hradčan, 31.5.2005, on *Rubus caesius*, adult emerged 31.3.2006, J. Macek coll. et det.). The adult did, however, closely resemble paratype specimens of *E. aridicola* from the same site.

Distribution. West Palaearctic. Confirmed country records are from Bulgaria, Czech Republic, France, Germany, Greece, Hungary, Russia (Ulyanovsk Oblast), and Slovakia.

Notes. This species could most easily be confused with *E. parvula* and *E. sexpunctata* by its external morphology (2 or 3 pairs of pale patches on posterior margins abdominal terga, tarsal claw with distinct subbasal tooth). The most reliable way to distinguish *E. parvula* from *E. aridicola* is to examine saws and penis valves (Figs 6, 13, 19, 20, 24, 25, 29). Serrulae are distinctly more flat in *E. parvula* (Figs 19, 20) compared to *E. aridicola* (Fig. 6). In *E. aridicola* males, the dorsal margin of the valviceps bends basally and apically in a rather similar way, so that the dorsal margin nearly forms a semicircle (Figs 13, 29). In *E. parvula*, the dorsal margin of the valviceps is quite asymmetric, bending basally much more abruptly than apically (Figs 24, 25). In *E. parvula*, the paired patches on abdominal terga are often detached from posterior margins of the terga, which can also be helpful in distinguishing the species. The best character to separate females of *E. sexpunctata* and *E. aridicola* is the position of paired patches on abdominal terga, which are detached from the posterior margin in *E. sexpunctata* (cf. Figs 1, 30). Head shape can also be helpful to distinguish females and males of *E. sexpunctata* and *E. aridicola*: the postocellar area is usually more than 2.5 times as broad as long in *E. sexpunctata* (Fig. 31), while in *E. aridicola* this ratio is less than 2.4 (Fig. 3), although there might be overlap. Although saws of *E. sexpunctata* and *E. aridicola* (Figs 6, 23) are hardly distinguishable, penis valves of these species are quite easy to separate (Figs 13, 28, 29). Many of the males of *E. sexpunctata* can be distinguished from *E. aridicola* also by the larger number (3–5) of pale patches on abdominal terga. Prous (2012) used the name *E. kuznetzovi* Dovnar-Zapolskij, 1929 for *E. aridicola* based on the original description (Dovnar-Zapolskij 1929), which is, however, consistent also with *E. parvula*. Because no type specimens of *E. kuznetzovi* Dovnar-Zapolskij, 1929 have been found in ZIN, we maintain the synonymy with *E. parvula* (Konow, 1892) as proposed by Conde (1940), who apparently did study the type specimen(s).

Empria liturata (Gmelin, 1790)*

Material. Varna: 1♂ (DEI-GISHym84164), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 06.04.2018. 2♂, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 09.04.2018. 1♂, locality as previous, 11.04.2018. 1♂, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

Confirmed records are from central Europe and Japan (Prous et al. 2011a).

Empria parvula (Konow, 1892)*

Poecilosoma parvula Konow, 1892 : 215. Lectotype ♂ GBIF-GISHym3784 (SDEI), here designated. Type locality: Fürstenberg in Mecklenburg, Germany, Brandenburg.

Empria pseudoklugi [*pseudo-klugi* sic!] Dovnar-Zapolskij, 1929: 39. Lectotype ♀ ZIN_Empria_8 (ZIN), here designated. Type locality: Sarepta, Volgograd Oblast, Russia.

Bulgarian material. Varna: 1♂ (DEI-GISHym88775), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 06.04.2018. 1♀, locality as previous, 08.04.2018. 1♀ (DEI-GISHym88802), Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 08.04.2018. 1♂, locality as previous, 09.04.2018. 1♀, 1♂, Goren Chiflik 1 km SW, 40 m, 43.001N, 27.621E, 13.04.2018.

Empria parvula has an extensive distribution in Europe (Taeger et al. 2006) and the Palaearctic (Sundukov 2017; Taeger et al. 2018). According to morphological characters and genetic data, the species is very closely related to *E. pravei*. The only clear difference between them is the colouration of the legs in the adults. Legs in *E. parvula* are usually mostly black with small pale areas, but occasionally the hind tibia can be basally 2/3 whitish or yellowish. Nevertheless, the metafemur appears to be always completely or nearly completely black in *E. parvula* (Fig. 32). In *E. pravei*, femora are apically and tibiae basally extensively yellowish (Fig. 33). There could be differences also in penis valves, but because of the variation within *E. parvula*, the differences are not always clear (Figs 24–27). The valviceps seems to usually expand basally less in *E. parvula* than in *E. pravei* (Figs 24–27). Host plants and at least colouration of larvae are not different between *E. parvula* and *E. pravei* (Figs 34, 35). Based on the sequence data of three genes that we currently have, *E. parvula* does not form a monophyletic group, particularly because an *E. parvula* specimen sampled from Bulgaria is closer to *E. pravei* than to other *E. parvula* specimens (from Estonia, Greece, and Russian Far East) (Figs 16, 36). Ignoring morphological evidence, our genetic data could be interpreted as indicating either that *E. pravei* is a synonym of *E. parvula*, or that *E. parvula* consists of more than one species. Because in Bulgaria we found *E. pravei* and *E. parvula* in the same places at the same time and never observed overlap with regard to leg colouration, we consider *E. pravei* to be a distinct species. Although the existence of more than one species under the name *E. parvula* cannot be excluded, the data is also consistent with a single species exhibiting large genetic variation, perhaps connected with the significantly larger population size in *E. parvula* (distributed throughout the Palaearctic) compared to *E. pravei* (possibly restricted to areas not far from the Black Sea and

Figures 17, 18. *Empria aridicola* larva.

south of the Caspian Sea). In other words, non-monophyly of *E. parvula* could be because of incomplete lineage sorting (maintaining of ancestral polymorphisms) due to large population size (e.g. Degnan and Rosenberg 2009). More specimens and genes of both species should be sequenced or mating experiments done to decide more reliably about species boundaries in this case.

Empria pravei Dovnar-Zapolskij, 1925*

Empria pravei Dovnar-Zapolskij, 1925: 37–38. Lectotype ♀ ZIN_Empria_11 (ZIN), here designated. Type locality: Stavropol, Stavropol Krai, Russia.

Bulgarian material. Burgas: 1♂ (DEI-GISHym88758), Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 04.04.2018. 1♀, locality as previous, 10.04.2018.

Varna: 3♀ (including DEI-GISHym84166), 3♂ (including DEI-GISHym88817, DEI-GISHym88735), Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 09.04.2018. 1♀, locality as previous, 11.04.2018. 2♂, Goren Chiflik 1 km SW, 40 m, 43.001N, 27.621E, 13.04.2018.

The specimens were collected in woodland, from the herb layer, at places where a *Geum* species (probably *Geum urbanum* L.) was rather abundant. Of other herbaceous Rosaceae, *Fragaria ?viridis* Weston, and *Rubus fruticosa* L. agg. were commonly present. Female DEI-GISHym84166 was sleeved on a potted *Geum* plant, taken from the collection locality, on which it then laid eggs in the leaf-blade (Fig. 37). Several larvae (Fig. 35; https://sdei.de/ecatsym/ecat_bild.php?NameNr=1003703&DateiName=25774.JPG) were reared to maturity on this plant.

Empria pravei was described from two female syntypes (one in ZIN, examined by MP) from Stavropol (Dovnar-Zapolskij 1925). This locality, in the North Cau-

casus, lies outside the area treated by Taeger et al. (2006) as "Europe". Other published records are from Armenia and Iran (Sundukov 2017). The species is very close to *E. parvula* (see discussion under that species). The record from Mongolia (Zombori 1972) is incorrect due to misidentification of *E. mongolica* (Konow, 1895). *Empria pravei* might be restricted to areas not far from the Black Sea and south of the Caspian Sea.

Empria pumiloides Lindqvist, 1968*

Material. Burgas: 1♂, Burgas 8 km SE, 40 m, 42.432N, 27.527E, 10.04.2018. 1♂, Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018. The first specimen was swept from *Filipendula vulgaris* Moench.

Previously only recorded in northern and central Europe (Taeger et al. 2006). *Filipendula ulmaria* (L.) Maxim. was the only known host plant (Heidemaa and Prous 2006), but this was absent at both of the above Bulgarian localities, whereas *F. vulgaris* was rather abundant. Therefore, it seems likely that *F. vulgaris* is also a host.

Empria tridens (Konow, 1896)*

Material. Varna: 1♂ (DEI-GISHym88776), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 06.04.2018. 3♂ (including DEI-GISHym88816, DEI-GISHym88736), Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 09.04.2018. 1♂, locality as previous, 11.04.2018. 2♂ (DEI-GISHym31967, DEI-GISHym88857), Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

The above specimens are unusually coloured. Abdominal terga (1–) 2–5 (–6) are more or less pale, including the normally black areas surrounding the pale unsclerotised patches (Fig. 38). The corresponding sterna are also more or less pale (Fig. 39). In life, the pale areas are whitish, and more conspicuous than in the pinned specimens, where the colour has become rather brown. No females were collected, so we cannot state whether this sex also exhibits unusual coloration in south-eastern Bulgaria. *Empria tridens* has a wide Palaearctic distribution (Prous et al. 2011b). Penis valves are not distinguishable from other *E. tridens* and genetic data (based on one male DEI-GISHym88776, Fig. 16) does not indicate the existence of an additional species either (based on three genes, closest specimens are always other specimens of *E. tridens* that were studied by Prous et al. 2019).

Endelomyia filipendulae Lacourt, 1998*

Material. Burgas: 1♂ (DEI-GISHym31826), Burgas 8 km SE, 40 m, 42.432N, 27.527E, 10.04.2018. Swept from low vegetation containing much *Filipendula vulgaris*.

The females of *Endelomyia filipendulae* are morphologically not easily separable from those of *E. aethiops* (Gmelin, 1790) using the ovipositor characters illustrated
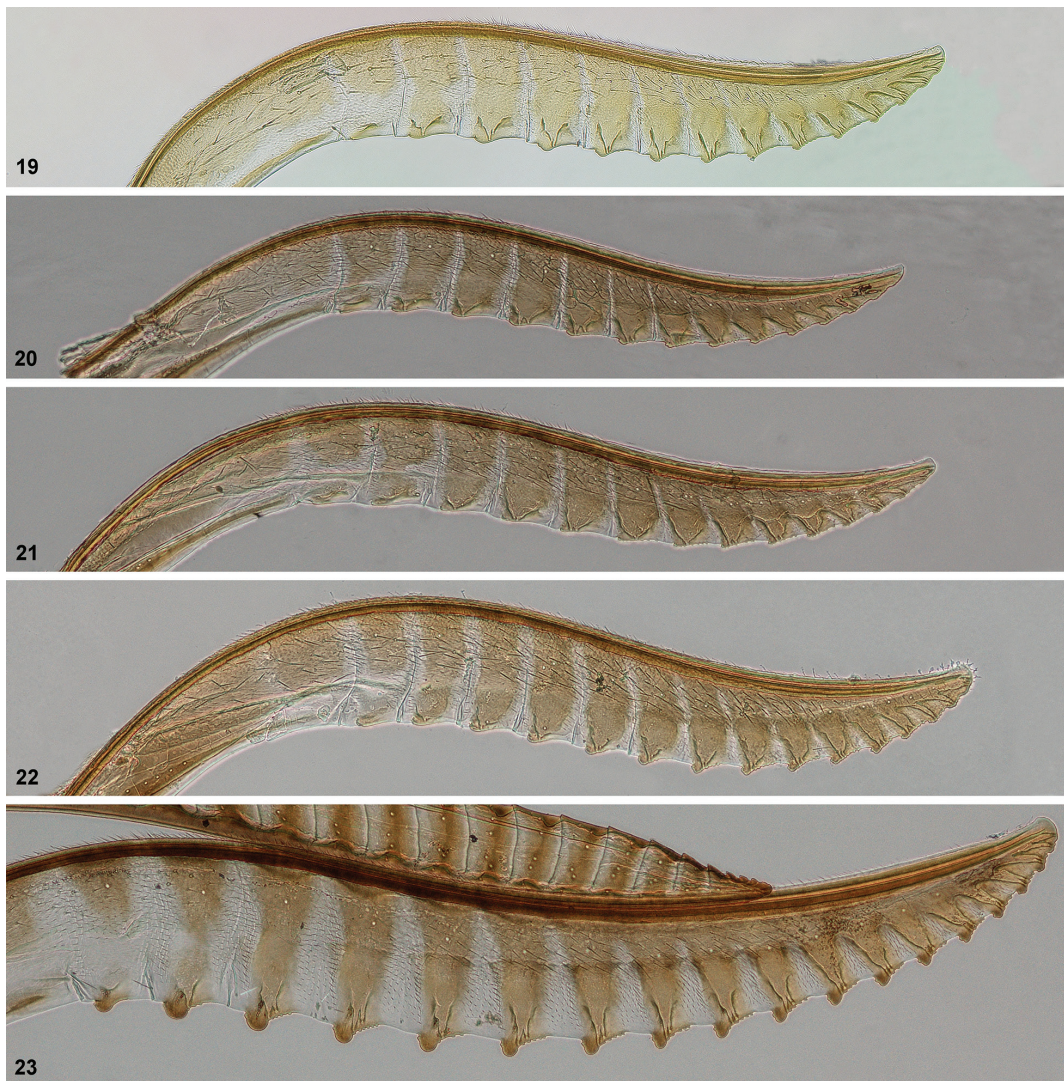
Figures 19–23. Saws of *Empria*. **19** *Empria parvula* DEI-GISHym18703 (Greece) **20** *E. parvula*, *E. pseudoklugi* lectotype ZIN_Empria_8 (Russia) **21** *E. pravei*, lectotype ZIN_Empria_11 (Russia) **22** *E. pravei* BMNH1967-364 (Iran) **23** *E. sexpunctata* DEI-GISHym15130 (Greece).

by Lacourt (1998). However, these species have clearly different COI barcodes (Schmidt et al. 2017) and different host plants: respectively, *Filipendula vulgaris* and *Rosa* species (Liston et al. 2006). Males of *E. filipendulae* were previously unknown and those of *E. aethiops* are rare. As far as we are aware, the penis valve of *E. aethiops* has not been figured. The penis valve of the Bulgarian *E. filipendulae* specimen is illustrated in Figure 40.

Endelomyia filipendulae was previously only known from France, Germany, and Italy (Schmidt et al. 2017).

Euura pedunculi (Hartig, 1837)*

Material. Sliven: 5♀, 1♂, Ichera 3 km SW, 730 m, 42.749N, 26.421E, 14.04.2018.
Swept from *Salix caprea* L.
Widely distributed in Europe and east to Sakhalin (Liston et al. 2017).

Euura venusta (Brischke, 1883)*

Material. Sliven: 1♀, Ichera, 490 m, 42.763N, 26.450E, 14.04.2018. 1♂, Ichera 3 km SW, 730 m, 42.749N, 26.421E, 14.04.2018.
Swept from *Salix caprea*.
Previously recorded in central and northern Europe and east to the Russian Far East (Liston et al. 2017).
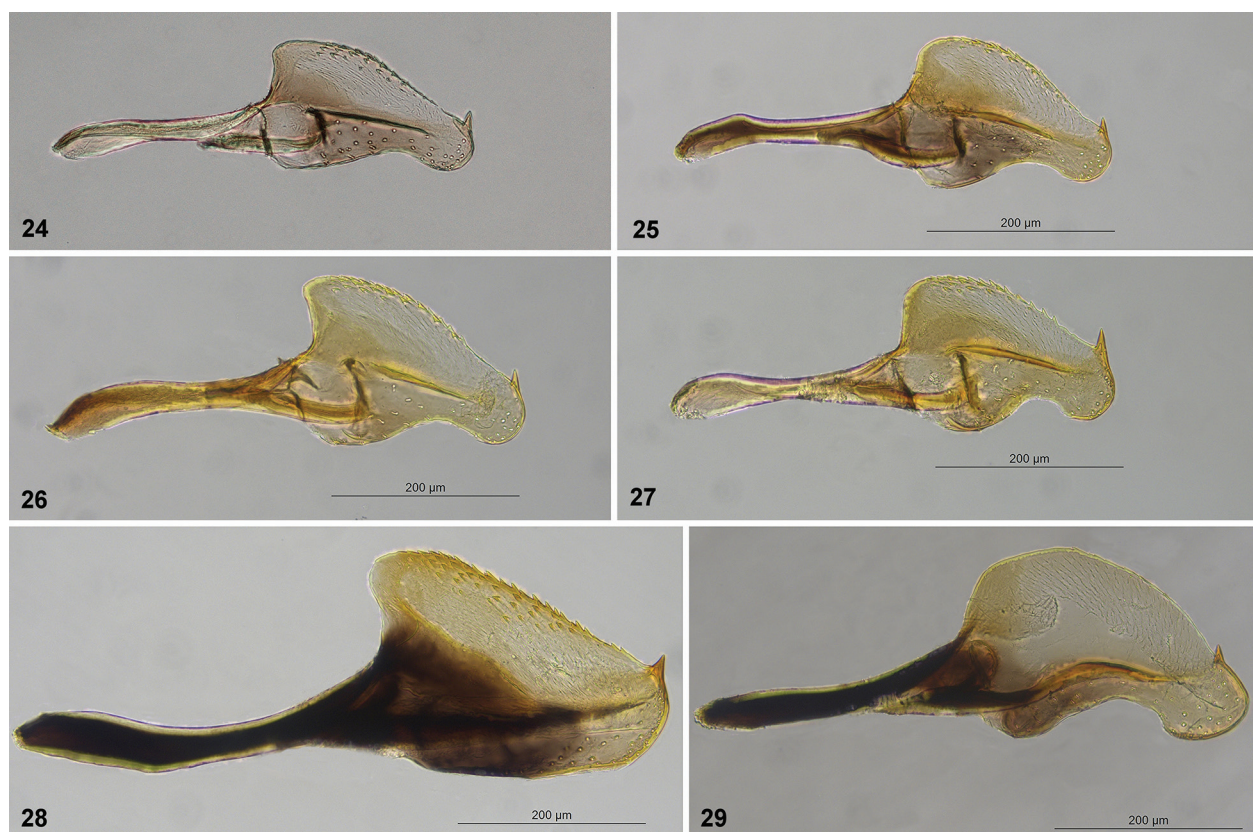
Euura vittata (Serville, 1823)*

Material. Sliven: 1♀, 3♂, Ichera 3 km SW, 730 m, 42.749N, 26.421E, 14.04.2018.
Swept from *Salix caprea*.
Euura vittata has a wide distribution in the Palaearctic (Lacourt 1999).

Figures 24–29. Penis valves of *Empria*. **24** *Empria parvula* TUZ615399 (Estonia) **25** *E. parvula* DEI-GISHym88775 (Bulgaria) **26** *E. pravei* DEI-GISHym88735 (Bulgaria) **27** *E. pravei* DEI-GISHym88758 (Bulgaria) **28** *E. sexpunctata* DEI-GISHym88818 (Bulgaria) **29** *E. aridicola* paratype DEI-GISHym80304 (Greece).

Euura humeralis (Serville, 1823)*

Material. Sliven: 1♂, Ichera 3 km SW, 730 m, 42.749N, 26.421E, 14.04.2018.

Swept from *Salix caprea*.

Previously recorded from northern and central Europe, south-east to Romania (Taeger et al. 2006), and also from the Eastern Palaearctic (Sundukov 2017).

Heterarthrus wuestneii (Konow, 1905)*

Material. Sliven: 1♀, Sliven 4 km NE, 440 m, 42.711N, 26.394E, 14.04.2018.

Heterarthrus wuestneii is widespread in the Western Palaearctic (Liston et al. 2015), but not known north of Denmark (Taeger et al. 2006).

Hinatara nigripes (Konow, 1907)

Material. We collected a total of 27♀ and 12♂ at various localities in Burgas, Sliven, and Varna provinces, mostly swept from *Acer campestre* L., the only known host plant.

Hinatara nigripes is only known from central and southern Europe (Taeger et al. 2006). The apparent abundance of the species in Bulgaria contrasts strongly with

its rare and sporadic occurrence on the northern edge of its range, such as in Germany (Liston et al. 2012).

Hoplocampa cantoti Chevin, 1986*

Material. Varna: 1♀, Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 02.04.2018. 1♀ (DEI-GISHym88748), locality as previous, 03.04.2018. 1♀, locality as previous, 06.04.2018. 5♀, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 05.04.2018. 1♀, locality as previous, 13.04.2018. Mostly swept from *Prunus spinosa* L., and once or twice from *P. domestica* L. growing among these.

Chevin (1986) suggested that the host of *H. cantoti* is *Prunus mahaleb* L., which is a characteristic component of the woody vegetation of the two known French localities. However, *Prunus mahaleb* was not seen at the Bulgarian localities. Therefore, we suppose that the host is *Prunus spinosa*, from which we collected most of the specimens.

Until now, this species was only known from the three female type specimens collected in northern France (Chevin 1986).

Hoplocampa flava (Linnaeus, 1760)

Material. Pazardzhik: 1♀, Vinogradets 3 km N, 300 m, 42.319N, 24.128E, 31.03.2018.
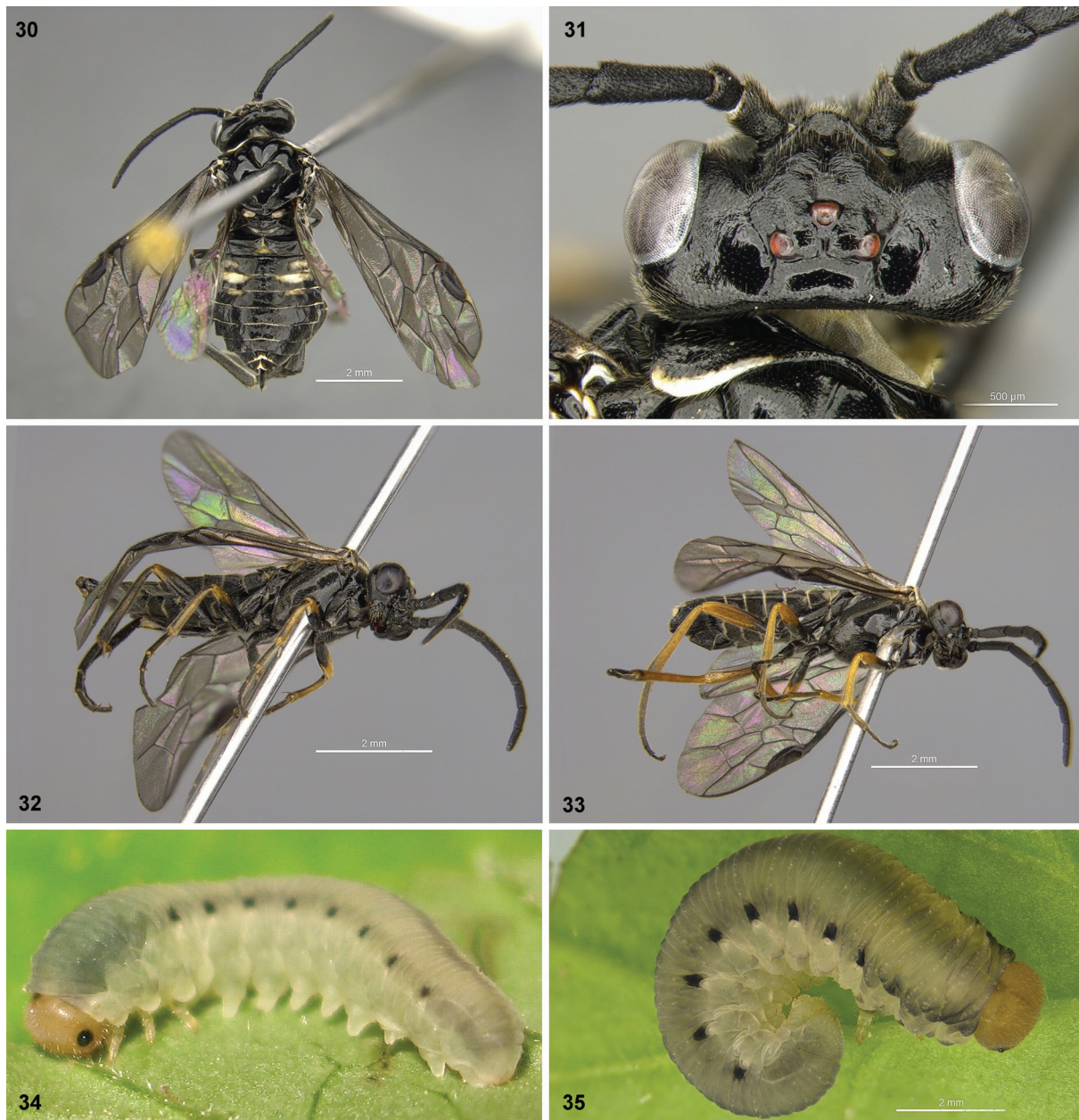
Figures 30–35. *Empria* species. **30** *Empria sexpunctata* DEI-GISHym88916, body dorsal; **31** head dorsal. **32** *E. parvula* DEI-GISHym88913, ventrolateral **33** *E. pravei* DEI-GISHym88735, ventrolateral. **34** *E. parvula* larva TUZ615249 (Estonia) **35** *E. pravei* larva, reared *ex ovo* from DEI-GISHym84166 (Bulgaria).

Not mentioned as occurring in Bulgaria by Vassilev (1978) or Taeger et al. (2006), although the species is a significant pest of cultivated plums in some parts of the country (Andreev and Kutinkova 2010).

Hoplocampa fulvicornis (Panzer, 1801)*

Material. Burgas: 1♀, Banya 3 km E, 40 m, 42.767N, 27.853E, 01.04.2018. 2♀, Slanchev Bryag 1 km N, 70 m, 42.718N, 27.725E, 01.04.2018. 2♀, 2♂, Sozopol 6 km S, 10 m, 42.361N, 27.700E, 04.04.2018. 1♀, Veselie 3 km NW, 50 m, 42.346N, 27.590E, 04.04.2018.

Pazardzhik: 3♀, 6♂, Vinogradets 3 km N, 300 m, 42.319N, 24.128E, 31.03.2018.

Varna: 4♀, 2♂, Rudnik 1 km SE, 100 m, 42.944N, 27.781E, 02.04.2018. 1♂, Tsonevo 1 km SW, 100 m, 43.016N, 27.428E, 02.04.2018. 2♀, 1♂, Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 02.04.2018. 1♀, locality as previous, 03.04.2018. 2♀, locality as previous, 06.04.2018. 10♀, 3♂, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 05.04.2018. 4♀, locality as previous, 13.04.2018. 1♀, Golitsa 1 km E, 240 m, 42.918N, 27.562E, 05.04.2018. 1♀, 3♂, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 08.04.2018. 3♀, 2♂, locality as previous, 13.04.2018.
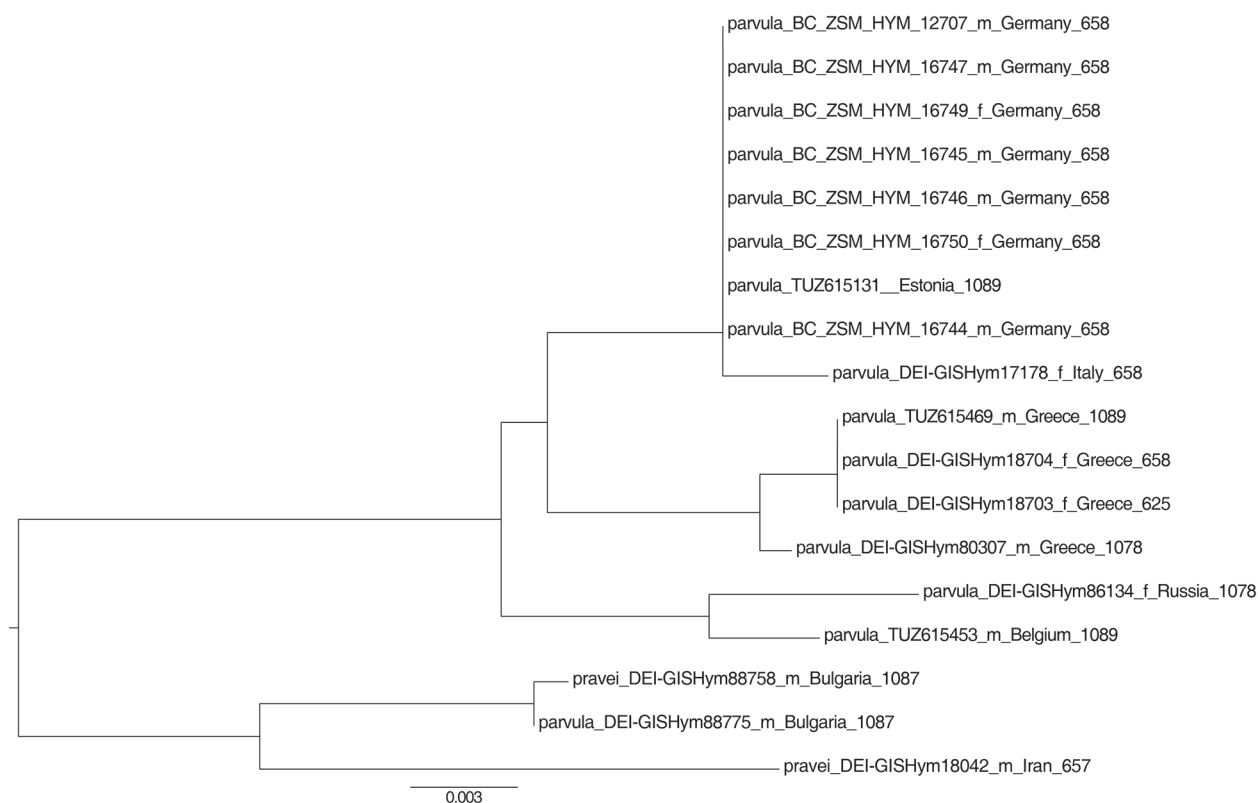
Figure 36. Maximum likelihood tree of *Empria parvula* and *E. pravei* specimens based on mitochondrial COI. Best-fit model chosen according to Bayesian information criterion was HKY+I. Numbers above branches show SH-aLRT support (%) / ultrafast bootstrap support (%) values. Support values for weakly supported branches (<90) are not shown. Letters "f" and "m" stand for "female" and "male". Numbers at the end of the tip labels refer to the length of the sequence. The scale bar shows the number of estimated substitutions per nucleotide position.

Hoplocampa fulvicornis occurs in Europe and Turkey (Lacourt 1999).

Macrophya recognata Zombori, 1979*

Material. Kyustendil: 1♂, Rila-Gebirge, Rila-Kloster [= Rilski Manastir], 42.133N, 23.350E, 20.06.1990, leg. A. Taeger & F. Menzel, det. A. Taeger (by exchange now in private collection of Matti Viitasaari, Helsinki).

Recorded from central and eastern Europe, and the Caucasus (Lacourt 1999).

Nematus lucidus (Panzer, 1801)*

Material. Burgas: 2♂, Mrezhichko 1 km W, 370 m, 42.860N, 27.397E, 07.04.2018. 1♂ (DEI-GISHym88830), Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 10.04.2018. 1♀, Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Varna: 1♂, Tsonevo 1 km SW, 100 m, 43.016N, 27.428E, 02.04.2018. 1♂ (DEI-GISHym88773), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 06.04.2018.

2♂, Goren Chiflik 1 km SW, 40 m, 43.001N, 27.621E, 13.04.2018. 1♀, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

Nematus lucidus is widespread in the Western and Eastern Palaearctic (Sundukov 2017).

Nematus umbratus (Thomson, 1871)*

Material. Varna: 1♀, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 09.04.2018.

Central and northern Europe (Taeger et al. 2006), to East Siberia (Sundukov 2017).

Neomessa steusloffi (Konow, 1892)*

Material. Varna: 1♂ (DEI-GISHym88743), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 02.04.2018. 1♀ (DEI-GISHym88749), locality as previous, 03.04.2018. 6♀ (including DEI-GISHym31831), 4♂ (including DEI-GISHym31830 and 31832), Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 05.04.2018. 1♀, locality as previous, 13.04.2018. 1♂, Staro Oryahovo 2 km SW, 120 m,

Figure 37. *Empria pravei* DEI-GISHym84166 ovipositing on *Geum ?urbanum.*

Figures 38, 39. Unusually coloured *Empria tridens* DEI-GISHym31967 male from Bulgaria. **38** dorsal **39** ventrolateral.

42.976N, 27.787E, 09.04.2018. 1♀, locality as previous, 11.04.2018.

Other material examined. Germany, Mecklenburg-Vorpommern: 1♂ [lectotype; in very poor condition], Neubrandenburg i. M. (SDEI). 1♀, near Teschen-

dorf [according to Konow 1897: "in hiesiger Gegend"] (SDEI).

Taxonomic history.

? *Fenusa* sp. nov. Konow 1885: 298–299. Description of male.

Fenusa steusloffi Konow, 1892: 213. Name proposed by indication on Konow (1885). Syntypes. Type locality: Neubrandenburg i. M. [Germany, Mecklenburg-Vorpommern, Neubrandenburg]. Konow 1897: 180–181, description of female.

Fenusa steusloffii. Dalla Torre 1894: 157. Name for *Fenusa steusloffi* Konow, 1892. Primary homonym of *Fenusa steusloffi* Konow, 1892.

Fenusella steusloffi. Enslin 1914: 306. New combination.

Metallus steusloffi. Benson 1959: 90. New combination, invalid lectotype designation [of the female specimen in SDEI collection].

Neomessa steusloffi. Koch 1990: 72–73. New combination, redescription, lectotype designation.

This species (and thus the monotypic genus to which it belongs) does not run unambiguously to a genus in the key to fenusine genera of the world by Smith (1976a), because it has the following combination of characters: winged; tarsal claw with one outer tooth and an acute basal lobe; prepectus absent; genal carina absent; stub of vein 2A+3A of fore wing curved up. With the genal carina scored as absent (this character is difficult to see), *N. steusloffi* does not run past couplet 17, because the radial cell of the hind wing is open at the apex, but the stub of vein 2A+3A of the fore wing is curved. If the genal carina is scored as present, then in the final key couplet leading to *Scolioneura*, the character given by Smith "antennal segments 3 and 4 about equal in length" does not fit *N. steusloffi*, which has antennomere 4 about 0.6× as long as antennomere 3.

Both Konow (1885) and Koch (1990) have already described a distinctive character in the venation of *Neomessa*: fore wing vein Rs+M is largely obsolete except for a small stub on Rs, and Rs is strongly bent at this point (Fig. 41). All examined specimens show this. Within the Fenusini, this character is apparently unique to *Neomessa*. Furthermore, fore wing vein M is very straight, whereas it is basally curved in most other genera. The male (Fig. 43) is additionally easily distinguishable from other Western Palaearctic fenusines by the colour of the abdomen, which is black with the following yellow: apical terga from T5 or T6 (Fig. 45), sterna S8 and S9 and narrow distal margin of S7 (Fig. 44), and visible parts of genitalia. Only the male of *Parna tenella* (Klug, 1816) also has an extensively yellow abdomen; but it differs in only abdominal terga 1 and 2 being mainly black, and in its largely pale legs (legs nearly entirely black in *N. steusloffi*: Figs 42, 43). We illustrate the penis valve of one of the Bulgarian specimens (Fig. 46), because the drawing by Koch (1990) lacks detail.

Based on the combined analyses of mitochondrial COI and nuclear NaK genes (one sequenced male DEI-GISHym88743), the species forms a strongly supported clade with *Scolioneura* and *Fenusella*, but the relationships between the three genera are less well resolved (Fig. 47).

Figure 40. *Endelomyia filipendulae* DEI-GISHym31826 penis valve.

Biology. Host plant unknown. All the Bulgarian specimens were swept from the newly opened buds or fresh leaves of one or more unidentified *Quercus* species, with the exception of the first male, which was swept from low vegetation just outside an area of mixed woodland. According to Konow (1885), the small series of syntype males was collected from flowers of *Prunus spinosa*. Subsequent authors (e.g. Benson 1959) have therefore suspected *P. spinosa* to be the host plant. According to our observations, *Quercus* seems to be a more likely host.

Distribution. Previously only definitely known from Mecklenburg-Vorpommern, in north-eastern Germany, and now from south-eastern Bulgaria. Muche (1973) published a record of a female identified as this species from Großschönau (Germany, Saxony). However, because he mentioned that this specimen possessed four cubital cells in the fore wing (unlike any specimens which we have seen), it seems likely that it was misidentified.

Parna apicalis (Brischke, 1888)*

Material. Varna: 1♀, Goren Chiflik, 30 m, 43.014N, 27.626E, 13.04.2018.

The recorded distribution of this species stretches from southern Fennoscandia and the British Isles, through Central Europe (Taeger et al. 2006), reaching south-east as far as Croatia (Matoševic et al. 2009) and Hungary (Edmunds 2016). Muche (1977) briefly described a "*Parna* aff. *tenella* (Klug)" from a single female specimen collected on Mount Vitoscha. Although his description might be thought to refer to *P. apicalis*, the specimen, in the Museum für Naturkunde, Berlin, was examined by AL and found to be *Hinatara nigripes*.

Pristiphora abbreviata (Hartig, 1837)*

Material. Burgas: 1♀ (DEI-GISHym88845), Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Pristiphora abbreviata is widely distributed in the Palaearctic and has also been introduced to North America (Sundukov 2017).

Pristiphora armata (Thomson, 1863)*

Material. Burgas: 2♂ (including DEI-GISHym88846), Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Varna: 1♂ (DEI-GISHym88848), Goren Chiflik 1 km SW, 40 m, 43.001N, 27.621E, 13.04.2018. 1♀, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

Widespread in the West Palaearctic (Prous et al. 2017); records from the Russian Far East (Sundukov 2017) require confirmation because the characterisation of this species in earlier literature was inadequate for identification.

Pristiphora biscalis (Förster, 1854)*

Material. Burgas: 2♂, Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 10.04.2018.

Sliven: 1♀, Sliven 6 km NE, 470 m, 42.726N, 26.402E, 14.04.2018.

Varna: 1♂ (DEI-GISHym88850), Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

Widespread in the Western Palaearctic, north to southern Sweden (Prous et al. 2017). According to Sundukov (2017) also in the Eastern Palaearctic, but at least some of the earlier records of *P. biscalis* in the Russian literature are based on misidentifications (Zinovjev 1993).

Pristiphora depressa (Hartig, 1840)*

Material. Varna: 2♀, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 09.04.2018. 1♀, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

All specimens were swept from *Acer campestre*, which is almost certainly the larval host, because no other *Acer* species was present at these localities. *Pristiphora depressa* is under-recorded, because it was until recently mixed up with *P. subbifida* (Thomson, 1871), but apparently has a wide distribution in Europe from Sweden to southern Italy (Prous et al. 2017).

Pristiphora fausta (Hartig, 1837)*

Material. Varna: 2♂, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 08.04.2018. 1♀, locality as previous, 11.04.2018.

Recorded from Central and Southern Europe (Prous et al. 2017), as well as Moldavia (Ermolenko and Plugaru 1973).

Pristiphora maesta (Zaddach, 1876)*

Material. Burgas: 1♂ (DEI-GISHym88844), Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Occurs in Europe, Caucasus, East Siberia, and the Russian Far East (Sundukov 2017).

Figures 41–46. *Neomessa steusloffi*. **41, 42** Female habitus, bend on vein Rs arrowed, DEI-GISHym31831. **43** Male DEI-GISHym31832 habitus. **44** Male DEI-GISHym31832 abdomen ventral. **45** Male DEI-GISHym31830 abdomen dorsal. **46** DEI-GISHym88743 Penis valve.

Pristiphora monogyniae (Hartig, 1840)*

Material. Burgas: 2♂, Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 04.04.2018. 1♀, 1♂, locality as previous, 10.04.2018. 1♀, Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Sliven: 1♀, Sliven 6 km NE, 470 m, 42.726N, 26.402E, 14.04.2018.

Varna: 1♂, Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 06.04.2018. 1♂, locality as previous, 08.04.2018. 1♂, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 08.04.2018. 2♂, locality as previous, 09.04.2018. 1♀, 2♂, locality as previous, 11.04.2018. 3♀, 5♂, Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

Widespread in Europe, north to Sweden (Prous et al. 2017), also in the Caucasus (Sundukov 2017).
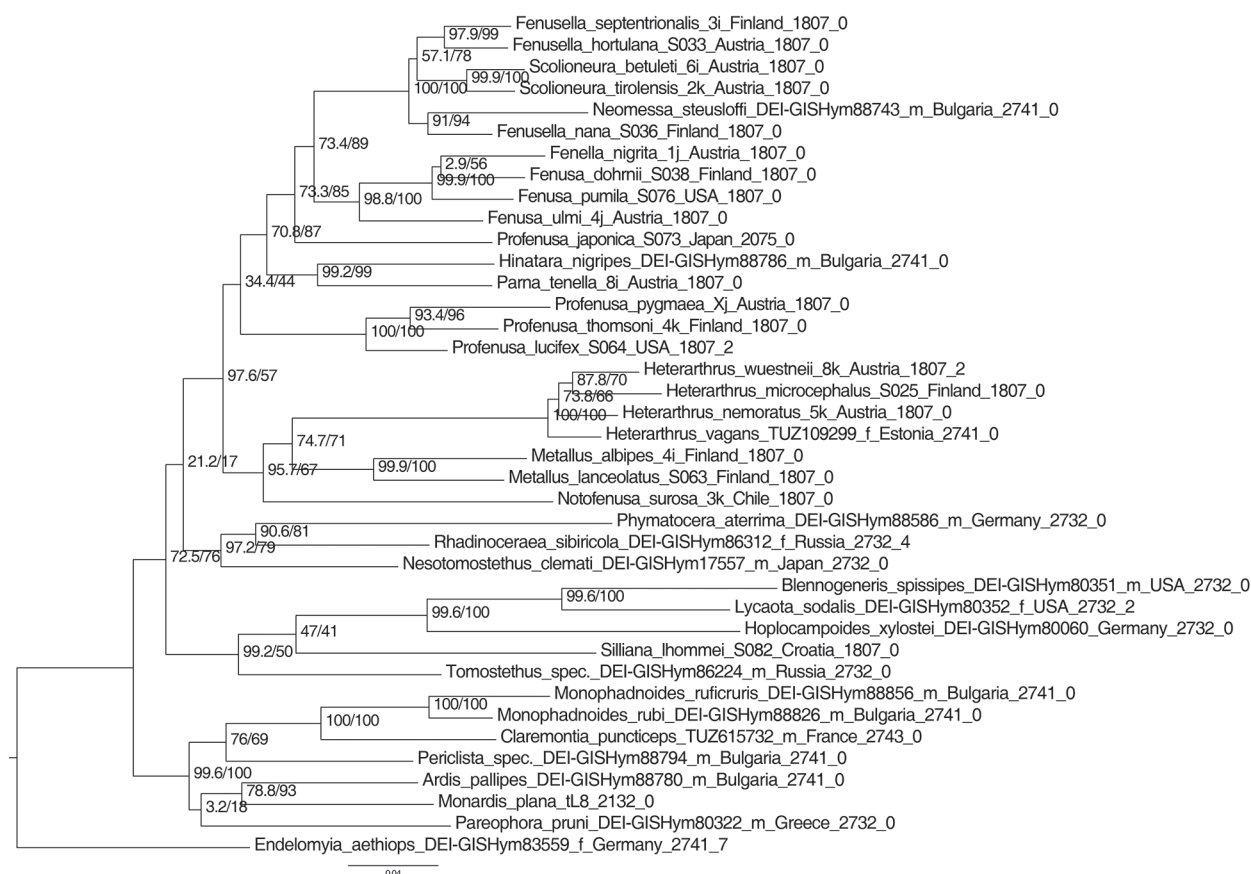
Figure 47. Maximum likelihood tree of Blennocampinae and Heterarthrinae based on two genes (COI and NaK). Best-fit model chosen according to Bayesian information criterion was GTR+I+G4. Numbers beside nodes show SH-aLRT support (%) / ultrafast bootstrap support (%) values. Support values for weakly supported branches (<90) are not shown. Letters "f" and "m" stand for "female" and "male". Numbers at the end of the tip labels refer to the length of the sequence and the number of ambiguous positions (e.g. polymorphisms). The tree was rooted according to the results of Leppänen et al. (2012). The scale bar shows the number of estimated substitutions per nucleotide position.

Pseudodineura fuscula (Klug, 1816)*

Material. Burgas: 1♀, Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 03.04.2018. 1♀, Mrezhichko 1 km W, 370 m, 42.860N, 27.397E, 07.04.2018.

Varna: 1♀, Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 02.04.2018. 1♀, locality as previous, 03.04.2018.

Southern, central and northern Europe, including British Isles (Taeger et al. 2006), Armenia, Kazakhstan, and eastern Siberia (Sundukov 2017), and introduced to North America (Smith 1976b).

Sciapteryx byzantina Benson, 1968*

Material. Burgas: 2♀, 1♂ (DEI-GISHym88755), Primorsko 4 km NW, 20 m, 42.300N, 27.729E, 04.04.2018. 1♂ (DEI-GISHym31834), locality as previous, 10.04.2018.

Varna: 2♂ (including DEI-GISHym88746), Tsonevo 5 km S, 100 m, 42.982N, 27.451E, 02.04.2018. 2♀, locality as previous, 03.04.2018. 1♀, locality as previous, 06.04.2018. 1♀, Goren Chiflik 1 km SW, 40 m, 43.001N,

27.621E, 13.04.2018. 1♀ (DEI-GISHym31835), Dolni Chiflik 2 km SE, 50 m, 42.983N, 27.743E, 13.04.2018.

All specimens were collected from patches of *Ranunculus constantinopolitanus* (DC.) d'Urv. in damp places, often at woodland edges.

Adults are morphologically similar to *S. consobrina* (Klug, 1816), and most easily distinguished from that and other *Sciapteryx* species by the pale parts of fore wing pterostigma, costa, and subcosta (Figs 48, 49, 52, 53), as described in the key by Benson (1968). The Bulgarian specimens agree well with the original description of this species (Benson 1968), except for the following details: body length is 8–9 mm (as given also by Benson), but one male only 7mm; labial and maxillary palps largely pale, but apical palpomeres more or less dark (Fig. 50) (Benson wrote only that the labial palps are yellowish white); distal margin of tergum 1 more or less pale, but entirely black in one female (Benson wrote that apical margins of all terga are more or less pale); outer margin of tegula more or less pale, and inside dark (Fig. 51) (Benson wrote that the "front half of tegula" is pale).

Figures 48–53. *Sciapteryx byzantina*. **48, 49** female DEI-GISHym31835 habitus; **50** head. **51** Male DEI-GISHym31834 thorax; **52, 53** habitus.

The COI barcode region of DEI-GISHym88746 shows a divergence of 5.3% from the closest neighbour, *Sciapteryx laeta* Konow, 1891 (DEI-GISHym4857).

The host plants of most *Sciapteryx* species remain unrecorded, but because at least *S. costalis* and *S. consobrina* are known to use *Ranunculus* species as hosts (Lorenz and Kraus 1957; Beneš 1960), we speculate that *R. constantinopolitanus* is the larval host of *S. byzantina*.

Sciapteryx byzantina was previously known only from the type specimens, collected in European Turkey near Istanbul, and at Rize in north-eastern Turkey (Anatolia) (Benson 1968).

Strongylogaster xanthocera (Stephens, 1835)*

Material. Varna: 5♂, Staro Oryahovo 2 km SW, 120 m, 42.976N, 27.787E, 08.04.2018. 1♀, 7♂, locality as previous, 11.04.2018. All specimens swept from very young growth of *Pteridium aquilinum* (L.) Kuhn, the main host plant. Males can be identified using the characters described by Welke (1959: 253–254).

Strongylogaster xanthocera has an extensive Palaearctic distribution (Sundukov 2017), including North Africa (Blank 2002).

Tenthredo giraudi (Taeger, 1991)*

Material. Sliven: 1♂, Sliven 4 km NE, 440 m, 42.711N, 26.394E, 14.04.2018, det. A. Taeger.

Previously recorded only from Austria, Italy, and Slovenia (Taeger et al. 2006).

Xiphydriidae

Xiphydria picta Konow, 1897*

Material. Dobrich: 1♀, 1♂, Albena Kranevo, 43.35N, 28.06E, 04–05.09.1981, leg. T.-E. Leiler (Swedish Museum of Natural History, Stockholm).

Xiphydria picta is infrequently recorded, but has an extensive range in the Western Palaearctic (Sundukov 2017).

Xyelidae

Xyela curva Benson, 1938*

Material. Burgas: 5♀, 1♂, Prosenik 1 km NW, 150 m, 42.805N, 27.436E, 07.04.2018. 1♀, Burgas 8 km SE, 40 m, 42.432N, 27.527E, 10.04.2018. 1♀, Indzhe Voivoda 3 km NE, 250 m, 42.235N, 27.451E, 12.04.2018.

Varna: 1♂, Goren Chiflik, 30 m, 43.014N, 27.626E, 13.04.2018.

Most specimens swept from *Pinus nigra*.

Widespread in the Western Palaearctic throughout the natural range of *Pinus nigra* J.F.Arnold, and also on introduced *P. nigra* in more northern areas of Europe (Blank et al. 2013, with distribution map as fig. 11).

Xyela menelaus Benson, 1960*

Material. Burgas: 1♀, Prosenik 1 km NW, 150 m, 42.805N, 27.436E, 07.04.2018.

Swept from *Pinus nigra*.

The known range includes several other Balkan countries, as well as Austria and Sicily (Italy) (Blank et al. 2013).

Other species recorded in Bulgaria by MP and AL in 2018

The following species are already more or less well documented as occurring in Bulgaria. Nevertheless, in the con-

text of their presence in the coastal areas of south-eastern Bulgaria (all of our localities in Burgas and Varna provinces), they are collectively of biogeographical interest. We list them here only with the names of the provinces in which we collected specimens.

Argidae: *Arge nigripes* (Retzius, 1783) (Burgas, Sliven), *A. ustulata* (Linnaeus, 1758) (Burgas). Cephidae: *Cephus nigrinus* Thomson, 1871 (Burgas). Pamphiliidae: *Acantholyda erythrocephala* (Linnaeus, 1758) (Burgas), *Neurotoma nemoralis* (Linnaeus, 1758) (Sliven), *Pamphilius alternans* (Costa, 1860) (Burgas, Sliven). Tenthredinidae: *Aglaostigma aucupariae* (Klug, 1817) (Burgas, Varna, Sliven), *A. fulvipes* (Scopoli, 1763) (Sliven), *Ametastegia carpini* (Hartig, 1837) (Burgas), *A. tenera* (Fallén, 1808) (Varna), *Athalia bicolor* Serville, 1823 (Burgas), *A. cordata* Serville, 1823 (Burgas, Varna, Sliven), *A. liberta* (Klug, 1815) (Sliven), *Cladius compressicornis* (Fabricius, 1804) (Burgas), *C. pectinicornis* (Geoffroy, 1785) (Burgas), *Claremontia alternipes* (Klug, 1816) (Burgas, Varna), *C. waldheimii* (Gimmerthal, 1847) (Varna), *Dolerus gonager* (Fabricius, 1781) (Burgas, Varna), *D. haematodes* (Schrank, 1781) (Pazardzhik), *D. nigratus* (O.F. Müller, 1776) (Varna), *D. picipes* (Klug, 1818) (Burgas), *D. puncticollis* Thomson, 1871 (Burgas, Varna), *D. sanguinicollis* (Klug, 1818) (Sliven), *D. triplicatus* (Klug, 1818) (Burgas), *D. vestigialis* (Klug, 1818) (Burgas, Varna), *Empria sexpunctata* (Serville, 1823) (Burgas, Varna), *Eutomostethus luteiventris* (Klug, 1816) (Varna), *Halidamia affinis* (Fallén, 1807) (Burgas, Varna, Sliven), *Hoplocampa brevis* (Klug, 1816) (Burgas, Pazardzhik), *H. minuta* (Christ, 1791) (Burgas), *Macrophya albicincta* (Schrank, 1776) (Sliven), *M. alboannulata* Costa, 1859 (Burgas, Pazardzhik, Varna, Sliven), *Mesoneura opaca* (Fabricius, 1775) (Burgas, Varna), *Monophadnoides rubi* (T. W. Harris, 1845) (Burgas), *M. ruficruris* (Brullé, 1832) (Varna, Sliven), *Monophadnus pallescens* (Gmelin, 1790) (Burgas, Varna, Sliven), *Monsoma pulveratum* (Retzius, 1783) (Varna, Sliven), *Periclista* species (approx. 7 species, not yet determined: Burgas, Varna, Sliven). *Phymatocera aterrima* (Klug, 1816) (Varna, Sliven), *Pristiphora insularis* Rohwer, 1910 (Burgas, Varna), *Rhogogaster chambersi* Benson, 1947 (Sliven), *Tenthredo dahlii* Klug, 1817 (Burgas, Sliven), *T. zona* Klug, 1817 (Burgas).

Discussion

The majority of species which MP and AL encountered in south-eastern Bulgaria have a wide European distribution (e.g. *Ardis pallipes*, *Euura pedunculi*, *Gilpinia frutetorum*, *Strongylogaster xanthocera*, and nearly all those listed above under "Other species"). They are mostly Euro-Siberian faunal elements. Many of our other records significantly extend the known range of these species to the south or south-east (e.g. *Empria pumiloides*, *Endelomyia filipendulae*, *Euura venusta*, *Parna apicalis*, and *Pristiphora depressa*). This is in keeping with the recog-

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nition of the Euxinian Province as part of the southern boundary of the Euro-Siberian Region in south-western Asia (Browicz 1989). Most of the remaining sawfly species that we collected are known either to occur rather widely in southern Europe (e.g. *Xyela menelaus*) or in South-Eastern Europe (e.g. *Tenthredo dahlii*), or at least already known from other territories in South-Eastern Europe (*Tenthredo giraudi*). Only *Empria pravei* and *Sciapteryx byzantina* are, according to the data currently available, possibly restricted in Europe to the coastal regions of the Black Sea. Note that neither species is absolutely confined to the Euxinian Province as currently defined in its restricted modern sense (Browicz 1989). According to Browicz, this extends north only to the Ropotamo River (on which lies our locality "Primorsko 4 km NW"), or perhaps to Burgas, whereas our records for both species are partly from localities a little further north, in southern parts of Varna Province.

The newly recorded localities in Bulgaria of the fenusine *Neomessa steusloffi*, far from its previously only known area of occurrence in north-eastern Germany, where it was last found more than a hundred years ago, are particularly noteworthy, but difficult to interpret. Generally, adult fenusines are under-recorded, probably as a result of their small size, often short flight period, and difficulties of identification (Smith 1976). On the other hand, the males of *N. steusloffi* are so distinctively coloured, that they should be readily recognisable. The leaf-mines of fenusines are much more easily collected than adults, and the hosts and larval stages of most European species are quite well known, so that records based on leaf-mines and larvae have greatly helped in clarifying their distribution. However, the current sum of accumulated knowledge is founded largely on morphological identification of reared adults. Although the circumstances of the Bulgarian records of *N. steusloffi* strongly suggest *Quercus* to be the larval host, we have no proof of this. Should *Quercus* really be its host, we must discard the hitherto widespread assumption that all sawfly leaf-mines found in Europe on *Quercus* belong to *Profenusa pygmaea* (Klug, 1816). Therefore, the definite identification of sawfly leaf-mines on *Quercus* requires either rearing or sequencing of the larvae, at least until characters become known which distinguish the larvae or leaf-mines of *N. steusloffi* from *P. pygmaea*. The discovery in Bulgaria of *Hoplocampa cantoti*, previously known only from three type specimens from northern France, is also surprising, but the current lack of records may only be because *H. cantoti* is not included in any of the standard identification works and superficially resembles *Hoplocampa fulvicornis* and *H. minuta*.

Acknowledgements

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First known larva of omicrine genus *Psalitrus* d'Orchymont (Coleoptera, Hydrophilidae)

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Key Words

Abstract

The larval morphology of the water scavenger beetle *Psalitrus yamatensis* Hoshina & Satô, 2005 is described based on a specimen collected from Fukuoka Prefecture, Kyushu, Japan. This is the first description of the larval morphology of the hydrophilid genus *Psalitrus* d'Orchymont, 1919, as well as the first description of larval chaetotaxy of the tribe Omicrini. Species-level identification of the larva was performed using DNA barcoding of a molecular marker: a 658 bp fragment of the mitochondrial cytochrome oxidase I. A description including chaetotaxy of head capsule and head appendages, diagnosis, and illustrations of the larva is provided. *Psalitrus* larvae can be distinguished from other known larvae of the tribe Omicrini by the morphology of the head and legs. The larva shares characters with other known larvae of Omicrini; potential plesiomorphies are shared with Cylominae and aquatic hydrophilids; some characters are also shared with larvae of Megasternini and Sphaeridiini.

Introduction

The tribe Omicrini, comprising 15 genera worldwide, is a group of small, terrestrial hydrophilid beetles belonging to the subfamily Sphaeridiinae (Hansen 1999; Short and Fikáček 2011). Members of the tribe inhabit various terrestrial habitats, such as decaying matter (Bameul 1992; Hoshina 2007) and bromeliads (Hansen and Richardson 1998; Albertoni and Fikáček 2014), or they are associated with termites (Schödl 1995). They are rarely collected relative to other groups of hydrophilid. The monophyly of Omicrini was not supported in the tree proposed by Short and Fikáček (2013); Fikáček et al. (2015) subsequently proposed an alternative hypothesis, in which Omicrini is monophyletic and an early-branching clade; however, the sister-group of Omicrini was still unstable in that study. Larvae of the tribe are only known from two species and one unidentified larva: *Peratogonus reversus*

Sharp, 1884 briefly illustrated by Hayashi (1986), *Omicrus ingens* Hansen & Richardson, 1998 described by Hansen and Richardson (1998), and an unidentified larva of *Noteropagus* Orchymont, 1919 or *Paromicrus* Scott, 1913 by Fikáček (in press).

Psalitrus d'Orchymont, 1919 is an omicrine genus containing 36 species from the Afrotropical, Oriental, Palaearctic, and Australian regions (Short and Fikáček 2011, 2013). The known species of the genus are small, oval beetles which inhabit decaying matter, and most typically they are sifted from various types of leaf litter (Bameul 1992; Hoshina 2007). The phylogenetic position of the genus remains unclear; *Psalitrus* is in an early-branching clade of Sphaeridiinae together with *Aculomicrus* Smetana, 1990 and *Peratogonus* Sharp, 1884 in the tree proposed by Short and Fikáček (2013), but it was revealed as sister to *Tylomicrus* Schödl, 1995 + *Omicrogiton* Orchymont, 1919 by Fikáček et al. (2015). *Psalitrus* also stands

apart from the remaining omicrine genera because of its antennal morphology, as its antenna has eight antennomeres and a loosely segmented antennal club (in contrast to nine antennomeres and compact antennal club in all remaining Omicrini), further obscuring its phylogenetic placement. Larval morphology has played an essential role in systematic studies, and discovery of the *Psalitrus* larva is expected to provide useful information to enlighten omicrine systematics.

A tiny larva of a terrestrial hydrophilid resembling omicrine larvae was recently collected in Kitakyushu, Kyushu Island, Japan. The larva was collected together with two omicrine species: *Psalitrus yamatensis* Hoshina & Satô, 2005 and *Peratogonus reversus*. In this study, the larva is identified using a DNA barcoding method, described as the first known larva of the genus *Psalitrus*, and compared with other known larvae of the Sphaeridiinae and Cylominae.

Material and methods

Morphological study

A single larva extracted from leaf litter using Tullgren funnels was available for study (Table 1). The larva, unfortunately, completely dried up in a microtube after DNA extraction and thoracic and abdominal characters were strongly deformed. Moreover, most of thoracic and abdominal segments of the larva bear large amounts of dust, which did not wash off during DNA extraction (20 μl proteinase K and 180 μl Buffer ATL, approximately 48 h at 55 °C, mixed by vortexing several times). Detailed observation of the characters was therefore impossible. Under these circumstances thoracic and abdominal characters are only briefly described, and I mainly focus on characters of the head, which was not affected by the DNA extraction. The larva was mounted on HS-slides (Shirayama et al. 1993; Kanto Rika, Tokyo) with Euparal (Waldeck, Münster) for examination and preservation. It is deposited at the Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan (Y. Minoshima) (KMNH).

The specimen was examined using a Leica MZ16 (Leica Microsystems, Wetzlar) and an Olympus BX50 (Olympus, Tokyo). Illustrations were prepared with the aid of a drawing tube attached to the BX50; line drawings were prepared using the software Paint Tool SAI (Systemax Inc., Tokyo). Photographs were taken with digital cameras (Olympus OM-D E-M5 Mark II and E-M1 Mark II) attached to an Olympus SZX12 and the BX50. Composite images were created using focus stacking software Helicon Focus (Helicon Soft Ltd, Kharkov). Photographs were subsequently adapted in Adobe Photoshop Lightroom and Photoshop CC (Adobe Systems Inc., San Jose) as needed.

Morphological terminology follows Hansen and Richardson (1998) and Minoshima and Hayashi (2011) for general morphology; chaetotaxy follows Fikáček et al.

Table 1. List of specimens and GenBank Accession Number used in this study. AD: adult; L: larva.

Taxon	Stage	Extraction ID	Locality data / reference	Accession No.
Psalitrus yamatensis	L	YNME#16-9	JAPAN: Fukuoka Pref., Kitakyushu-shi, Yahata-nishi-ku, Narumizu, Gôtôyama, 33°51.16'N, 130°46.51'E, 170 m; leaf litter; 11 Jun. 2016; YN Minoshima (Loc#2016-11)	LC484174
Psalitrus yamatensis	AD	YNME#85	Same as above (Loc#2016-11)	LC484175
Psalitrus yamatensis	AD	YNME#86	Same as above (Loc#2016-11)	LC484176
Psalitrus yamatensis	AD	YNME#16-4	JAPAN: Ôita Pref., Nakatsu-shi, Hon-yabakei-machi, Atoda, 33°28.57'N, 131°11.81'E, 120 m; leaf litter; 28 May 2016; YN Minoshima (Loc#2016-8)	LC484173
Peratogonus reversus	AD	YNME#16-2	Same as above (Loc#2016-8)	LC484172
Armostus ohyamatensis	AD	YNME#90	Same locality as Loc#2016-11; see Minoshima (2018)	LC422744

(2008) and Byttebier and Torres (2009). Classification follows Short and Fikáček (2013) and Seidel et al. (2016). The following abbreviations are used: AN: antenna; FR: frontale; gAN: group of the apical antennal sensilla; gAPP: group of sensilla on inner appendage of maxilla; gFR: group of sensilla on frontale; gLA: group of the apical sensilla on labial palpus; gMX: group of the apical sensilla on maxilla; LA: labium; MN: mandible; MX: maxilla; PA: parietale; SE: sensorium.

Molecular study

Total genomic DNA was extracted from the whole body using a DNeasy Blood & Tissue Kit (Qiagen, Hilden) (Cruickshank et al. 2001). Vouchers and GenBank accession numbers are listed in Table 1; all vouchers are preserved at KMNH. I extracted and sequenced the presumed *Psalitrus* larva, three adults of *Psalitrus yamatensis*, and a single adult of *Peratogonus reversus* (both Omicrini). In addition, I used *Armostus ohyamatensis* Hoshina & Satô, 2006 (Megasternini) (Gen Bank Accession #LC422744; Minoshima 2018) to compare the generic distance. A single fragment of 658 bp of mitochondrial cytochrome c oxidase I (COI) was sequenced using the primers LCO1490 and HCO2198 (Folmer et al. 1994). Protocols for the PCR were identical to those described in Minoshima et al. (2013). PCR products were purified using ExoSAP-IT (Affymetrix, Santa Clara). Each fragment was sequenced using the primers in both directions by Macrogen Japan Corporation (Kyoto). The sequenced data were assembled and edited manually in MEGA 7.0.26 (Kumar et al. 2016). I used pairwise *p*-distance analysis to associate the larva with adult individuals with the software.

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Results

Identification

Pairwise *p*-distance analysis (Table 2) shows that the COI sequence of the presumed *Psalitrus* larva is identical to the sequenced adults of *Ps. yamatensis* collected at the same locality, as well as in Ôita Prefecture. Its pairwise *p*-distance from the adults of *Peratogonus* and *Armostus* is 15.7–17.9%. Hence, the larva is unambiguously identified as *Ps. yamatensis*. The head appendages of the examined larva lack secondary sensilla; on the basis of this, I infer that the larva likely represents the first instar, even though two additional setae are present close to PA8 on head capsule (Fig. 3A).

Description of larva

Psalitrus d'Orchymont, 1919

Diagnosis. Larva of *Psalitrus* can be distinguished from other known omicrine larvae (*Omicrus* Sharp, 1879, *Peratogonus*, and unidentified larva of *Noteropagus* or *Paromicrus*) by: (1) nasale with four distinct teeth; (2) asymmetrical median projection on nasale absent; (3) epistomal lobe absent; (4) mentum very deeply emarginate dorsally; and (5) legs four-segmented.

The *Psalitrus* larva is also similar to other terrestrial sphaeridiine larvae; however, it can be distinguished by the addition of following combination of characters: (1) coronal line absent; (2) PA6 and PA13 absent; (3) anten-

Table 2. Pairwise distances between individuals in analysis expressed as a percentage of nucleotide differences (*p*-distances).

	1	2	3	4	5
1. Larva (YNME16-9)					
2. *Psalitrus yamatensis* (YNME16-4)	0.0%				
3. *Psalitrus yamatensis* (YNME85)	0.0%	0.0%			
4. *Psalitrus yamatensis* (YNME86)	0.0%	0.0%	0.0%		
5. *Peratogonus reversus* (YNME16-2)	15.7%	15.5%	15.5%	15.5%	
6. *Armostus ohyamatensis* (LC422744)	17.9%	17.8%	17.8%	17.8%	18.4%

nomere 2 with a small basal additional pore dorsally; (4) antennal sensorium slender, long; (5) mandibles almost symmetrical, both mandibles with two teeth; (6) MN1 close to MN2; (7) MN2–4 forming a triangular group; (8) maxillae symmetrical; (9) maxilla with well-sclerotised inner appendage; (10) submentum without large lateral extension; (11) labium without hypopharyngeal lobe; (12) LA10 stout seta; (13) legs short, four-segmented; and (14) median lobe of spiracular atrium with median emargination posteriorly.

Psalitrus yamatensis Hoshina & Satô, 2005
Figs 1–4

Material examined. 1 presumably first instar larva; see Table 1.

Diagnosis of larva. See generic diagnosis.

Description of presumably first instar larva. General morphology. Length 1.2 mm in the specimen fixed
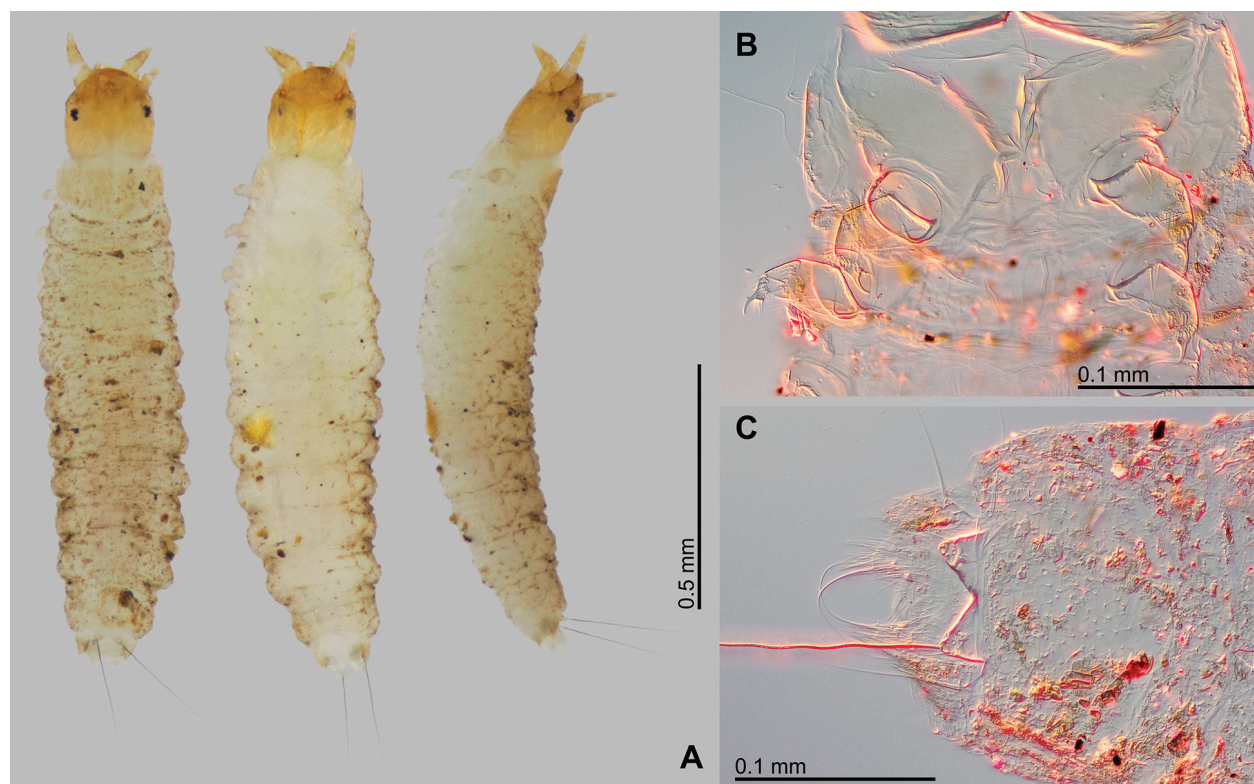
Figure 1. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A.** Habitus, dorsal (left), ventral (middle), and lateral (right) view; **B.** Thorax, ventral view; **C.** Spiracular atrium, dorsal view.

Figure 2. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A, B.** Head, dorsal (A) and ventral (B) view; **C.** Foreleg, anterior view.

by ethanol; head width 0.2 mm. Body (Fig. 1A) maggot-like in shape, widest between abdominal segments 3–6. **Colour.** Head capsule and thoracic sclerites yellowish, membranous parts milky white.
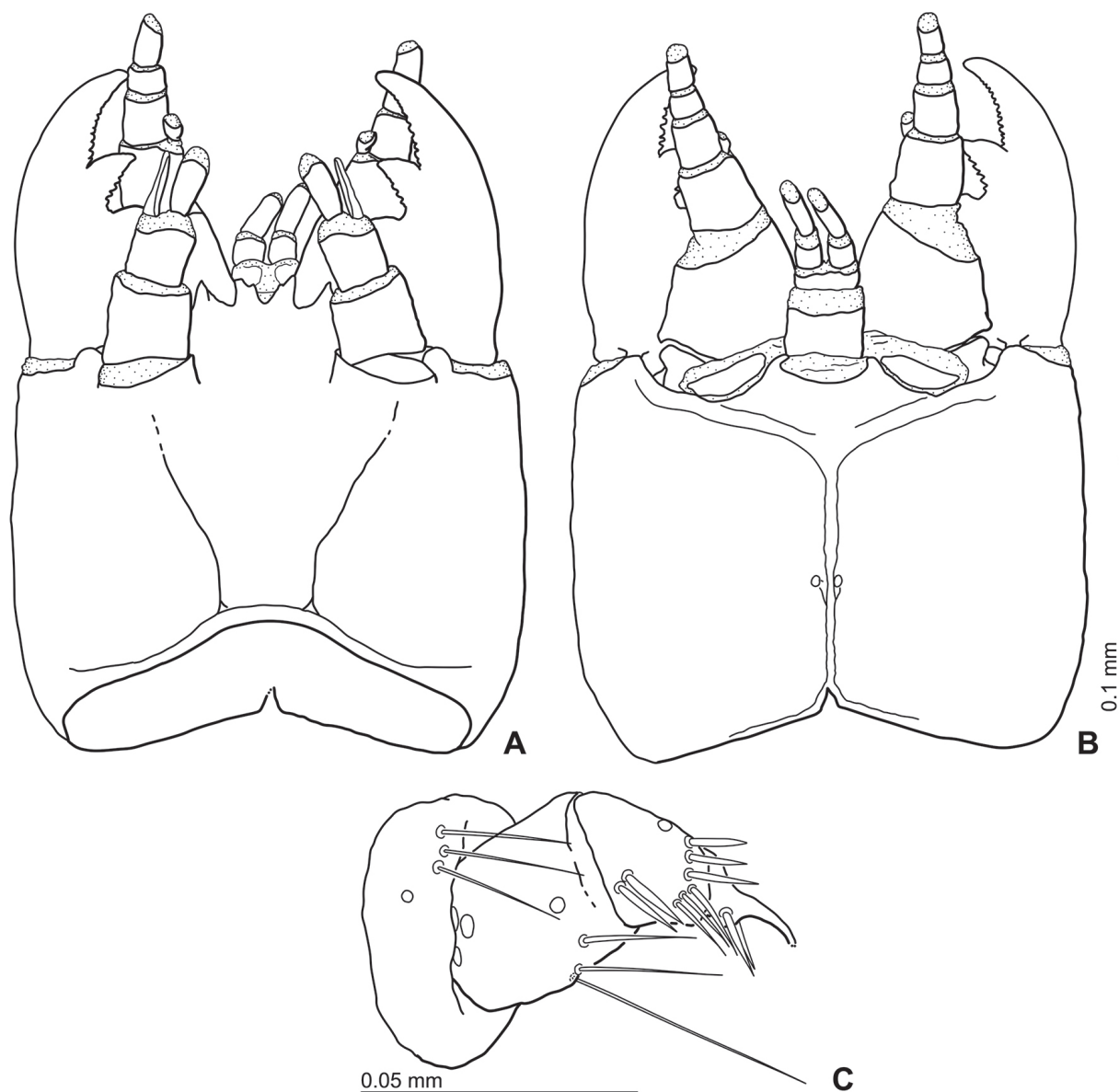
Head. Head capsule subquadrate (Fig. 2A); cervical sclerites undetectable. Frontal lines U-shaped at base, then divergent laterally, ending behind outer margin of antennal socket; coronal line absent. Surface of head capsule smooth; stemmata present on each anterolateral portion of head capsule; number of stemmata unclear but two (groups of) stemmata detectable: posterior one oval; anterior one wider than posterior one. Posterior tentorial pits present, on midlength of and close to submental sulcus. Clypeolabrum symmetrical in shape (Fig. 3C) but asymmetrical in arrangements of setae (see description of chaetotaxy). Nasale distinctly projecting, with four

large teeth; all teeth almost similar in size and equidistant. Asymmetrical median projection absent. One pair of presumably egg-bursters present behind median two teeth of nasale. Epistomal lobe absent (Fig. 3C); lateral part of epistome almost straight.

Antenna (Fig. 4A) three-segmented, short and stout; surface of antenna smooth. Antennomere 1 widest, distinctly wider than antennomere 2; antennomere 3 narrowest. Antennomeres 2 slightly shorter than antennomere 1; antennomere 3 slightly shorter than antennomere 2. Antennal sensorium present, as long as antennomere 3.

Mandibles (Fig. 4B) stout, distinctly widened in basal part, almost symmetrical; median part with two inner teeth; incisor area and basal margin of inner teeth weakly serrate.

Maxilla (Fig. 4C) six-segmented, stout, longer than antenna, asymmetrical. Cardo irregularly triangular.

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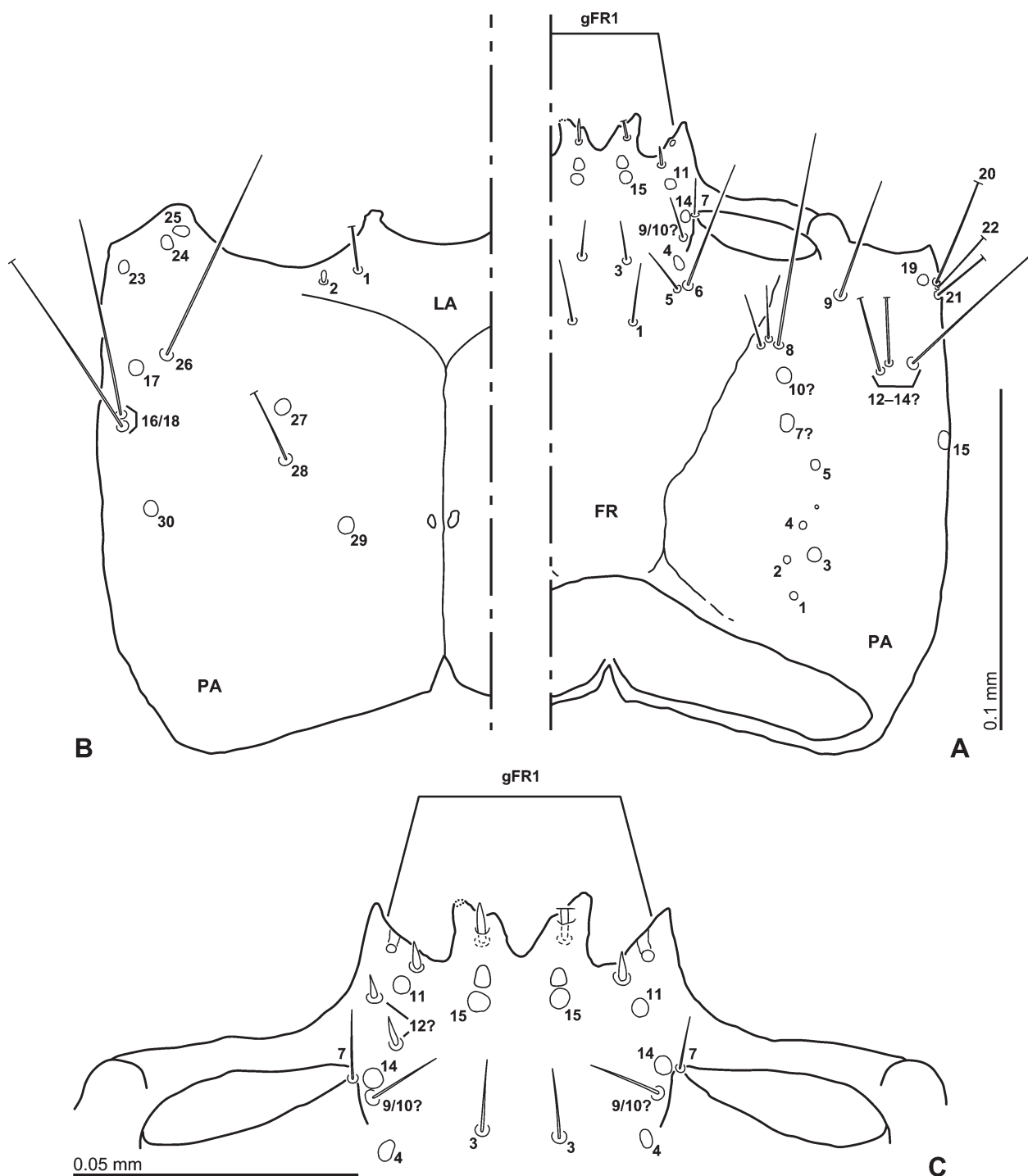
Figure 3. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A, B.** Head capsule, dorsal (**A**) and ventral (**B**) view; **C.** Anterior part of head capsule, dorsal view.

Stipes widest and longest, shorter than palpomeres 1–4 combined; maximum length of stipes as long as maximum width. Maxillary palpus somewhat stout, four-segmented; palpomeres 1–3 wider than long, 4 longer than wide. Approximate ratios of length of palpomeres 1–4 as follows: 1:0.6:0.6:0.7. Palpomere 1 widest and longest, completely cylindrically sclerotised; inner process small, sclerotised. Palpomere 2 shorter and narrower than pal-

pomere 1, as long as palpomere 4. Palpomere 3 shortest, narrower than palpomere 2. Palpomere 4 narrowest.

Labium (Fig. 4D) developed. Submentum subpentagonal, transverse, fused with head capsule; submental sulcus present. Submentum without large lateral extension, i.e., not fused with associate sclerites of cardo. Mentum subquadrate from ventral view; sclerite of dorsal face very deeply emarginated medially, narrowly and very strongly
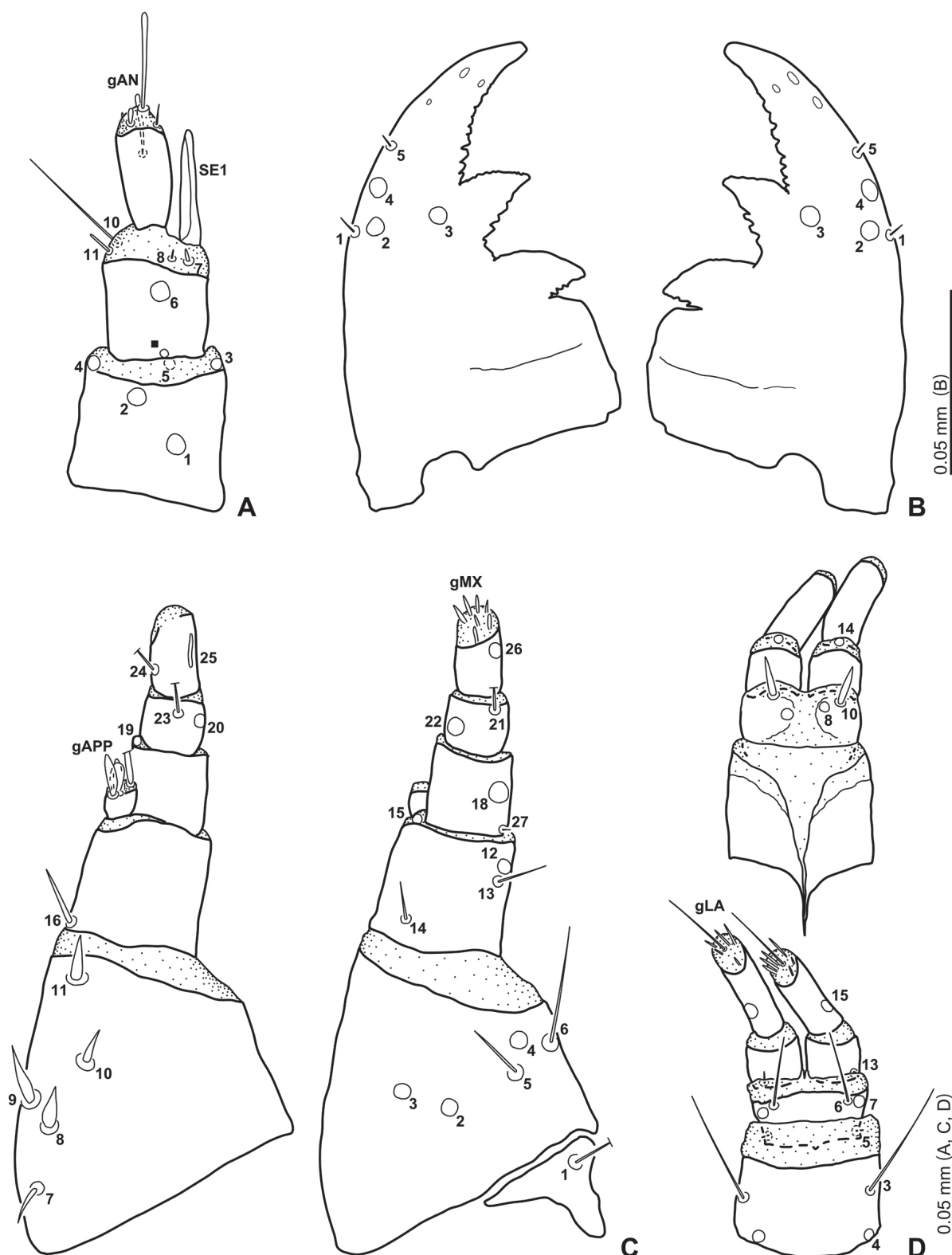
Figure 4. Larva of *Psalitrus yamatensis* Hoshina & Satô. **A.** Antenna, dorsal view; **B.** Mandibles, dorsal view; **C.** Maxilla, dorsal (left) and ventral (right) view; **D.** Labium (excluding prementum), dorsal (top) and ventral (bottom).

projected posteriorly at midwidth; border of sclerotised and membranous portions indistinct. Prementum subquadrate, transverse; median part of dorsal surface membranous. Ligula apparently absent or reduced to a minute membranous projection between palpomeres. Labial palpus moderately long, palpomere 1 wide, palpomere 2 narrower and distinctly longer than palpomere 1.

Thorax. Thoracic segments bearing microtrichiae, which may catch and securely keep the dirt on its integument, except for ventral area between legs; this area bare

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and not bearing dust as other parts. Prothorax slightly wider than head capsule (Fig. 1A). Proscutum formed by one large plate bearing several very long setae, subdivided by fine sagittal line, anterior and posterior margins weakly sclerotised. Prosternal sclerite transverse, not clearly detectable in the specimen. Mesothoracic spiracles forming small tubercle. Legs short, reduced to four segments, well sclerotised (Figs 1B, 2C). Trochanter and femur fused into a segment or trochanter reduced; coxa, tibiotarsus and claw (pretarsus) well defined.

Abdomen 10-segmented, widest in anterior half, then tapering posteriad (Fig. 1A). Membranous part densely bearing microtrichiae, covered with dirt. One pair of spiracles on lateral part of dorsal surface, weakly tuberculate. Spiracular atrium (Fig. 1C): segment 8 with oval dorsal sclerite bearing sparse microtrichiae and setae. Segment 9 trilobed, bearing long microtrichiae except for dorsal surface; median lobe of spiracular atrium with median emargination posteriorly. A pair of sclerotised urogomphi short, conical, bearing extremely long seta, fused basally, thus, outline of urogomphi looks to be V-shaped.

Primary chaetotaxy of head. Frontale (Fig. 3A, C). Rather long seta FR1 situated mesally at midlength of frontale. FR2 absent. FR3 short seta, anterior and slightly mesal to FR1. FR4–6 located behind inner margin of antennal socket; FR4 pore-like, slightly elongate, anterior to FR5 and FR6; rather long seta FR5 and long seta FR6 very closely situated, FR5 mesal to FR6. FR7 on inner margin of antennal socket. Two sensilla close to inner margin of antennal socket; pore-like sensillum FR14 mesal to antennal socket, rather short seta FR"9/10?" behind FR14. FR13 absent. Pore-like sensillum FR11 between FR14 and gFR1; left FR11 situated more anteriorly on than right one. Two short, stout setae (FR12 and additional seta) present between FR11 and FR14 (both marked as "12?" in Fig. 3C) on left; these absent on right. Pair of pore-like sensilla FR15 behind median two setae of gFR1. Six sensilla (gFR1) present on anterior margin of nasale; mesal four short, stout setae; character state of lateral ones unclear.

Parietale (Fig. 3A, B). Dorsal surface with a group of five sensilla (PA1–5) forming irregular longitudinal row in posterior part; PA1–2 and 4–5 may be short setae, PA3 pore-like. Minute additional pore present between PA4 and PA5. PA6 absent. Probable PA7 situated anterolaterally to PA5; PA7 may be a seta which is missing in the specimen. Very long seta PA8 and pore-like sensillum (probable PA10) anterior to PA7; PA8 close to frontal line; PA10 between PA7 and PA8. Two rather short additional setae close and mesal to PA8. Group of three long to very long setae lateral to PA8 and PA10; homology of them unclear (probably PA12–14); PA11 likely absent. Pore-like sensilla PA15 situated laterally at anterior two-fifths. Long seta PA9 posterolateral to antennal socket. PA19–22 situated dorsolaterally on anterior corner of head capsule; PA19 pore-like, dorsal to PA20–22; PA20–22 assumed very long to long setae, very closely aggregated; PA20 anterior to PA21; PA22 ventral to PA20

and PA21. Pore-like sensilla PA23–25 lateroventral, close to ventral mandibular articulation; PA23 lateral to PA24; PA24 and PA25 closely situated; PA24 posterolateral to PA25. Pore-like sensilla PA17 situated lateroventrally on anterior fourth of head capsule. Two very long setae (PA16 and PA18) posterior to PA17, precise homology of respective sensilla unclear. Very long seta PA26 close and mesal to PA17. PA27 and PA28 situated on median part of parietale, slightly anterior to midlength of head capsule; PA27 pore-like, anterior to PA28, PA28 seta. PA29 pore-like, posteromesal to PA28. Pore-like sensillum PA30 laterally on midlength of ventral surface.

Head appendages. Antenna (Fig. 4A). Antennomere 1 with five pore-like sensilla (AN1–5). AN1 situated dorsally on midlength of dorsal surface of sclerite. AN2 anterolateral to AN1, close to borderline between sclerite and membrane. AN3 and AN4 apically on intersegmental membrane or borderline between sclerite and membrane; AN3 on inner face, AN4 lateral face. AN5 apically on ventral surface. Antennomere 2 with seven sensilla. AN6 dorsally on subapical part of sclerite. One small additional or secondary pore-like sensillum on basal margin of sclerite. Minute setae AN7 and AN8, long seta AN10, short seta AN11, and sensorium SE1 on intersegmental membrane between antennomeres 2 and 3. AN7 and AN8 dorsally on lateral part, behind SE1. AN9 absent. AN10 and AN11 on lateral face. SE1 situated on outer face, slender and long, as long as antennomere 3, partly sclerotised. Antennomere 3 with group of apical sensilla (gAN) in apical membranous area. One ventral seta of gAN situated posterior to remaining sensilla; although borderline between membrane and sclerite hardly visible and almost undetectable, the seta seems to be on the borderline based on examination of very fine line indicated borderline.

Mandibles (Fig. 4B). Five sensilla (MN1–5) on anterior one-third to two-fifths; MN1 and MN5 short setae, MN2–4 pore-like sensilla. MN1 on anterior to midlength of mandible. MN2 mesal to MN1. MN4 anterior to MN2, between MN2 and MN5. MN3 lateral to MN2 and MN4. MN5 anterior to MN4. MN6 undetectable; three sensilla-like structures present on subapical part of mandible.

Maxilla (Fig. 4C). Cardo with one ventral seta (MX1). Inner face of stipes with irregular longitudinal row of five rather short setae (MX7–11); MX7 at base, slenderer than others; MX8–11 stout. Pore-like sensilla MX2 and MX3 situated ventrally on median part, MX2 posterolateral to MX3. Pore-like sensilla MX4, rather long seta MX5, and long seta MX6 situated subapically and ventrally on lateral face. MX6 lateral to MX4, MX5 posterior to MX4. Rather long seta MX16 basally on inner face of palpomere 1. Pore-like sensillum MX12 and rather long seta MX13 situated subapically on lateral face; MX12 anterior to MX13. MX14 ventrally and subbasally on inner part of sclerite. Pore-like sensillum MX15 ventrally on membrane behind inner appendage; MX17 absent. Inner appendage with few short apical setae of variable length (gAPP). Palpomere 2 with pore-like sensillum MX18 and minute seta MX27 on sclerite. MX18 lateroventral-

ly at midlength; MX27 basally on lateral face. Pore-like sensillum PA19 on inner face of intersegmental membrane between palpomeres 2 and 3. Palpomere 3 with two pore-like sensilla (MX20 and MX22), and two setae (MX21 and MX23). MX23 and MX20 on subapical part of sclerite; MX23 dorsal, MX20 lateral. MX21 apically on lateroventral part. MX22 on posteroventral part of inner face. Palpomere 4 with three sensilla (MX24–26) on sclerite. MX24 seta on inner face; digitiform (MX25) and pore-like (MX26) sensilla on lateral face, MX25 dorsal, MX26 ventral. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Fig 4D). Submentum with two pairs of setae (LA1 and LA2); LA1 trichoid, situated mesally to LA2; LA2 short, leaf-like, on lateral part. Mentum with one pair of very long setae (LA3) and pore-like sensilla (LA4) on lateroventral face; LA4 at base, LA3 anterior to LA4. Prementum with 5 pairs of sensilla (LA5–8, LA10). LA5–7 situated laterally on ventral face; minute seta LA5 at base; long seta LA6 and pore-like sensillum LA7 on apical part of sclerite; LA7 lateral to LA6. LA8 pore-like, dorsally on median part. Stout short seta LA10 anterolateral to LA8. LA9, LA11, and LA12 absent. Labial palpomere 1 with minute seta LA13 lateroventrally at base. Pore-like sensillum (LA14) dorsally on intersegmental membrane between palpomeres 1 and 2. Palpomere 2 with one pore-like sensillum (LA15) situated subbasally on outer face; several minute sensilla of variable shape and length (gLA) on apical membranous area.

Biology. Adults and the larva were collected from leaf litter (for the photograph of collecting locality, see Minoshima 2018: fig. 1H). They were collected together with adults and larvae of *Peratogonus reversus* (Omicrini), *Cercyon* sp., and *Armostus ohyamatensis* Hoshina & Satô, 2006 (both Megasternini).

Discussion

The larva of *Psalitrus* shows us multiple differences from other known larvae of Omicrini (*Omicrus*, *Peratogonus*, and an unidentified larva of *Noteropagus/Paromicrus*; Hayashi 1986; Hansen and Richardson 1998; Fikáček in press). The nasale bears clearly separated teeth in *Psalitrus* and *Peratogonus* (e.g., Fig. 3C), whereas it has aggregated irregular teeth in *Omicrus* and *Noteropagus/Paromicrus*. The median projection of the nasale is absent in *Psalitrus* (Fig. 3C), whereas *Omicrus* has the projection (the projection seems to be also present in *Peratogonus*; Y.N. Minoshima pers. obs. 2018). The epistomal lobe is absent in *Psalitrus* (Fig. 3C), whereas it is present in *Omicrus*, *Peratogonus*, and *Noteropagus/Paromicrus*. The surface of the head capsule is smooth in *Psalitrus*, whereas it is granulated in *Noteropagus/Paromicrus*; however, the surface structure is often different between first and third instar larvae. Although shape and relative length of head appendages are different between instars, short antenna and very wide and short maxillary stipes

are possible apparent characters of *Psalitrus* (Fig. 4A, C). The morphology of the dorsal surface of the mentum (Fig. 4D) is unique within the known larvae of Hydrophilidae; the mentum is morphologically variable between genera but never deeply emarginate as in *Psalitrus* (e.g., Archangelsky 1997; Archangelsky et al. 2016a). The legs are reduced to four segments (Fig. 2C), whereas they are five-segmented in *Omicrus* and *Noteropagus/Paromicrus*.

The phylogenetic position of the members of Omicrini, which is an early-diverging clade within the subfamily Sphaeridiinae (Short and Fikáček 2013; Fikáček et al. 2015), is reminiscent of ancestral characters of omicrine larvae. Short and Fikáček (2013) supposed two plesiomorphic characters of the larvae: the presence of teeth on the nasale (Fig. 3C) and well-developed legs (Fig. 2C). Larval morphology of *Psalitrus* supports their hypothesis, as *Psalitrus* larva shares several symplesiomorphies with aquatic clades as discussed below (Table 3).

The *Psalitrus* larva have distinct teeth on the nasale (Fig. 3C). Within Sphaeridiinae, the larvae of Megasternini and Protosternini do not have distinct teeth on the nasale (Archangelsky 1997, 1999; Fikáček et al. 2015, 2018a); the larvae of Sphaeridiini bear a simple, low, median projection (Archangelsky 1997); the nasale of Coelostomatini is more or less variable, ranging from that with a simple median projection resembling that of *Sphaeridium* Fabricius, 1775 (e.g., *Dactylosternum cacti* (LeConte, 1855) in Archangelsky 1994) to closely aggregated teeth-like projections resembling that of *Omicrus* (e.g., *Phaenonotum exstriatum* (Say, 1835) in Archangelsky et al. 2016b). In comparison to Cylominae, which is a sister taxon of Sphaeridiinae, distinct teeth on the nasale are common in the known aquatic or semi-aquatic larvae of Cylominae (*Anticura* Spangler, 1979, *Cylomissus* Broun, 1903, *Cylorygmus* Orchymont, 1933, and *Rygmodus* White, 1846; Minoshima et al. 2015, 2018; Seidel et al. 2018), and only the terrestrial genera *Andotypus* Spangler, 1979 and *Austrotypus* Fikáček, Minoshima & Newton, 2014 do not have distinct teeth on the nasale (Fikáček et al. 2014). It seems probable that the reduction of the toothed nasale corresponds to specialized prey preference and feeding behaviour in many terrestrial hydrophilid larvae. The reduction of teeth on the nasale is often associated with further modifications of mouthparts, i.e., asymmetry of nasale, mandibles and maxillae, and presence of an asymmetrical hypopharyngeal lobe (Archangelsky 1999; Fikáček et al. 2018a). The *Psalitrus* larva does not show such modifications, thereby resembling the larvae of the aquatic Cylominae and the majority of Acidocerinae (sister taxon of Cylominae + Sphaeridiinae) (e.g., Archangelsky 1997; Minoshima and Hayashi 2011). This outgroup comparison illustrates that the toothed nasale of larval Omicrini is a plesiomorphy as supposed by Short and Fikáček (2013), and a reduced nasale is an apomorphy that evolved independently in the Sphaeridiinae and the Cylominae.

Asymmetry of mandibles and maxillae are characteristics of megasternine and sphaeridiine larvae. Asymme-

Table 3. Morphological characters of Sphaeridiinae and Cylominae larvae.

	Sphaeridiinae					Cylominae
	Omicrini	Coelostomatini	Protosternini	Sphaeridiini	Megasternini	
Nasale	With teeth	With median projection to aggregated teeth-like projection	Without teeth	With a median projection	Without teeth	With/Without teeth
Asymmetrical median projection on nasale	Present/absent	Absent	Absent	Absent	Absent	Absent
Epistomal lobe	Present/absent	Present	Present	Absent	Absent	Present
Notch on left side of nasale	Absent	Absent	Absent	Present	Present	Absent
FR2	Absent	Present	Present	Present	Present	Present
FR7	Present	Present	Present	Absent	Absent	Present
PA6	Absent	Present	Present	Present	Present	Present
Mandibles	Symmetrical	Symmetrical/Asymmetrical	Symmetrical/Asymmetrical	Asymmetrical	Asymmetrical	Symmetrical/Asymmetrical
Stipes	Symmetrical	Symmetrical	Symmetrical/Asymmetrical	Asymmetrical	Asymmetrical	Symmetrical/Slightly asymmetrical
Chaetotaxy of inner face of stipes	MX7–11	gMX2	MX7–11	gMX2	gMX2	MX7–11/gMX2
MX17	Absent	Present	Present	Present	Absent	Present
Hypopharyngeal lobe	Absent	Present/Absent	Absent	Present	Present	Present/Absent
LA9	Absent	Present	Present	Absent	Absent	Present
LA10	Stout	Trichoid	Trichoid	Trichoid	Trichoid	Trichoid
LA11	Absent	Present/Absent	Present	Present	Absent	Present
LA12	Absent	Present/Absent	Present	Present	Present	Present
Legs	Reduced to 4 segments/5-segmented	5-segmented	5-segmented	Short rod-like, 5-segmented	Reduced, unsclerotized to 2-segmented	5-segmented
Basal additional pore on dorsal surface antennomere 2	Present	Absent	Absent	Absent	Present	Absent

try of mandibles has evolved multiple times in different clades within Hydrophilidae, including Coelostomatini and Protosternini; in contrast, asymmetry of maxillae is less common in Hydrophilidae (Archangelsky 2016; Fikáček et al. 2018a). Symmetry of mandibles and maxillae in Omicrini could be considered as plesiomorphies.

Legs of *Psalitrus* larva are well sclerotised but short and reduced to four segments (Figs 1B, 2C) by the fusion of the trochanter and the femur or reduction of the trochanter. The reduction of the trochanter was observed by Hansen and Richardson (1998) in *Omicrus*, in which it is still present but rather narrowly ring-like. In contrast, the possible *Noteropagus* or *Paromicrus* larva has a moderately sized trochanter (Fikáček in press). The reduction of larval legs is an evolutionary trend of terrestrial Sphaeridiinae, especially in the Megasternini + Sphaeridiini clade, in which the segments of legs are more or less reduced, appearing as a minute tubercle (*Oosternum* and some *Cercyon*) to minute two segments (some *Cercyon* and *Armostus*) or five-segmented but short, rod-like (*Sphaeridium*) (Archangelsky 1997, 1999, 2018; Minoshima 2018). The presence of legs in Omicrini is a plesiomorphy as supposed by Short and Fikáček (2013) based on the fact that terrestrial and aquatic cylomine larvae and acidocerine larvae have well-developed legs (e.g., Archangelsky 1997; Minoshima and Hayashi 2011; Fikáček et al. 2014; Minoshima et al. 2018).

This is the first detailed description of the larval chaetotaxy of Omicrini. Even though only one larva is available in this study and intraspecific variation is therefore still unclear, the chaetotaxy of *Psalitrus* larva shows apparent differences from the other larvae of Sphaeridiinae. Homology of some setae are still unclear, further investigations of omicrine larvae are essential to solve the homology of the sensilla.

Absence of FR2 (Fig. 3A) is unique within Sphaeridiinae; outside Sphaeridiinae, *Paracymus subcupreus* (Say, 1825) (Hydrophilinae, Laccobiini) exceptionally does not have the sensillum (Fikáček et al. 2008). On the clypeolabrum, two unique character states are observed: absence of the seta FR8 and pore FR13. Homology of the rather short seta behind FR14 is unclear; it is likely FR9 or FR10 than FR8 based on the position of the seta. Absence of gFR2 is shared with the larvae of Megasternini and Sphaeridiini; in contrast gFR2 is present in Coelostomatini and Protosternini (Archangelsky 2016). This is a possible convergence associated with the reduction of the epistomal lobe.

On the parietale (Fig. 3A, B), absence of PA6 is unique within Hydrophilidae. Homology of PA7 and PA10 is unclear because of a possibly broken seta; anterior and posterior sensilla may be PA10 and PA7 based on their position, respectively. Closely aggregated setae PA12–14 are similar to other megasternine larvae, whereas the

position of PA18 resembles some aquatic clades rather than Megasternini (e.g., Fikáček 2006; Minoshima and Hayashi 2011; Minoshima et al. 2017). Anterolateral position of PA26 seems to be similar to sphaeridiine larvae; however, this character is relatively variable within the subfamily (e.g., Archangelsky 2016, 2018; Fikáček et al. 2018a). A small basal additional pore on the dorsal surface of antennomere 2 is present in *Psalitrus* (Fig. 4A); Archangelsky (2016, 2018) considered this is an essential character for Megasternini. The character has been likely overlooked until Archangelsky (2016, 2018) pointed it out, and, therefore, it has not been described in detail in the majority of Hydrophilidae. Although the sensilla or sensilla-like structures on the basal part of antennomere 2 may be observed in the wider spectrum of Hydrophilidae taxa (e.g., Minoshima and Hayashi 2011, 2015; Minoshima et al. 2015, 2017), a distinct large pore is surely notable in Megasternini and *Psalitrus* only.

Arrangements of mandibular sensilla MN1–3 (forming a transverse row) and MN2–4 (forming a triangular group) (Fig. 4B) of *Psalitrus* and *Noteropagus/Paromicrus* (Fikáček in press) are expected to be potential synapomorhphies of Omicrini; however, these characters are often rather variable within the tribe and subfamily and therefore they shoule be carefully evaluated. Arrangements of MN1–4 resembles the myrmecophilous genus *Sphaerocetum* Fikáček, 2010 (Protosternini) and Coelostomatini (Clarkson et al. 2014; Fikáček et al. 2015; Archangelsky et al. 2016b); MN1 is situated more posteriorly than in other genera of Sphaeridiinae (e.g., Archangelsky 2018). Outside Sphaeridiinae, somewhat similar character states are present, e.g., in *Andotypus* and *Austrotypus* of Cylominae (Fikáček et al. 2014), and *Berosus* and *Regimbartia* of Berosini (Minoshima and Hayashi 2015; Rodriguez et al. 2018).

The inner face of stipes of maxilla bears five setae (MX7–11) (Fig. 4C); the character is shared with Protosternini and the majority of hydrophilids outside Sphaeridiinae, whereas Coelostomatini, Sphaeridiini, and Megasternini bear more than five setae (gMX2) (Fikáček et al. 2008, 2015, 2018a). The character is likely plesiomorphic because bearing gMX2 is a rather rare character outside Sphaeridiinae. The group of setae gMX2 is present in some Cylominae, and *Hydramara* of Hydrobiusini (Spangler 1979; Fikáček et al. 2014; Minoshima et al. 2015). The number of the setae rarely increases during larval development; five in the first instar larva but more than five in later instars in *Enochrus japonicus* (Sharp, 1873) (Minoshima and Hayashi 2011). Absence of MX17 is only shared with Megasternini, except for *Amphiops* Erichson, 1843 of Amphiopini, which does not bear MX17 and MX15 (Minoshima and Hayashi 2012).

The arrangement of LA1 and LA2 is unique, as LA1 is posterolateral to LA2 in other known hydrophilid larvae. The character state of LA10 (stout setae; Fig. 4D) is notable, as this sensillum is present as trichoid seta in the majority of Hydrophilidae with the exception of Megasternini and Sphaeridiini, in which LA10 is absent

(Fikáček et al. 2008). This character is shared with *Omicrus* (Hansen and Richardson 1998), and this is a possible synapomorphy of Omicrini. LA9, LA11, and LA12 are absent because of the reduction of labial structures. The reduction of labial sensilla is an evolutionary trend in several Hydrophilidae, which have modified labrum. Absence of LA9 is shared with Megasternini and Sphaeridiini, and absence of LA11 is shared with Megasternini, Sphaeridiini, and *Dactylosternum* (Coelostomatini); absence of LA12 is shared with *Dactylosternum* and *Laccobius* Erichson, 1837 (Laccobiini) (Archangelsky et al. 2016b; Minoshima et al. 2017; Archangelsky 2018; Fikáček et al. 2018b).

Psalitrus larva have characters shared with other known larvae of Omicrini, including potential synapomorphies of the tribe, the presumable plesiomorphies shared with aquatic hydrophilids and Cylominae, and the supposed derived characters, which are shared with Megasternini + Sphaeridiini, for an adaptation to terrestrial habitats.

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