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Notes on the identity of *Oiketicoides tedaldii* (Heylaerts, 1882) (Psychidae, Oiketicinae)

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Abstract. The identity of a group of species around *Oiketicoides tedaldii* (Heylaerts, 1882) is discussed. The comparison of the taxa in question shows that there is considerable uncertainty about the taxonomic classification of the various described populations of *Oiketicoides* around the Mediterranean. The type material of *O. tedaldii* was found to be lost and therefore it is necessary to define a neotype, in order to maintain the stability of the nomenclature. The distribution of *O. tedaldii* and related taxa is discussed and morphological and molecular differences are presented.

Zusammenfassung. Die Identität einer Gruppe von Arten um *Oiketicoides tedaldii* (Heylaerts, 1882) wird diskutiert. Der Vergleich der in Frage kommenden Taxa zeigt, dass eine beträchtliche Unsicherheit über die taxonomische Einordnung der verschiedenen beschriebenen Populationen von *Oiketicoides* im Mittelmeerraum besteht. Da das Typusmaterial von *O. tedaldii* verloren gegangen ist, ist es für die Stabilität der Nomenklatur zwingend notwendig, einen Neotypus festzulegen. Die Verbreitung von *O. tedaldii* und verwandten Arten wird diskutiert und die morphologischen und molekularen Unterschiede werden dargestellt.

Introduction

The genus *Oiketicoides* Heylaerts, 1881 comprises more than 40 species described in the Palaearctic (Sobczyk 2011; Sobczyk, Arnscheid and Nuss 2013; Arnscheid and Weidlich 2017). Others are of Afrotropical and Oriental distribution. In addition to the Central Asian steppes and arid areas of the Iberian Peninsula and the Mediterranean, the mountains of North Africa are the main distribution area of the genus. From the end of the 19th to the first half of the 20th century several species of this genus have been described by different authors but most descriptions, however, are based on only one or very few specimens. The taxa were rarely illustrated, and essential characteristics like the male genitalia were not been presented. This has led to considerable confusion about taxonomy of *Oiketicoides* up to the present.

In this context, a group of species around *Oiketicoides tedaldii* (Heylaerts, 1882) deserves special consideration. The taxon was first mentioned by Heylaerts (1881), who named “*tedaldii*” without description. It was been made nomenclaturally available by Heylaerts himself in 1882.

Since that time, *O. tedaldii* has been mentioned in numerous faunistic works, but also in works on systematics and taxonomy of Psychidae in various fields. Meanwhile it is unclear whether reported specimens represent *O. tedaldii* or another species, because it is very difficult for taxonomists or other workers who are less familiar with psychids to distinguish this species from the next closest related species that shares its distribution area. In the meantime, in addition to the sparse material in collections, various molecular data are now available, so that a more clearly defined picture of the taxonomic and zoogeographic relationships concerning *O. tedaldii* is now available. We attempt to explain these relationships and to provide diagnostic information for further investigations.

Material and methods

Abbreviations

CMZ	Research collection of Michael Zerafa, Naxxar, Malta
CTS	Research collection of Thomas Sobczyk, Hoyerswerda, Germany
CWA	Research collection of Wilfried R. Arnscheid, Bochum, Germany
DC	Discal cell
ICZN	International Code of Zoological Nomenclature
MFNB	Museum für Naturkunde Berlin
MWM	Museum Witt München
NMNL	National Museum of Natural History Naturalis Leiden
SMNK	Staatliches Museum für Naturkunde Karlsruhe
UWCP	University of Wrocław, Poland
ZSM	Zoologische Staatssammlung München

Indices

FI	Forewing index (maximum length from base to apex divided by the maximum width of the wings)
EI	Eye index (= smallest eye distance divided by the vertical eye diameter)

Images of male genitalia (procedure as described in Arnscheid and Weidlich 2017) were taken with an Olympus OMD EM10 Mark II digital camera using an Olympus stereomicroscope with photo adapter and stacked with COMBINE ZP using Soft Stack; sharpened and denoised with Neat Image V8 and post-processed with PHOTOSCAPE V.37. Images of the adults were taken with an Olympus E1 digital camera with a 35–50 mm macro lens and a series of 12 single shots stacked with COMBINE ZP using Soft Stack; sharpened and denoised with NEAT IMAGE V8.

DNA barcode sequences in BOLD are based on a 658 base-pair long segment of the mitochondrial COI gene (cytochrome c oxidase 1). DNA samples (dried legs) were prepared and successfully processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) to obtain DNA barcodes using the standard high-throughput protocol described in deWaard *et al.* (2008). Degrees of interspecific variation of DNA barcode fragments were calculated under the Kimura 2 parameter model of nucleotide substitution.

The taxonomic and collection data, voucher image, COI sequence and/or GenBank accession numbers are available for all specimens in the BOLD database (<http://www.boldsystems.org>). The neighbor-joining tree is based on the Kimura 2 parameter (K2P) model of nucleotide substitution

(Kimura 1980) as recommended in the barcoding protocol (Ratnasingham and Hebert 2007, 2013) was obtained using MEGA 7.

The terminology in the description of the morphology follows Arnscheid and Weidlich (2017).

Taxonomic problems

O. tedaldii plays a key role in the clarification of which *Oiketicoides* species are distributed around the Mediterranean Sea. It is also the first species of the genus described from North Africa. Nevertheless, it is possible that the specimens on which the description is based belong to a mixed series. Both the *Oiketicoides* species from the Near East and the European and North African species have a rather localised distribution none of which known more than one continent. Looking at the details in Heylaerts' original description of 1882, it is clear that he only had two male adult specimens at his disposal. He named this new species after Luigi Failla-Tedaldi, (1853–1933 from Palermo, Sicily, Italy). However, no adult specimen from Sicily is specified. Heylaerts only mentioned several larval cases, which he had received from Zeller in 1847 from the vicinity of Anapo in Sicily, as well as further caterpillars taken by Failla-Tedaldi from Sicily, also without males, since both breedings failed. These larval cases are the only evidence for a possible occurrence of *O. tedaldii* on Sicily. The total number of syntypes is unknown, but must be larger than four. Thus, there were only larval cases from Sicily, which cannot be assigned today with absolute certainty to *O. tedaldii* since the whereabouts of the two male adults cannot be ascertained. At the end of 1881 Heylaerts received from M. Chevalier a male with the corresponding characteristic larval case from Algiers. At the same time, he mentions that this specimen corresponds “in every respect” to another specimen from Syria, which he had received from O. Staudinger to compare and describe. It can be assumed that it was from these two specimens that the description of *O. tedaldii* was made. Just as the type specimens have equal rights for primary type designation, the type localities (Sicily, Algiers, Syria) are those of the syntypes. Heylaerts further noted, however, that he compared the specimens in his possession with *O. febretha* (Boyer de Fonscolombe, 1835) and *O. lutea* (Staudinger, 1871). Here a new taxonomic problem begins. With the means and comparative collections for determination available at the time, at least *O. tedaldii* and *O. lutea* could not be separated with absolute certainty. Hence, the type material had to be studied for this paper.

The Heylaerts Collection at NMNL does not contain any of the specimens mentioned above. Six specimens (pins with one or more larval cases, some with female exuvia and label) with the numbers RMNH.INS.1283464–1283469 have been subsequently marked by an unknown person with red labels “Museum Leiden, SYNTYPE, *Acanthopsyche tedaldii* Heylaerts, 1882”. This is a mistake. Three larval cases bear female exuviae and one of these is labelled “*Heylaertsii*”. In the description of *Amicta tedaldii* Heylaerts points out that females are unknown. But Heylaerts had females of *Psyche heylaertsii* available to him because Millière reported on Heylaerts' observation that a female of “*Psyche*” *heylaertsii* laid 210 eggs. However, there is no evidence that the case specimens in NMNL actually belong to the syntypic series of *P. heylaertsii*. Thus there are no males and larval cases which can be safely identified as *O. tedaldii*. The syntypes of *O. tedaldii* must be considered lost.

The descriptions of *P. heylaertsii* and *A. tedaldii* remain of primary importance. Heylaerts does not compare Millière's description of *P. heylaertsii* with his *A. tedaldii* and lists it in contrast as a further species. It is therefore probable that Heylaerts detected differences between these two species. Later, Kirby (1892) listed *P. heylaertsii* as a subjective junior synonym of *Psyche febretha*

var. *lutea* (Staudinger, 1871). On the other hand, Millière expressly points out that the specimens on which the description of *P. heylaertsii* is based, were also given to him by Failla-Tedaldi. They were collected in North-Eastern Sicily at an altitude of 1800 m in the Nebrodi Mountains, therefore, they may have been found in the summit area of Mt. Soro (1847 m). So, it appears there were two different consignments from Failla-Tedaldi, the first with *P. heylaertsii* Millière, reaching Heylaerts in 1878 or earlier. The other could have been the result of a targeted search in the Anapo Valley, which reached Heylaerts in 1881. Except for Sicily, records of *P. heylaertsii* from southern Italy come from Puglia, Calabria, Molise and Abruzzo (Porcelli and Parenzan 2006).

Millière described and depicted *Psyche heylaertsii* in 1878. However, this name has fallen into oblivion mainly because Millière's description lacks a geographic origin of this taxon. However, in a further publication (Millière 1881), he left no doubt that as already mentioned he referred to specimens from the Nebrodi Mountains in Sicily. Kirby (1892) synonymized *P. heylaertsii* and *P. sera* in his catalogue, but obviously he did not know the correct year of the description of *P. heylaertsii* and therefore he refers erroneously to Millière's work of 1881. In his monograph Heylaerts (1881) listed among the genus *Amicta* the taxon *tedaldii* as a separate species besides *Psyche heylaertsii* Millière, 1878. *Psyche sera* Wiskott, 1880 is listed as a synonym of *Psyche heylaertsii*. Thus, it is not *P. sera*, as Kirby states, but *P. heylaertsii*, that is the older and therefore the valid name for the taxon in question here.

During the studies for this paper, we examined in the Staudinger Collection at MFNB *Oiketicoides* specimens that might be considered as syntypes of *O. tedaldii*. One of these specimens is labelled "*lutea* var. *timona* Heyl.". No taxon bearing this name has ever been described. In any case, the name "*timona*" indicates an origin from Syria, because it is the name of a deacon of the ancient Christian community in the 1st century, who later lived in Aleppo. As already shown, Syria may be a possible locality for *O. tedaldii*. But unfortunately, we found this and another questionable specimen in the Staudinger collection which is labelled "*lutea* var." both belonging to another species, probably *O. jordana* (Staudinger, 1899).

Despite intensive searches, the syntypes of *O. tedaldii* could not be found and they must be considered as lost. It can be recognised without doubt that Heylaerts knew two different species of *Oiketicoides* from Sicily, which according to current understanding are *O. tedaldii* and *O. lutea* (respectively; *Psyche sera* and *Psyche heylaertsii* being probably synonyms of the latter). Even today this situation has not changed. Furthermore, the frequency of the cases of *O. tedaldii* at several locations described by Heylaerts allows the conclusion that it was and is a widespread species. Altogether it was impossible to verify true *O. tedaldii*, neither from the Near East nor from North Africa. The exclusion of *O. lutea* and the presence of another *Oiketicoides* species in Sicily allows at least the identity of the Sicilian species to be established with respect to *O. tedaldii*. This is also the case with the two *Oiketicoides* species occurring on Malta. One of these species could be identified as *O. tedaldii* by its morphological characters, larval cases and DNA barcode (Arnscheid, Weidlich and Zerafa, unpubl.). Such a reconstruction is not possible for the North African and Near Eastern species due to their much higher diversity (Sobczyk and Arnscheid, in prep.) and low proportion of undescribed species.

Molecular analysis of the *Oiketicoides* species mentioned here

In the BOLD, the database of the Canadian Centre for DNA Barcoding (CCDB) as well as on the GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>), several publicly accessible samples are

Table 1. Pairwise DNA barcode divergences between two *Oiketicoides* taxa from South Europe.

Species	Sequence No.	Locality	Pairwise distance (%)					
<i>Oiketicoides tedaldii</i>	GBGL32882-19	Malta						
	GBGL32883-19	Malta	0.00					
<i>Oiketicoides lutea</i>	GWORU342-10	Cosenza, Italy	13.8	13.8				
	GWORZ165-10	Cosenza, Italy	13.6	13.6	0.3			
	PSYCH086-11	Zagoria, Greece	13.7	13.7	0.2	0.2		
	PSYCH140-12	Calabria, Italy	13.8	13.8	0.1	0.2	0.1	

**Figure 1.** Neighbor-joining tree of the *Oiketicoides* species from South Europe.

available, which belong to the taxa *O. tedaldii* and *O. lutea*. The samples are generated from the following Barcode Index Numbers (BIN) BOLD:AAM0038 (GWORZ165–10), BOLD:AAP3634 (GWORU342-10), BOLD:ABU7325 (PSYCH086–11). The Sequence No. PSYCH140–12 has no BIN. The Sequence Nos. GBGL32882–19 and GBGL32883–19 were generated from GenBank Access Numbers KX399366 and KX399372. This shows that the infra-specific divergence is a maximum of 0.3 % or zero whichever is applicable in *O. lutea* but negligible in *O. tedaldii*. In contrast, the interspecific divergence between *O. lutea* and *O. tedaldii* is 13.3–13.8% (Tab. 1, Fig. 1). This also shows, that in South Europe two distinct *Oiketicoides* species exist, from which one must be the previously enigmatic *O. tedaldii*.

The identity and distribution of *O. tedaldii* (Heylarts, 1882)

Considering the taxa of the genus *Oiketicoides* in the western Mediterranean area, starting from the presumed distribution area of *O. tedaldii*, three taxa are questionable according to previous knowledge. One of them is *O. febredda*. However, a confusion with *O. tedaldii* (sensu lato) can be excluded, as *O. febredda* is an easily recognisable species, which was certainly understood correctly in the past. Thus the taxa *O. lutea* and *Psyche sera*, which some authors considered as separate species, are preserved remain, but according to Heylarts (1881) *Psyche sera* is a junior synonym for *Psyche heylaertsii* and thus, according to Kirby (1892) to *O. lutea*.

Wiskott's (1880) description of *P. sera* is very short: “♂, Alis cinereis; capillis inferiore capitis parte, antennis, margine anteriore alarum anticarum, ciliis nigro-cinereis; capillis superiore capitis parte, thorace, abdomine, pedibus, cano-flavescentibus. Lutea propinqua, sed minor, colore obscuriore, antennis, tenuioribus, alis magis rotundatis, Esp. 21 mm. ♀: Ignota. Patria: Sicilia (Litus septentrionale).“

Translation: “♂, Wings grey; the lower part of the head, antennae and the edge of the forewings darker black-grey, the upper part of the head, the thorax and the feet are greyish yellow-brown. Closely related to *O. lutea* Stgr., but smaller, darker colours and more rounded, thin wings, span 21 mm. ♀: unknown. Region: Sicily.”

The description partly correlates with both *Oiketicoides* species occurring on the island of Sicily. Especially the statement that *O. lutea* has rounder wings does not allow to exclude with absolute certainty that Wiskott's specimen might not have been *O. tedaldii*. The surprising recovery of the only syntype of *P. sera* in the Wiskott Collection in UWCP, however, shows that this taxon is without question the one also known as “*sera*” in today's sense.

Looking closer to the distribution areas of these three taxa known from literature shows the following result: The type locality of *O. lutea* is Mt. Veluchi in Greece. The species is also mentioned from Albania, Bulgaria, Crete, Sicily, Italy, North-Macedonia, Croatia and Serbia. Furthermore, Armenia, Georgia, Turkey, Iraq, Lebanon, Palestine, Syria and Russia are mentioned, however, the latter records will most likely be confused with other species. Concrete evidence of distribution is only available from the wider Balkan region.

Since it was not possible to find syntypes of *O. tedaldii*, and in regard to the taxonomic problems outlined above, there is an urgent need for the stability of the nomenclature to define a neotype. The determination of a neotype is in accordance with Art. 75 of the ICZN (Kraus 2000). For this purpose, the diagnostic characteristics of the specimens considered for this taxon are compared below. One indication of Heylaerts (1882) in his description can be considered as particularly important: the larval cases of the species he describes are characteristically covered with fragments of shells of small molluscs. We therefore assume that the specimens with the corresponding larval cases now available to us represented the taxon that Heylaerts described in 1882 as *O. tedaldii*. Oberthür (1909) pictured a male, female, and such a typical larval case as *O. tedaldii* from Algeria (Khenchala). Last but not least, due to the fact that no certain specimen (with the characteristic larval case) of *O. tedaldii* from North Africa nor from the Near East is available, we select a specimen with a larval case from Sicily for neotype:

***Oiketicoides tedaldii* (Heylaerts, 1882)**

Figs 2(1), 4

The neotype is labelled as follows:

1) Sicilia, Ficuzza, 16.ix., Krüger Geo. C. 2) det. Dr. Wehrli *A. tedaldii* Heyl. 3) *Oiketicoides tedaldii* Heyl., det. Arnscheid, Präp. 4077 4) Slg. Daniel. 5) red label: NEOTYPUS, *Oiketicoides tedaldii* (Heylaerts, 1882).

The neotype is deposited in the MWM.

Description. Head dorsolaterally long, yellowish brown, hair-shaped scaled. Eyes ovoid, AI: 0.54. Antennae bipectinate with 29 pecten. Pecten ciliated and scaled. Antennae length 5 mm. Wings light brown, forewings costa straight, apex roundish, termen oblique. Underside equally coloured. Fringes yellowish brown with a whitish gloss distally. Wingspan 22 mm, wing length 9 mm, wing



Figure 2. 1, 1a. Neotype of *Oiketicooides tedaldii* (Heylaerts, 1882) and labels in MWM. 2, 2a. Holotype and labels of *Psyche lutea* Staudingee (1871) in MFNB. 3. Holotype of *Amicta sera* Wiskott, 1880 in UWCP. 4, 5. Case and labels of *Psyche heylaertsii* Millière, 1878, erroneously labelled as syntype of *Acanthopsyche tedaldii* Heylaerts, 1882 (NMNL).

width 5 mm, FI: 1.8. Scales short, unstalked or short stalked. Mostly with two dentations, partially with 3 dentations (classes 1–2, after Sauter 1956). Fringes yellowish brown with a whitish gloss distally. Fringe scales with 3–5 dentations. Forewing venation with 10 veins from discal cell. Discal cell divided, veins r3+r4 stalked of 1/3 length. Hindwing venation with 7 veins, m1 and m2 short stalked. Genitalia (slide 4077 Arnscheid): Tegumen and vinculum fused. Tegumen ovoid, folded laterally. Valva short and broad, of tegumen length. Distinctly indented above vinculum laterally. Vinculum stretched, triangle shaped. Clasper of sacculus short and slender, covered distally with 6 short spines. Saccus long and stretched, of tegumen length. Phallus very long, thick, weakly curved, vesica without cornuti but with a broad pointed process laterally.

The confirmed distribution of *O. tedaldii* with both specimens and cases is thus from Italy: Sicily [Ficuzza, Madonie, Caltanissetta], Malta [Imtähleb, Bingemma, Naxxar Gap, Għarghur: Ġebel San Pietru, Mellieħa]. As has already been shown, there are hints that this species also occurs in Algeria and Tunisia (Fig. 8a, b).

Redescription of the male morphology of *O. tedaldii* (Heylaerts, 1882)

Figs 3 (1–3), 4, 6 (1–4), 7 (1, 4)

Head dorsolaterally long, yellowish brown, hair-shaped scaled. Eyes ovoid, AI: 0.54–0.55. Antennae bipectinate with 29–30 pecten. Pecten long ciliated. Antennae length 5 mm. Wings light brown, forewings costa straight, apex roundish, termen oblique. Underside equally coloured. Wingspan 20–24.5 mm. Forewing with 10 veins from discal cell, r3+r4 and m2+m3 stalked. Junction of vein m1 to DC complete. Hindwing with 7 veins from DC. Veins m2+m3 stalked. Sometimes with small, intercalated cells at the base with the DC, FI: 1.8–1.9. Scales short, unstalked or short stalked. Mostly with two dentations, partially with 3 dentations (classes 1–2, after Sauter, 1956). Fringe scales whitish, light brown basally, distinctly glossy, with 3–5 dentations. Less indented than in *O. lutea*. Genitalia: Tegumen and vinculum fused. Tegumen ovoid, folded laterally. Valva short and broad, of tegumen length. Distinctly indented above vinculum laterally. Vinculum stretched, triangle shaped. Clasper of sacculus short and slender, covered distally with 6 short spines. Saccus long and stretched, of tegumen length. Phallus very long, thick, weakly curved, vesica without cornuti but with a broad pointed process laterally. Larval Case: Male length 20–25 mm, diameter 5.5–6 mm. Cylindrical, slightly curved with circular cross section, covered with fine particles of soil and bits of broken snail shells, twigs, mineral debris and dry plants matter. Front opening is covered with smaller plant material and soil.

Redescription of the male morphology of *O. lutea* (Staudinger, 1871)

Figs 3 (4–10), 5, 6 (5–6), 7 (2, 3, 5, 6)

Head dorsolaterally long, brown hair-shaped scaled. Eyes ovoid, AI: 0.67–0.68. Antennae bipectinate with 33–34 pecten. Pecten long ciliated. Antennae length 5 mm. Wings light brown, forewings costa mostly slightly concave in the basal half, apex roundish, termen oblique or roundish. Underside equally coloured. Wingspan 21–25.5 mm. Forewing with 10 veins from discal cell, r3+r4 and m2+m3 stalked, rarely from one-point rising or completely divided. Junction of vein m1 to DC complete. Hindwing with 7 veins from discal cell. Veins m2+m3 stalked. Small, intercalated cells at the base of the DC absent, FI: 1.82–1.93 (the southern populations of Greece and Italy mainland and

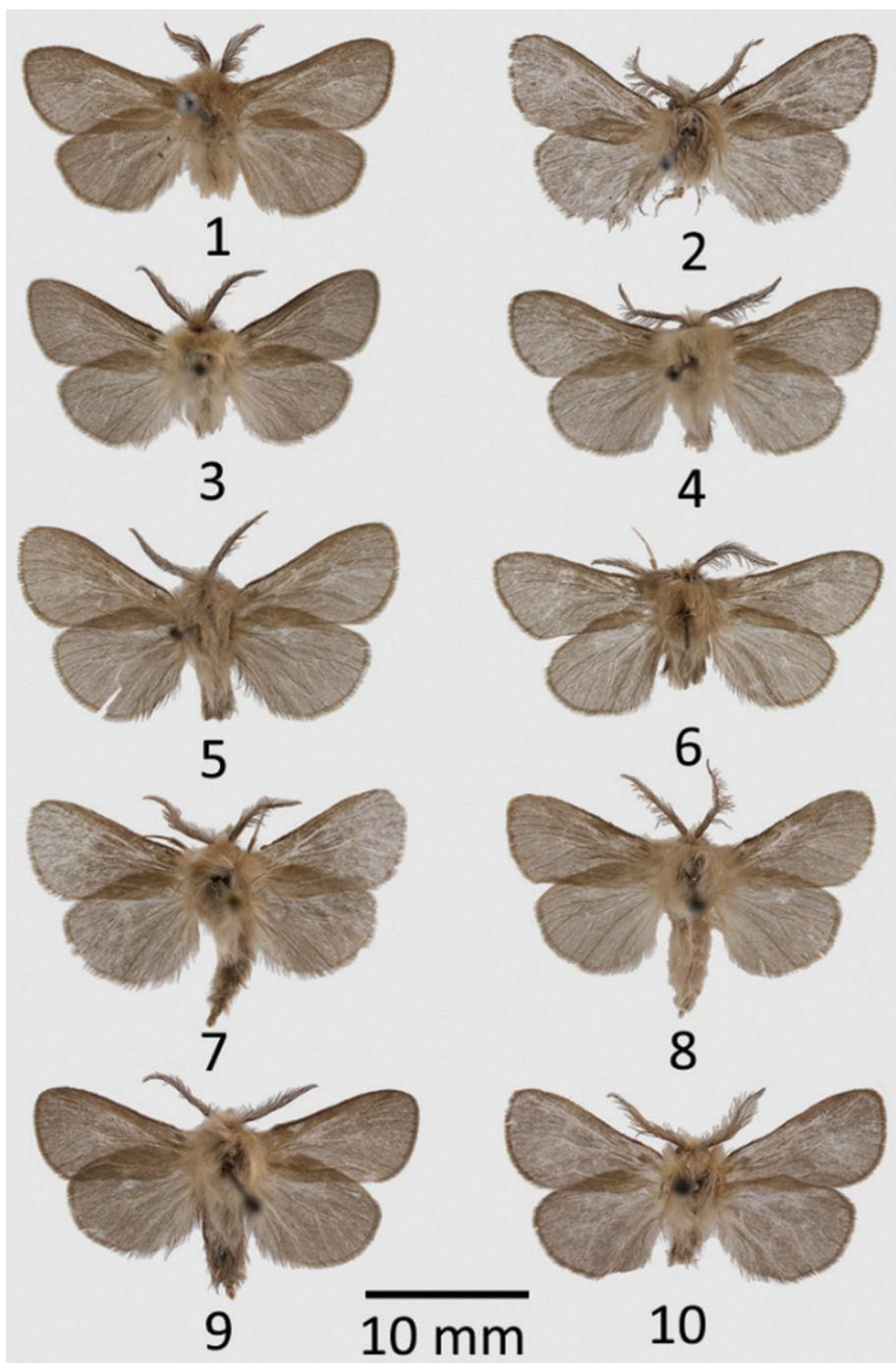


Figure 3. Males of *Oiketicoides tedaldii* and *O. lutea* from Europe. **1.** *O. tedaldii*, neotype, Italy, Sicily, Ficuzza. **2.** *O. tedaldii*, Italy, Sicily, Madonna. **3.** *O. tedaldii*, Malta. **4.** *O. lutea* Italy, Sicily, Madonna. **5.** *O. lutea*, Italy, mainland, Sila mts. Spaviera. **6.** *O. lutea* Italy, Taranto, San Paolo. **7.** *O. lutea*, Italy, Sicily, Agrigento. **8.** *O. lutea* Italy, Caltanissetta, Barburra. **9.** *O. lutea*, North Macedonia, Lake Ohrid. **10.** *O. lutea*, Greece, Zachlarou.

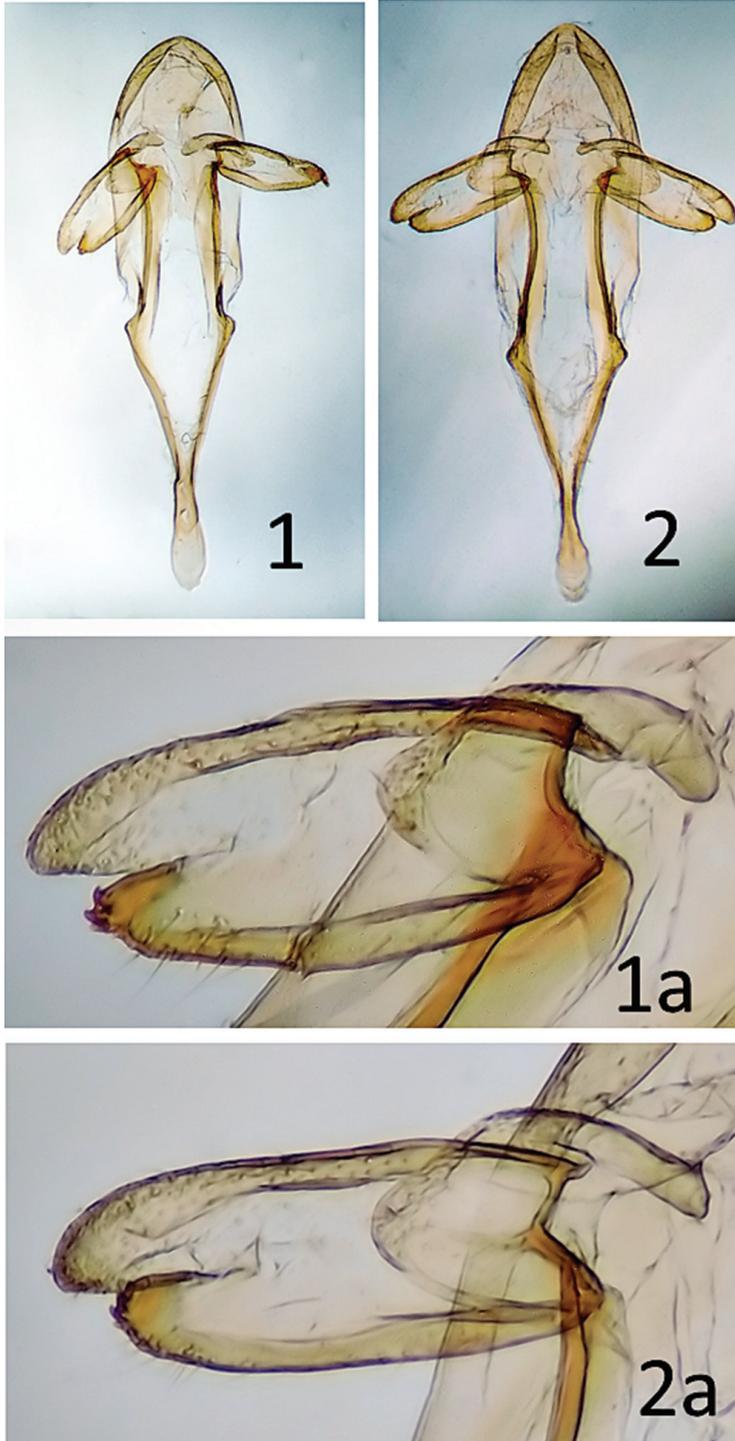


Figure 4. Male genitalia of *Oiketicoides tedaldii* (Heylaerts, 1882). **1, 1a.** Neotype, Italy, Sicily, Ficuzza, (genital slide 4077, CWA). **2, 2a.** Italy, Sicily, Caltanissetta (genital slide 4084, CWA).

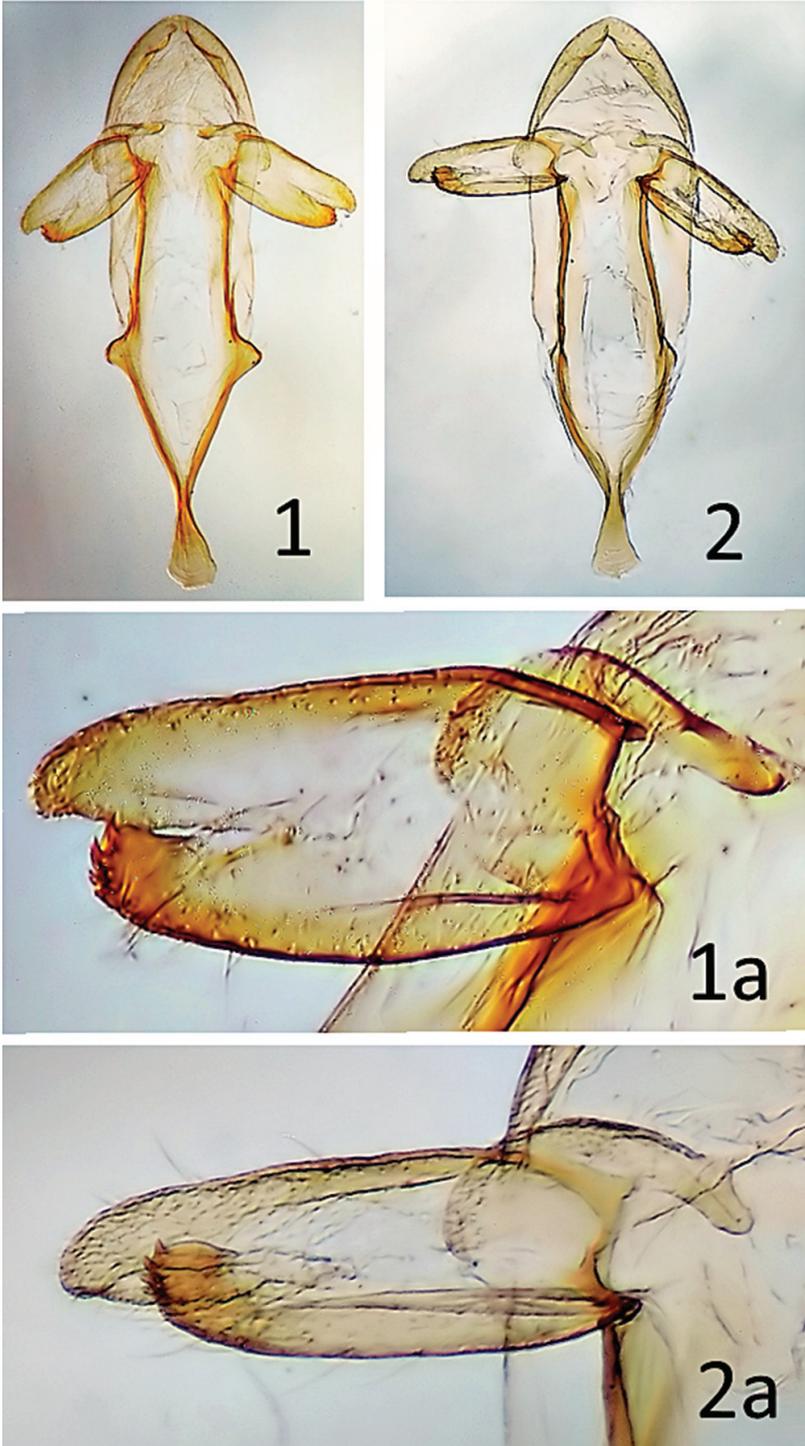


Figure 5. Male genitalia of *Oiketicoides lutea* (Staudinger, 1871). **1, 1a.** Italy, Sicily, Madonic (genital slide 4079, CWA). **2, 2a.** Italy, Sicily.



Figure 6. The larval cases of *Oiketicoides tedaldii* (Heylaerts, 1882) and *O. lutea* (Staudinger, 1871). *O. tedaldii*: **1, 2.** Italy, Sicily, **3.** Tunisia, **4.** Malta. *O. lutea*: **5, 6.** Sicily.

Sicily, n = 17) and 2.14 (Populations of northern Balkans, n = 15). Scales elongated, lanceolate, unstalked or short stalked. Mostly with 1–2 dentations (classes 1–2, after Sauter 1956). Fringe scales whitish, light brown basally, distinctly glossy, with 3–5 dentations, deeper indented than in *O. tedaldii*. Male Genitalia: Tegumen and vinculum fused. Tegumen ovoid, folded laterally. Valva short and broad, of tegumen length. Not or only slightly indented above vinculum laterally, with distinctly visible or intimated triangle-shape projects laterally. Vinculum broad, triangle shaped or slightly rounded laterally. Clasper of sacculus short and mostly broader than in *O. tedaldii*, covered distally

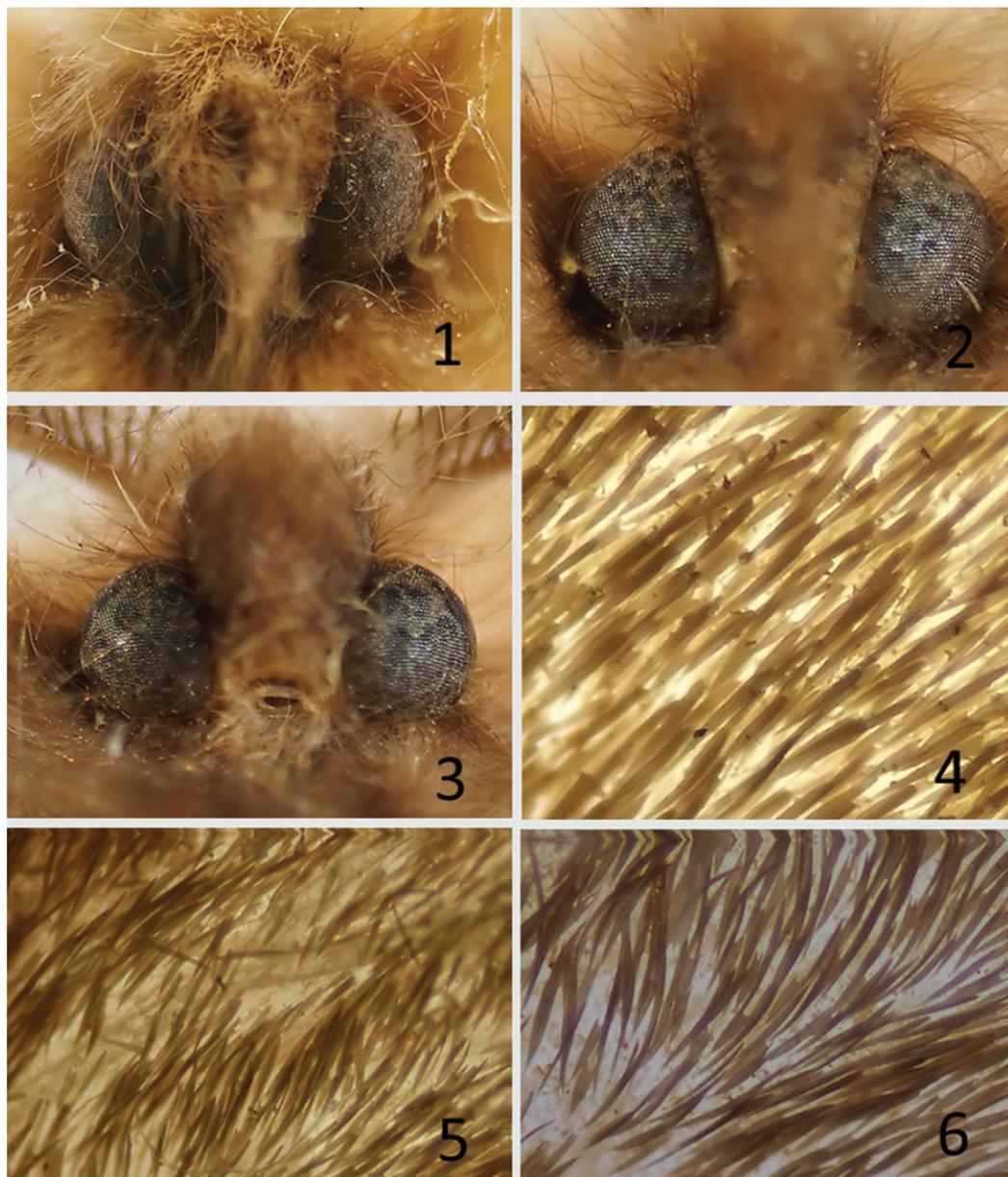


Figure 7. Eye area and forewing scales of the *O. tedaldii*-species group. **1, 4.** *O. tedaldii*, neotype, Italy, Sicily. **2, 5.** *O. lutea*, Italy, Sicily, Madonie. **3, 6.** *O. lutea*, North-Macedonia, Lake Ohrid.

with 5–6 longer spines. Saccus short and widened and rounded distally, fishtail-shaped. Phallus very long, thick, weakly curved, vesica without cornuti but with a broad pointed process laterally. Larval Case: Length 19–25 mm, diameter 5–6 mm. Cylindrical, covered with fine particles of soil, twigs, mineral debris and dry plants matter. Front opening is covered with smaller plant material.

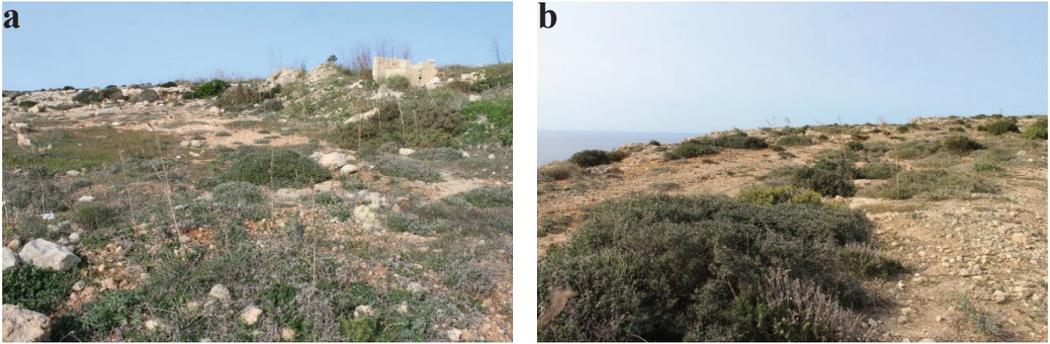


Figure 8. a, b. Habitat of *O. tedaldii*, Malta, Imtahleb, 184 m. Photos: M. Zerafa

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Without the help of our friends and colleagues this work would not have been possible. Thomas J. Witt (†) generously enabled us to work on the material of his extensive collection for many years. The same applies to Robert Trusch and Michael Falkenberg (both SMNK) as well as Wolfram Mey, Viola Richter and Théo Léger (all MFNB). Furthermore, we would like to thank Peter Hättenschwiler (Uster), Marek Wanat (UWCP) and Ana Nahirnic (Sofia) for their valuable help in different ways. Our special thanks goes to Rob de Vos (NMNL) for his support while searching for the type material of *O. tedaldii*. We also thank one reviewer for helpful discussion and careful review of the manuscript.

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DNA barcoding and genomics reveal *Perizoma barrassoi* Zahm, Cieslak & Hausmann, 2006 as new for the fauna of Central Europe (Lepidoptera, Geometridae, Larentiinae)

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<http://zoobank.org/7669F4FC-EB0C-4EB7-A0F4-8BDD14D3EF6F>

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Subject Editor: Sven Erlacher.

Abstract. *Perizoma barrassoi* Zahm, Cieslak & Hausmann, 2006, previously considered a central Italian endemic, shows a much wider distribution with additional records from the Alps and the Pyrenees, in partial sympatry with its sister species, *Perizoma incultaria* (Herrich-Schäffer, 1848) which is widespread in the Alps, Pyrenees, Carpathians and Dinaric mountains. The disruptive genetic patterns of both species involve the COI barcode gene as well as nuclear genomic data and are confirmed by correlated differential features in male and female genitalia. To fix nomenclatural stability a neotype is designated for *P. incultaria*.

Introduction

In his outstanding revision of European Perizomini and Eupitheciini, Mironov (2003) presented *Perizoma incultaria* (Herrich-Schäffer, 1848) as a species with montane distribution in the Alps, Pyrenees, Carpathians and western Balkan peninsula with comparatively narrow vertical distribution in the south (from 1500 m up to 2200 m), but with a much wider range in the Alps (from 1000 m up to 3200 m). *Perizoma incultaria* is known as the only European geometrid species which has leaf-mining first larval stages (on Primulaceae).

Three years after the publication of Mironov's monograph, Zahm et al. (2006) described a Central Italian sister species, *P. barrassoi*, based solely on a singleton male specimen from Maiella mountains that was designated as the holotype, and a female paratype from the same locality, the latter subsequently found out to be a misidentified, unusually small specimen of *Colostygia aqueata* (Hübner, 1813) (Müller et al. 2019). One additional specimen of *P. barrassoi* was collected by H. Rietz at high elevation on the Central Italian Monte Terminillo, just 100 km from the type locality, and could successfully be DNA barcoded, revealing a very large genetic divergence of 8.9% to *C. incultaria* (Müller et al. 2019). The reasons for attributing this Central Italian specimen to *P. barrassoi* are outlined below under the 'Remarks' to the Results section.

Müller et al. (2019) mentioned a genetic haplotype within the Alpine populations of '*Perizoma incultaria*' which is very close to that of *P. barrassoi* (at just 1.1% distance) and thus far distant from the genetic cluster of *P. incultaria*. The distinctness of this second Alpine COI cluster compared

with *P. incultaria* was confirmed by ddRAD sequencing involving hundreds of genome-wide nuclear loci (Mutanen *et al.* 2017; Müller *et al.* 2019). In this paper we present new insights from Sanger-sequenced DNA barcodes and from additional High-Throughput Sequencing (HTS) of the COI barcode gene fragment of material collected close to the type localities as well as from extended dissections. We show that *P. barrassoi* is much more widespread than originally thought.

Material and methods

The study is based on more than 250 specimens of *Perizoma incultaria* and *P. barrassoi*, including 46 dissections, 29 DNA barcodes and ddRAD-data for eight specimens. The material is housed at the following collections:

- HNS** Haus der Natur, Salzburg, Austria;
- RCTM** Research Collection Toni Mayr, Feldkirch, Austria;
- TLMF** Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria;
- ZSM** SNSB – Zoologische Staatssammlung München, Germany.

Taxon delineation

The taxa were delimited on the basis of combining data from various sources: morphology, bionomy (mainly phenology, partly vertical distribution) and DNA barcodes. The genitalia and the abdomens were prepared following methods described by Hardwick (1950). Morphological analyses were performed with a Wild microscope (308700), measurements were taken with a calibrated measuring eyepiece, slide photographs were taken with multilayer automontage technique (Helicon software) at a Leica microscope (DM2700M).

DNA barcoding

For the DNA barcoding analyses, one or two legs were removed from each dried specimen and transferred to lysis plates. DNA extraction, amplification, and sequencing of the barcode region of the mitochondrial cytochrome c oxidase I (COI) gene (658 base pairs) were carried out in the Canadian Centre for DNA Barcoding, Guelph, Ontario, Canada (CCDB), using standard high throughput protocols (Ivanova *et al.* 2006), those are described at CCDB (2020). Sequence divergences within and between species were calculated using the Kimura 2-parameter model (Kimura 1980) and the Neighbor-joining algorithm (Saitou and Nei 1987), as implemented in the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007). High Throughput Sequencing (HTS) of old museum material was performed at the CCDB following the methodology presented by Prosser *et al.* (2016) and Speidel *et al.* (2015).

ddRAD library preparation and bioinformatics

We used DNA aliquots that were extracted at the Canadian Centre for DNA Barcoding (CCDB) following laboratory protocols used routinely in CCDB as explained in DeWaard *et al.* (2008). The quantity of genomic DNA (gDNA) extracts was checked using PicoGreen kit (Molecular Probes). To reach sufficient gDNA quantity and quality, whole genome amplification was performed using the REPLI-g Mini Kit (Qiagen) due to its low concentrations of gDNA in the original extracts. The ddRAD library was implemented following protocols described in Lee *et al.* (2018) with two exceptions: gDNA was

digested with *Pst*I and *Msp*I and the size distribution and concentration of the pools was measured with Bioanalyzer (Agilent Technologies). The de-multiplexed fastq data are archived in the NCBI SRA: SRP155304. Raw paired-end reads were de-multiplexed with no mismatches tolerated using their unique barcode and adapter sequences using *ipyrad* v.0.7.23 (Eaton and Overcast 2016). All *ipyrad* defaults were used, with the following exceptions: the minimum depth at which majority rule base calls are made was set to 3, the cluster threshold was set to 0.95, the minimum number of samples with data for a given locus to be retained in the final dataset was set to 2 to 8, and the assembly method was set to ‘denovo’ and ‘reference’ for independent testing. The ‘denovo’ method assembled sequences without any reference resources. The ‘reference’ assembly method mapped sequences to *Operophtera brumata* (Linnaeus, 1758) whole genome sequences (GenBank, GCA_001266575) with *BWA* using the default *bwa-mem* setting (Li 2013) based on 95% of sequence similarity.

Analyses of ddRAD data

To infer maximum likelihood (ML) trees, we used RAxML v.8.2.0 (Stamatakis 2014) with bootstrap support estimated by a 1,000 replicates of rapid-bootstrap analysis from the GTR+GAMMA model. We visualised the resulting phylogeny using FigTree v.1.4.2 (Rambaut 2015). To investigate genetic variation between individuals, we inferred population clustering with admixture from SNP frequency data using STRUCTURE (Pritchard et al. 2000). We ran 10 independent analyses for each value of *K*, between 1 and 3, each consisting of 50K burnin generations and 500K post-burnin generations. Results were summarized and compared in CLUMPP (Jakobsson and Rosenberg 2007). The optimal *K* value was inferred using StructureHarvester (Earl and VonHoldt 2012) according to the ad hoc ΔK statistics (Evanno et al. 2005). Genetic assignments were visualized using DISTRUCT (Rosenberg 2004).

Examination of *Wolbachia* infection

To check for the presence of bacterial parasite *Wolbachia*, we sequenced two markers, FstZ and Wsp, using primers and laboratory procedures of Ivanov et al. (2018).

Results

Perizoma barrassoi Zahm, Cieslak & Hausmann, 2006

Perizoma barrassoi Zahm, Cieslak & Hausmann, 2006: 95:31, figs 1a, b, 2a, b (Locus typicus: Italy, Abruzzo: Maiella Mts., Valle Cannella, Manzini-Hütte). Holotype male (coll. Zahm/ZSM, examined and dissected, DNA barcoding failed). Associated female paratype a misidentification of *Colostygia aqueata* (Hübner).

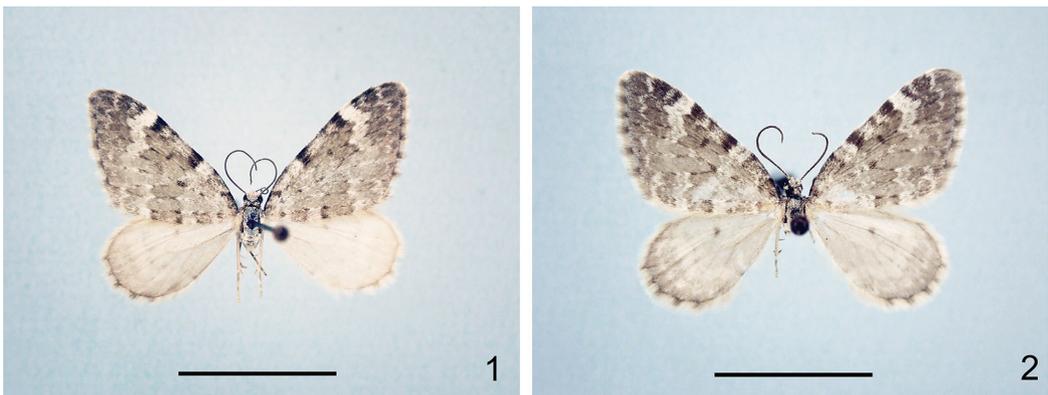
Material examined. Italy: *Holotype* male, central Italy, Abruzzo, Maiella, Valle Cannella, Manzini-Hütte, 2530 m, 23.vii.1988, leg. N. Zahm, coll. ZSM (gen.prp. ZSM G 20836; DNA barcode sample ID BC ZSM Lep 54528, 77874 (failures); 1 female, central Italy, Lazio, Rieti, Mt. Terminillo, 1800 m, 18.vii.2004, DNA barcode sample ID BC ZSM Lep 82927, gen.prp. ZSM G 15840; 2 males, Trentino, Adamello, Rifugio Mandrone, 2450 m, 26.vi.2014, leg. T. Mayr, DNA barcode sample ID TLMF Lep 25428 (RCTM); **France:** 1 male, France, Hautes Alpes, Pelvoux, [2000 m], 1.–10.viii.1972, leg. L. Hinterholzer, gen.prp. ZSM G 21237 (ZSM); 1 male, France, Alpes Maritimes, Col des Champs, [2100 m], 5.vii.1931, [leg. C. Herbulot], gen.prp. ZSM G 21238 (ZSM); 1 female, France, Alpes Maritimes, Cayolle, 2100 m, 31.vii.1975, leg. Lukasch, gen.prp. ZSM G 21259 (ZSM); 1 female, France, Hautes Alpes, la Moutieres, 2100 m, 3. viii.1975, leg. Lukasch (ZSM); 1 female, France, Valloire, 1500 m, 31. vii.1954, leg. G. Bernardi (ZSM); 1 male, France,

Pyrenees orientales, Porté, 1650–2100 m, 25.VI.–21. vii.1948, leg. H. de Toulgoet, gen.prp. ZSM G 14302 (ZSM); 1 female, France, Pyrenees orientales, Col de Puymorens, 1900 m, 10.vii.1975, leg. G. Behounek, gen.prp. ZSM G 21255 (ZSM); **Germany**: 1 female, Germany, Bavaria, Allgäu, Oberstdorf, Oytal, Oybach E Oytalhaus, 1036 m, 01.vi.2014, leg. D. Doczkal, DNA barcode sample ID BC ZSM Lep 86512, gen.prp. ZSM G 21249 (malaise trapping, ZSM); 2 males, Germany, Bavaria, Eschenlohe, [700 m], 12.vi.1977, leg. L. Hinterholzer, gen.prp. 21229 (ZSM); 3 females, Germany, Bavaria, Bergen, Weißachtal, 700 m, 24.v.1980, leg. A. Beyerl (ZSM); **Austria**: 16 males and females, Austria, North Tyrol, Riedenberg / Landl, 800–900 m, 16.v–19.vi.1974–1979 leg. Scheuringer, Wolfsberger, gen.prp. ZSM G 21228, 21248 (ZSM); 1 male, Austria, northern Tyrol, Ötztal Alps, Feichten, 1300 m, late May 1986, leg. E. Scheuringer, gen.prp. ZSM G 21233 (ZSM); 1 male, id., late May 1992 (ZSM); 1 female, id., early June 1983, gen.prp. ZSM G 21257 (ZSM); 1 female, id., leg. [coll.] Wolfsberger (ZSM); 2 males, Austria, North Tyrol, unterhalb Farst / Umhausen N, 1100 m, 10.iv.2017, leg. P. Huemer, DNA barcode sample ID TLMF Lep 22852, 22853 (TLMF); 1 male, id., 28.v.2013, DNA barcode sample ID TLMF Lep 12589; 1 male, Austria, East Tyrol, Matreier Tauerntal, Aussergschloess Umgebung, 1700 m, 14.vi.2013, leg. P. Huemer, DNA barcode sample ID TLMF Lep 13024 (TLMF).

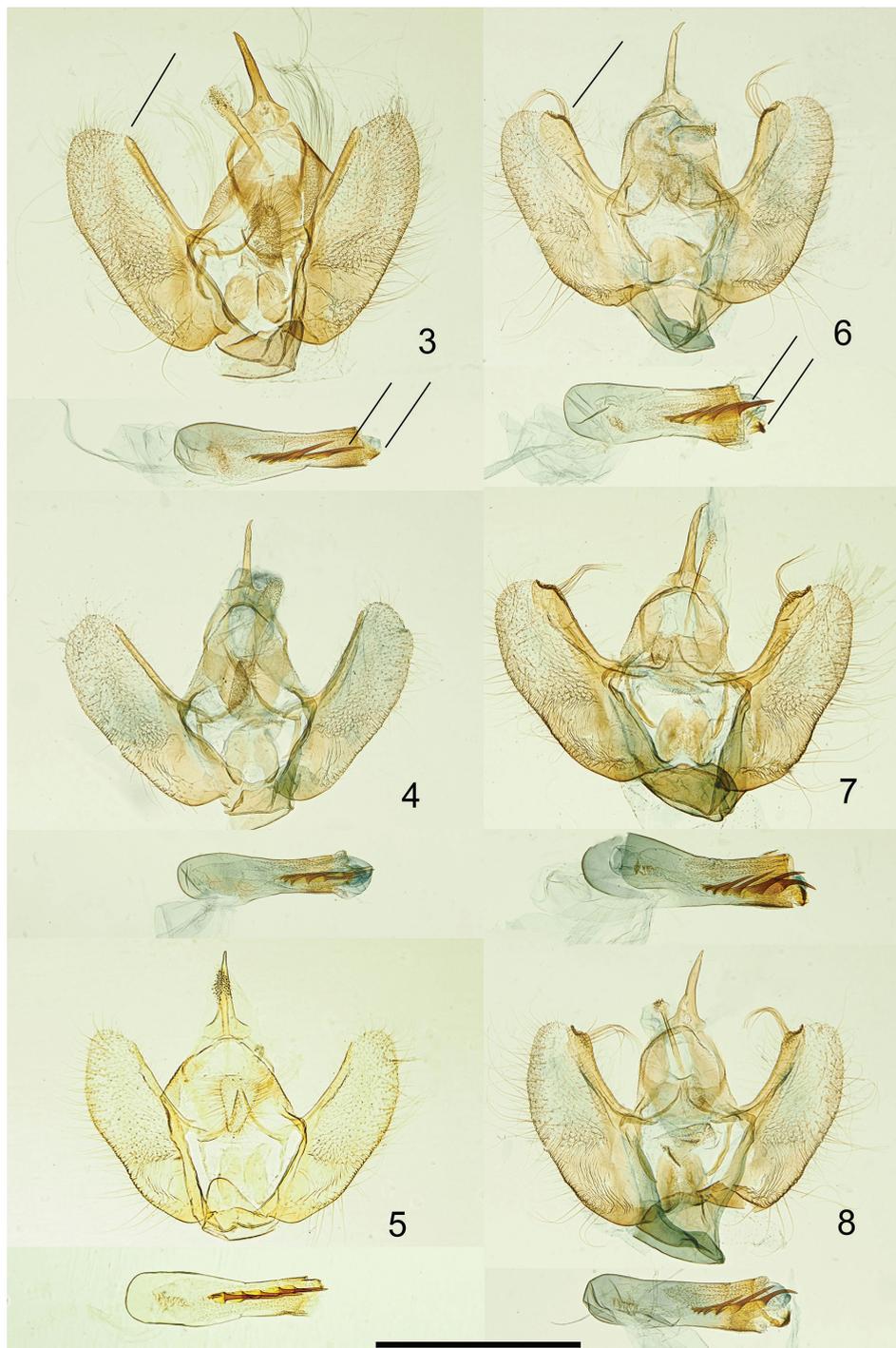
External characters and abdomen (Fig. 1). See description in Müller *et al.* (2019). The newly attributed Alpine populations with wingspan of 17–21 mm in males, 19–22 mm in females. Ground colour whitish pale grey, silky shining. Wing pattern varying in a similar way as in the sister species *P. incultaria*, no constant and reliable differential feature in wing pattern and coloration was found that would allow discrimination between the two sibling species. Palpi short, length 0.5–0.7 mm, hardly exceeding frons. Male antennae ciliate-setose, flagellum dorsally chequered grey and white.

Male genitalia (n = 7; Figs 3–5). The genitalia of the newly attributed Alpine populations are well matched to those of the holotype, i.e. showing comparatively narrow valvae, ventral and dorsal margins approximately parallel, costa of valva narrow from base to apex, at apex narrowly tapering (cf. Müller *et al.* 2019). Anal tube strongly developed, spinulose at tip. Head of (fused) labides comparatively large. Aedeagus with five to nine small cornuti of 0.1 mm (basalmost) to 0.25 mm (distalmost), cornuti not dilated at base. Length of aedeagus 0.9–1.1 mm.

Female genitalia (n = 6; Figs 9–11). The genitalia of the newly attributed Alpine populations are well matched to those of the central Italian female as figured in Müller *et al.* (2019). Apophyses fine, tapered at apices. Colliculum (in earlier publications referred to as ‘ductus bursae’ but homol-



Figures 1, 2. Adults (females). **1.** *Perizoma barrassoi* (Austria, Riedenberg); **2.** *Perizoma incultaria* (Germany, Hirschberg). Scale bars: 1 cm.



Figures 3–8. Male genitalia. 3–5. *Perizoma barrassoi* (3. Austria, Riedenberg; 4. Germany: Eschenlohe; 5. France, Pyrenees, Porté); 6–8. *Perizoma incultaria* (6. Austria, Brandenburg; 7. Italy, Friuli, Altiplano Montasio; 8. Italy, southern Tyrol, Sulden). Scale bar: 1 mm.

ogy with colliculum postulated in Mironov 2003) elongate, length 0.37–0.5 mm, in one specimen 0.6 mm), parallel-sided almost over the whole length. Corpus bursae small, often globular. Sclerobinate signum small, round, lateral spinules weak, diameter 0.10–0.17 mm.

Differential diagnosis. In external appearance (wing shape, wing coloration, pattern), the newly attributed populations of *P. barrassoi* from the Alps and the Pyrenees do not exhibit significant and constant differences from the sympatric *P. incultaria*. The latter differs in male genitalia ($n = 23$; Figs 6–8) with much broader costa of valva which is dilated towards apex and ending in a small, sclerotized, beak-shaped process and bearing a conspicuous setal tuft. Aedeagus with stout cornuti (5–7), the distalmost being the largest, usually curved and dilated at base. Female genitalia of *P. incultaria* ($n = 10$; Figs 12–14) are similar to those of *P. barrassoi*, but in the former the colliculum is longer (0.6–0.7 mm), signum larger, more elongate, often triangular, length 0.13–0.3 mm, lateral spinules stout.

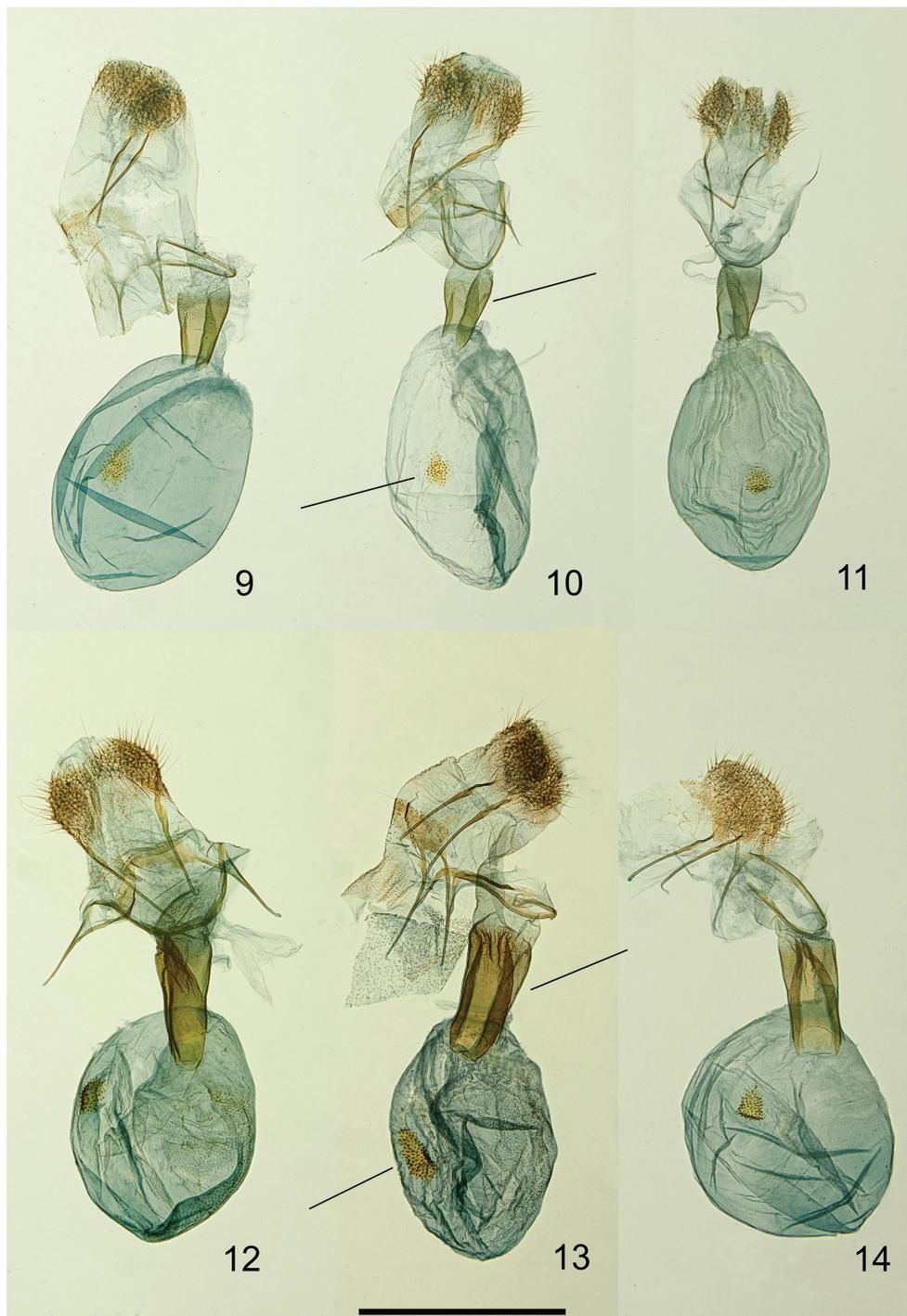
Distribution. Recorded in central Italy (locus typicus: Maiella mountains; Mt. Terminillo), Pyrenees, French Alps, and in a section of the central part of the Alps with records, so far, restricted to eastern and northern Tyrol (Austria) and to southernmost Bavaria (Germany), as a sympatric, sibling species of *P. incultaria* (see examined material and genetic data). Furthermore an isolated occurrence was detected in northern Italy (Adamello).

Phenology. Univoltine, the two central Italian records are from mid-July and late July, in the Pyrenees and French Alps the species flies from early July to early August. The remaining records from the Alps, however, refer to much earlier dates, from mid-April to late May, the single specimen from eastern Tyrol in mid-June and specimens from northern Italy in late June. Therefore, when occurring sympatrically, *P. barrassoi* flies earlier than *P. incultaria* whose Alpine populations are usually on the wing from early June to early August.

Biology. The larval stages are unknown. Larvae of the sister species *P. incultaria* feed on Primulaceae (first stages), later instars also on Saxifragaceae. Representatives of both plant families are abundant at the collecting sites of *P. barrassoi*.

Habitat. Montane. Collected on karstic slopes at 2500 m in the Maiella and 1800 m on Mt. Terminillo. In French Alps and Pyrenees from 1500 m up to 2100 m and in northern Italy (Adamello) occurring at 2450 m. In the Bavarian and Austrian Alps collected from much lower elevations in valleys from 1000 m up to 1300 m (Bavaria; northern Tyrol) ($n = 29$) with only one specimen from eastern Tyrol recorded at 1700 m, while the vertical distribution of sympatric *P. incultaria* ranges from 1700 m up to 3200 m, with very few exceptions.

Genetic data (DNA barcodes and nuclear genomic data). The specimen from Mt. Terminillo was DNA barcoded with an HTS approach, resulting in a 658 bp sequence including an 89 bp n-gap. BIN: BOLD:ACJ5976 ($n = 1$ from central Italy). Six specimens from Austria, south-western Bavaria and northern Italy are BIN-sharing, at a distance of only 1.1% from central Italian *P. barrassoi*. The genetic divergence from *P. incultaria* is strongly correlated with the differential features in genitalia and bionomic traits (see above). Nearest species: *P. incultaria* (8.5%; $n = 19$ from Germany, Austria and northern Italy; BIN BOLD:AAF5044). The distinctness of Alpine *P. barrassoi* and *P. incultaria* at species level was confirmed by ddRAD-sequencing involving nuclear loci (Mutanen *et al.* 2017). Two specimens of *P. incultaria* from the type locality near Gastein (Austria, Salzburg) could be sequenced, using the HTS approach for old museum material and revealed to belong to BIN BOLD:AAF5044, confirming the suggestion of species identity as *P. incultaria* as inferred from the comparatively high elevation (1800–2000 m).



Figures 9–14. Female genitalia. 9–11. *Perizoma barrassoi* (9. Austria, Feichten; 10. French Alps: Cayolle; 11. France, Pyrenees, Col de Puymorens); 12–14. *Perizoma incultaria* (12. Germany, Hochfelln; 13. Germany, Koblat; 14. Italy, Mt. Grappa). Scale bar: 1 mm.



Figures 15–20. Details of female genitalia: Signum. **15–17.** *Perizoma barrassoi* (same slides as Figures 9–11); **18–20.** *Perizoma incultaria* (same slides as Figures 12–14). Scale bar: 0.1 mm.

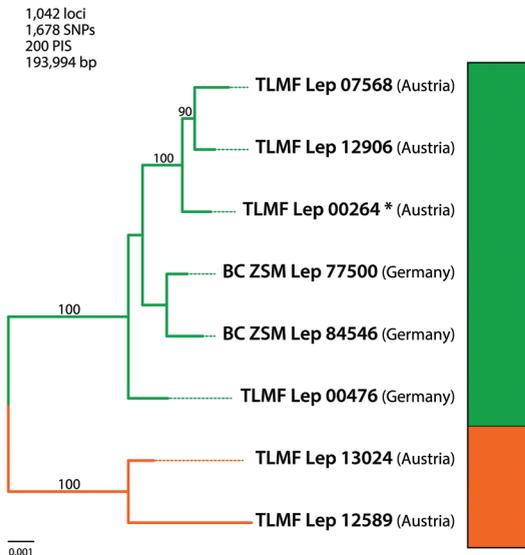
Data exploration and phylogenetic analyses based on SNP data. We generated a genome-wide set of genetic clusters from 8 individuals of *Perizoma incultaria* using ddRAD sequencing, and used this data set to perform phylogenetic analyses. We obtained 1.54 million reads per individual on average, of which 84.8% were retained after stringent quality filtering steps. After filtering and clustering at 95% sequence similarity using ‘*de novo*’ assembly method, we recovered 1,042 putative orthologues shared across more than three samples, for a total length of 193,994 base pairs (Fig. 21A). These data include 1,678 SNPs, of which 200 are parsimony informative. For the ‘reference’ assembly, an average of 1,298 reads per sample was mapped to the *Operophtera brumata* genome, while an average of 107,289 reads per sample remained unmapped. Because the reference species is only distantly related to *Perizoma*, the sample ‘BC ZSM Lep 84546’ was dropped out in the reference assembly due to the lack of mapped reads to the reference genome. After filtering, 222 clusters per sample were obtained, with 45.13 per sample for cluster depth on average. The final dataset from the reference assembly consisted of 50 recovered loci across more

than three individuals (Fig. 21B). Phylogenetic analysis using the concatenated ddRAD dataset produced robust support for the relationship between the individuals (Fig. 21). The ML tree based on the reference assembly produced a remarkably congruent tree with the tree of *de novo* assembly. In both ML trees, the two revealed lineages correspond to cluster A (*P. incultaria*, marked with green) and cluster B (*P. barrassoi*, marked with orange) that was supported by 100% bootstrap support values. STRUCTURE also identified two discrete clusters (Fig. 21). Only one of the eight examined samples ('TLMF Lep 00264') was *Wolbachia* infected.

Discussion

The shape and pattern of the wings of the barcoded, Central Italian female collected at Monte Terminillo (just 100 km from the type locality of *P. barrassoi* in the central Apennines) clearly showed it to belong to the *Perizoma incultaria/barrassoi* species complex although the large geographical distance of 500 km from the nearest Alpine populations of *P. incultaria* and the scarcity of high alpine habitats in the northern Apennines supported the initial hypothesis of conspecificity of that Central Italian specimen with *P. barrassoi*. This hypothesis was corroborated by the fact that the male genitalia of the holotype from the Maiella mountains agree perfectly with the male genitalia of one of the Alpine DNA barcode clusters, the latter corresponding to the barcoded central Italian female.

(a) ddRAD data, *de novo* assembly



(b) ddRAD data, reference assembly

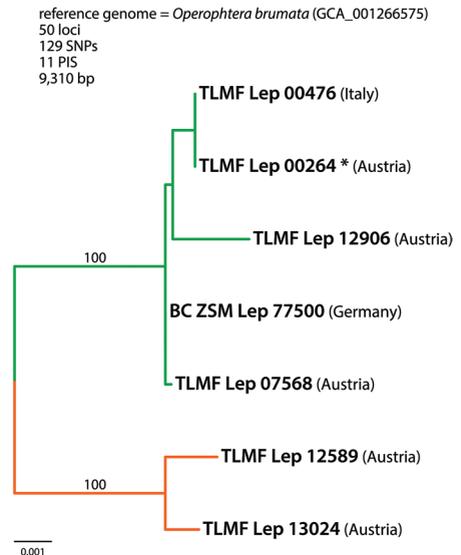


Figure 21. Maximum likelihood trees inferred from the ddRAD data matrices based on (a.) *de novo* assembly and (b.) reference assembly method against *Operophtera brumata* genome (GCA_001266575). Bootstrap support values are indicated above the branches and only the values > 50% are shown. The barplot shows the assignments of individuals into two genetic clusters, the green clusters referring to *Perizoma incultaria*, the orange clusters to *P. barrassoi*. Each bar represents one individual and colors represent the proportion of the individuals that belong to each of the genetic cluster. Samples infected with *Wolbachia* are marked with an asterisk.

Larentia incultaria was described from two males and a single female collected in the Alps (Herrich-Schäffer 1843–1855). In the original description two collectors are mentioned, Kindermann, without further details to his material, and Koch, with Gastein (Salzburg, Austria) as collecting locality. The type material is presumed destroyed (not traced in the museums in London and Berlin). Since this species cannot be separated externally from *P. barrassoi* and both taxa may co-occur in the area of Gastein, we, in accordance with ICZN (1999), designate a neotype to preserve nomenclatural stability. The male specimen was collected at the type locality of *P. incultaria* and it is labelled as follows: [Austria], Salzburg, Bad Hofgastein, Schlossalm, 2000 m, 06.viii.1975, leg. G. Embacher; DNA Barcode ID: BC ZSM Lep 103434. The Neotype was successfully DNA barcoded with a HTS approach to a 658 bp (200 n) fragment, unambiguously clustering with *P. incultaria*.

The discovery of a cryptic species of Geometridae in the Alps and Pyrenees comes as a surprise, although, recently, a similar case has been discovered in the genus *Perizoma* when *P. juracolaria* (Wehrli, 1919) was recognized as a cryptic species differing from its sister species, *P. obsoletata* (Herrich-Schäffer, 1838) in morphology and DNA barcodes (Bérard *et al.* 2005; Müller *et al.* 2019). The zoogeographical pattern of species pair *P. obsoletata* / *P. juracolaria* is reminiscent of that of *P. incultaria* / *P. barrassoi* with *P. juracolaria* being distributed in the Alps, southern France, in the Apennines and in the Balkan Peninsula (Müller *et al.* 1919). In the herewith presented case of *P. barrassoi*, the advantages of a comprehensive DNA barcode screening of local faunas are demonstrated once again (*cf.* Huemer and Hebert 2011; Huemer and Mutanen 2012; Huemer *et al.* 2013). Hardly anyone would have come up with the idea to study series of the widespread *P. incultaria* morphologically. Only the discovery of two highly divergent DNA barcode clusters was the trigger for such an exploration.

Perizoma barrassoi shows, according to current data, an unusual distribution pattern which is presumed to be due to a patchy recording. The distinctly isolated sub-areas in parts of the Alps and in the Pyrenees as well as in the central Apennines seem implausible when compared with the zoogeographical patterns of other geometrids inhabiting alpine and sub-alpine habitats, e.g. the above mentioned *P. juracolaria*. There is a large probability that *P. barrassoi* has still unrecorded relic populations in the northern Apennines and it will show a wider distribution in the western Alps including Switzerland, Piedmont and Valle d’Aosta. In particular, the early flight time, which starts shortly after the snowmelt, as well as the morphological similarity with *P. incultaria* are obvious reasons for the possibility that the species has simply been overlooked in many places.

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with material of *P. incultaria* from the type locality, Toni Mayr (Feldkirch, Austria) with Italian samples of *P. barrassoi*. We thank Laura Törmälä for the invaluable help in the molecular laboratory and CSC – IT Centre for Science, Finland for computational resources. This work was supported by the Academy of Finland (grant number 277984) to MM and the Kvantum Institute to KML.

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New taxa of extant and fossil primitive moths in South-East Asia and their biogeographic significance (Lepidoptera, Micropterigidae, Agathiphagidae, Lophocoronidae)

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Abstract. We report some surprising recent distributional range extensions of one extant genus and two more families of primitive moths discovered in amber fossils from South-east Asia which were previously only known from Australia and/or the southwestern Pacific, with the possible exception of an undescribed Siberian fossil attributed to Lophocoronidae. During entomological field work in rain forests of central Vietnam a new species of Micropterigidae was discovered. It is described herein as *Aureopterix bachmaensis* sp. nov. based on male and female specimens collected at light in the Bach-Ma National Park. The identification was corroborated by a molecular analysis. This is the first record of this genus in the Northern Hemisphere, previously thought to be restricted to the Australian Region (including New Caledonia). First results of investigations of Burmese amber inclusions now reveal the presence of the Australian Region families Agathiphagidae and Lophocoronidae in the Cretaceous of Asia. The fossil taxon *Agathiphagama perdita* gen. nov., **sp. nov.** is established on the basis of two females and this is assigned to Agathiphagidae. The fossil genus *Acanthocorona* gen. nov. is established in Lophocoronidae and includes seven species described here as *A. skalskii* **sp. nov.**, *A. bowangi* **sp. nov.**, *A. muelleri* **sp. nov.**, *A. kuranishii* **sp. nov.**, *A. sattleri* **sp. nov.**, *A. spinifera* **sp. nov.** and *A. wichardi* **sp. nov.** The new species can be distinguished by the male genitalia which are illustrated together with wing venation and other morphological characters. The disjunct ranges of these taxa are discussed in a historical biogeographic context. Vicariance and dispersal hypotheses explaining the disjunct pattern are discussed. The discovery of these new species suggests a broader ancestral range of *Aureopterix*, Agathiphagidae and Lophocoronidae. Their extant ranges may be regarded as remnants or relicts of a wider distribution in the Mesozoic, or at least in the case of *Aureopterix* they could be the results of recent or ancient dispersal processes, since the calibration of molecular splits does not so far accord with plate tectonics.

Introduction

In continental South-East Asia the faunas of the Eastern Palaearctic and Oriental Regions share a common border. This borderline is not a clear-cut delimitation and separation of both faunas, but rather a broad transition zone extending from the slopes of the southern Himalayas in northern India to northern Myanmar, Thailand, Laos, Vietnam and southern China including Taiwan (Müller 1981).

This zone includes biodiversity hotspots for many insect groups (Balian *et al.* 2008; Konstantinov *et al.* 2009) and is also seen as a diversity centre of vascular plants (Barthlott *et al.* 1999). It does not simply combine taxa from different biomes, but is also home of a great number of endemic species. The existence of these species might be evidence of an enduring ecological stability and favourable conditions facilitating both the evolution of recent neo-endemics and the persistence of older palaeo-endemics (Fjeldså and Lovett 1997). Taxa belonging to old lineages dating back to the Mesozoic are of particular interest. In Lepidoptera, the following genera of homoneurous families, which represent these lineages, were documented with autochthonous species occurring in the area to date (Meyrick 1909; Issiki 1931; Issiki and Stringer 1932; Hwang 1965; Mutuura 1971; Davis *et al.* 1995; Mey 1997; Hashimoto and Mey 2000; Chen *et al.* 2009; Hirowatari *et al.* 2009; Lees *et al.* 2010):

Micropterigidae: *Micropterix* Hübner, 1825, *Paramartyria* Issiki, 1931, *Vietomartyria* Hashimoto & Mey, 2000

Eriocraniidae: *Eriocrania* Zeller, 1850, unpublished record (in coll. MfN)

Hepialoidea: *Ogygoses* Issiki & Stringer, 1932

Neopseustidae: *Neopseustis* Meyrick, 1909, *Nematocentropus* Hwang, 1965

A common feature of primitive moths is the low number of collected specimens for the majority of species. The species are rarely encountered in nature, and almost every new record merits communication. The scarcity of hitherto found specimens, however, suggests the occurrence of further relict species. Concerning Microlepidoptera, continental South East Asia has not been sufficiently explored, and new discoveries remain to be made, particularly in the mountain ranges of the Palaearctic-Oriental transition zone.

During the first field trip of the joint Vietnamese-German project VIETBIO to Central Vietnam in 2018, the first author was searching for caddisflies and micromoths in the Bach-Ma National Park (Mey *et al.* 2020). A single micropterigid female was collected at lights on 10.06.2018. Intensive searching at the locality for additional specimens yielded no results. Two days later, collecting in a different valley of the National Park, the corresponding male was found, again at the lights. Previous records of Micropterigidae were restricted to the north of Vietnam (Mey 1997), and the family was not expected to occur in the south.

Closer inspections of the specimens identified them as belonging to *Aureopterix* Gibbs, 2010, a genus reported so far only from Australia and New Caledonia (Gibbs 2010). Though similar in morphology to the two hitherto described species, the Vietnamese specimens represent a new, distinct species for this genus, which is described herein.

Examination of insect inclusions in Burmese amber resulted in the discovery of individuals which were identified as putative species of Agathiphagidae and Lophocoronidae. Both families are currently regarded as extant, endemic families of Australia and Southwest Pacific Islands. Interestingly, Skalski (1979) has tentatively determined a fossil individual from Siberian amber (Tajmyr region) of Upper Cretaceous (Santonian) as a representative of Lophocoronidae. The species was, however, not formally described and named. Burmese amber originates predominantly from the Hukawng Valley near Myitkyina, Kachin State, Myanmar (Fig. 1). It derives from an amber-bearing layer, which is not exposed at the surface but extends to a depth of 2–15 m (Cruickshank and Ko 2003). The amber deposits have been dated in detail by Shi *et al.* (2012). The age determination is of early Cenomanian (98.8 ± 0.6 Ma) given by U-Pb dating of zircons from the volcanoclastic

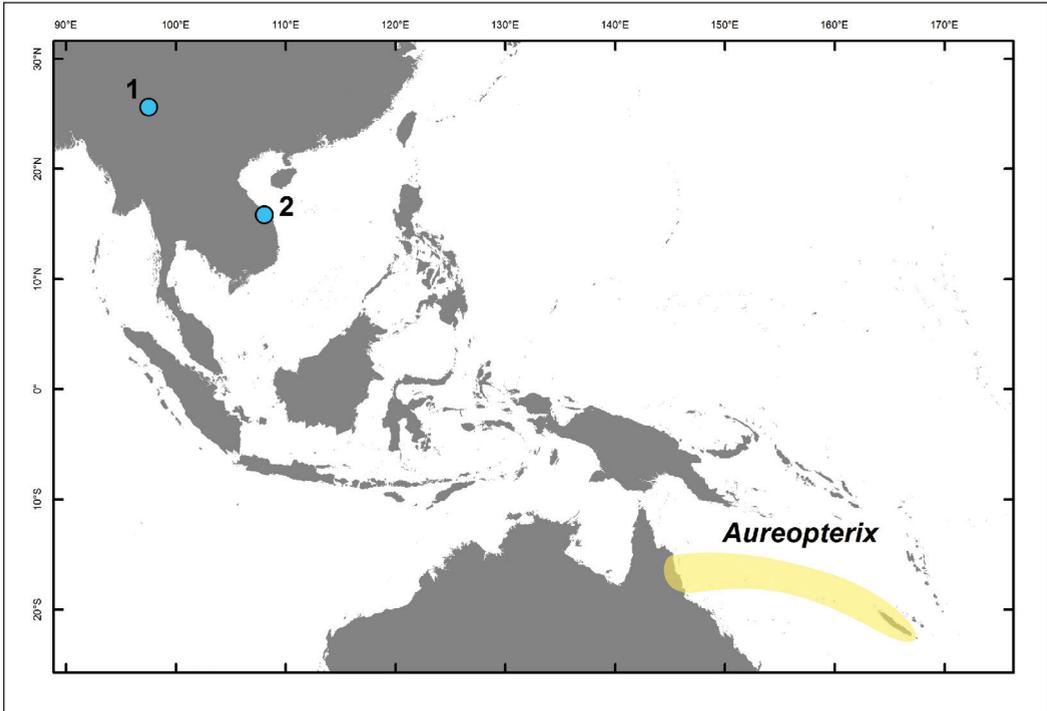


Figure 1. Map of the distribution of *Aureopterix* Gibbs, 2010 with disjunct ranges in Vietnam and (in yellow) Australia/New Caledonia, and locality of Burmese amber mines (**1.** Mine in Hukawng Valley, Kachin State, Myanmar; **2.** New record of *Aureopterix*, Bach-Ma National Park, Vietnam).

matrix of the amber (Shi et al. 2012). The first synopsis of identified biota from Burmese amber was published by Grimaldi et al. (2002). A regularly updated catalogue of described taxa is available online (Ross 2019). There are only a few species of Lepidoptera described from this class of amber (Sohn et al. 2012). Representatives of the family Micropterigidae were encountered quite often in inclusions, and therefore, led to the descriptions of five species (Zhang et al. 2017; Cockerell 1919) which were assigned to the extant genus *Sabatinca* (Walker, 1863). One species was described in Douglasiidae, a placement (Poinar 2019a) that needs to be confirmed. These are the only available descriptions of Burmese amber Lepidoptera. The Burmese amber, however, contains a diverse and rich fauna of Microlepidoptera of ancient and more derived forms, which are currently under investigation and documentation (see Mey 2019). The following descriptions are some first results and are included in this article for providing a biogeographical context in the discussion on the unexpected discovery of *Aureopterix bachmaensis* sp. nov. in Vietnam.

Material and methods

Extant taxa

The adult moths were pinned and set in the field. Genitalia drawings were performed prior to embedding in Euparal on a genitalia slide. A camera lucida attached to a Leica MZ12 compound microscope was used. Genital preparations were made according to the procedure described in

Robinson (1976). The genitalia were embedded in Euparal. Chlorazol Black was used to stain the membranous parts of the genitalia. Photographic documentation of imagines was done with a Leica Z 16 APOA Microscope in combination with a Leica DFC490 camera and Leica Application Suite programme, version 4.5.0 on a Windows PC. The map (Fig. 1) was produced with ArcGIS software.

DNA extraction and sequencing

DNA extraction were performed with a NucleoSpin Tissue kit (Macherey-Nagel, Düren, Germany). The standard forward and reverse primers LCO/Nancy for the DNA barcode region failed at amplifying the target region. The COI barcode was thus amplified in two parts referred to as COI fragment 1a and 1b, using primers from Léger *et al.* (2020). PCR-mix consisted of 17.8 µl ddH₂O, 2.5 µl 10× Puffer, 1 µl Mg (25 mM), 0.5 µl dNTP Mix, 0.5 µl of each primer, 0.2 µl of Taq polymerase (New England Biolabs, Ipswich, USA) and 2 µl of the DNA sample, totalling a volume of 25 µl. PCR program was that of Léger *et al.* (2020). PCR product cleaning and sequencing were performed by MACROGEN (Netherlands).

Sequence analysis

Sequences were eye-checked under PhyDE 0.9971 (Müller *et al.* 2005), also aligned visually with other DNA barcode sequences of *Aureopterix* and *Sabatinca* retrieved from BOLD (<http://v4.boldsystems.org/>). Phylogenetic analyses were performed on RAxML on the CIPRES portal (Miller *et al.* 2010), with Rapid Bootstrap Search stopped after 252 replicates. K2P distances were calculated on MEGA X (Kumar *et al.* 2018).

Fossil taxa

Photos of fossil species were taken using a Leica stereomicroscope M 420 Apozoom in combination with a Canon EOS 80D, EOS utility software and the Zerene Stacker software.

The fossils were examined under incident and transmitted light using a stereomicroscope (Leica MZ125). Line drawings were produced with a Leica camera lucida and digitally processed using Adobe Photoshop CS4. Measurements were made with the ocular micrometer of the stereomicroscope.

All taxonomic acts established in the present work have been registered in ZooBank, together with the electronic publication: <http://zoobank.org/FC32D2F4-5EE1-4484-8BAF-D873487DB332>.

The terminology of genitalia structures used in the descriptions of taxa follows Gibbs (2010) for Micropterigidae, Kristensen (1998) for Agathiphagidae and Nielsen and Kristensen (1996) for Lophocoronidae. For each of these families a separate superfamily taxon was established (see Kristensen and Skalski 1998). The use of these names was found to be dispensable here, because they provide no additional information for the families and the taxonomic contents of the present article.

Abbreviations of depository collections:

AMNH	American Museum of Natural History, New York
TF	ex coll. Thilo Fischer, München
PM	ex coll. Patrick Müller, Kähshofen (will be transferred to MfN later)
MfN	Museum für Naturkunde, Berlin
NIGP	Nanjing Institute of Geology and Palaeontology, Nanjing, P.R. of China
VNMN	Vietnam National Museum of Nature, Hanoi.

Systematic account

Micropterigidae

Aureopterix bachmaensis sp. nov.

<http://zoobank.org/59D2AADB-5BBF-4F8D-BED4-C7B9F2FF1964>

Figs 1–11

Type material. *Holotype* ♂, Vietnam, Thua Thien-Hue Province, Bach-Ma National Park, 12.vi.2018, above Rhododendron Trail, 1256 m, 16°11.757'N, 107°50.922'E, at light, leg. W. Mey, genitalia slide Mey 08/20, DNA voucher Lepidoptera, MFN LEP042 (VNMN).

Paratypes: 2 ♀, Vietnam, Thua Thien-Hue Province, Bach-Ma National Park, 10.vi.2018, Five Lakes Trail, 1190 m, 16°12.214'N, 107°50.441'E, at light, leg. W. Mey, genitalia slide Mey 09/20, 1 ♀ in alcohol, DNA voucher Lepidoptera, MFNLEP041 (MfN).

Etymology. The specific name is derived from the name of the Bach-Ma National Park.

Diagnosis. Vietnam. Male with long genitalia, projecting half the length of abdomen in dried specimens; abdomen and genitalia with long, scattered setae; tergum X of males with single setal tuft on each ventro-lateral margin on a raised base at mid-length.

Forewing ground colour and fascial pattern (Figs 1, 2) corresponding widely with the two other known species of *Aureopterix* Gibbs, 2010. The male genitalia of the new species are more similar to those of *A. micans* Gibbs, 2010, described from New Caledonia, and less similar to *A. sterops* (Turner, 1921) distributed in northern Queensland, eastern Australia. *A. bachmaensis* sp. nov. mainly differs from both species by the shape of the valvae and the slender segment X bearing one single setal brush on a knob-like process of the lateral margin in male genitalia.

Description. (Figs 3–6) Length of forewings 3.9 mm (male) to 4.1 mm (females). Antennae with 34 flagellomeres in male, 32 in female, extending to two-thirds of forewings; first four basal flagellomeres fused, clothed with white lamellar scales, following flagellomeres brown, with long, dark sensillae and ascoids, female flagellomeres 4 to 6 black; head capsule dark brown, with dense tufts of white, piliform scales on frons and vertex; eyes hemispherical; epicranial suture and ocelli absent; clypeus separated from frons by a deep, arched suture extending between the tentorial pits; labrum long, triangular with rounded tip; mandibles present, apical portions hidden under labrum; maxillae with long, five-segmented palpi, held in vertical position close to frons, inner endites two short, rounded processes (= galea and subgalea); labial palpi short, three-segmented, terminal segment with a garland of stiff sensillae. Pronotum and basal part of tegulae brown, dorsum of thorax with silvery white, lamellar scales. Ground colour of forewings pale white, shining silvery, some brown spots at base of costa, apical part of forewings with oblique, bronzy fascia, fringes white, hindwings shining bronzy on upper- and underside. Wing venation (Fig. 7) with Sc and R1 forked in forewing, simple in hindwing or absent (R1), R4 and R5 in both wings very short, forming forks encompassing the wing tips, hindwings with accessory cell absent, anal veins without looping. Wing coupling mechanism with short jugum of forewings and bundle of three erect bristles on costal base of male hindwings, females without those bristles. Legs with white coxae and femora, tibiae and tarsal segments dark brown, epiphysis present on foretibia, legs clothed with acute tipped scales, long or short spines in addition to spurs absent, spurs 0.0.4. Male abdomen with long bristles on ventral side, glands of sternite V present, orifice rounded, segment VIII of male present as tergum only, no traces of sternite visible.

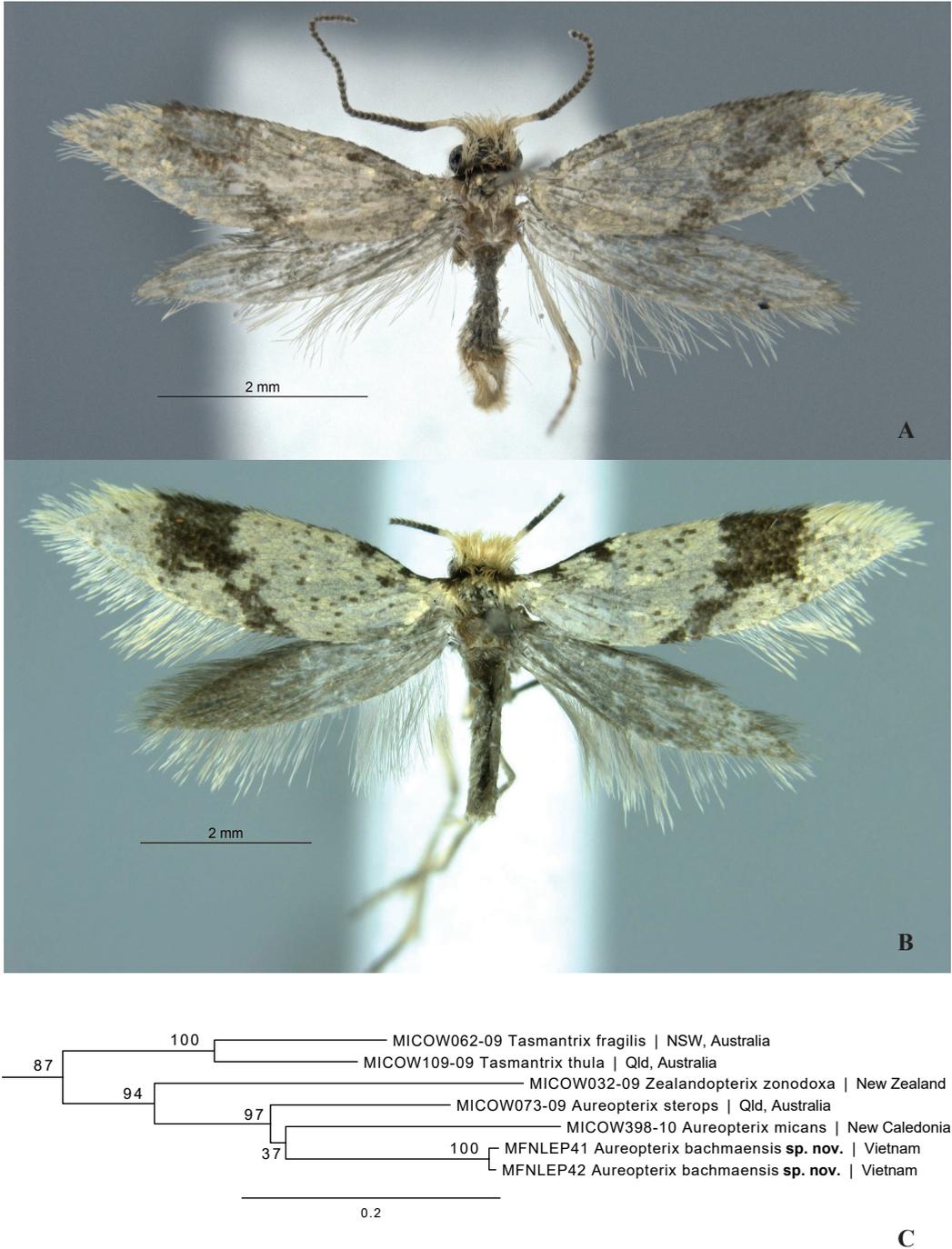
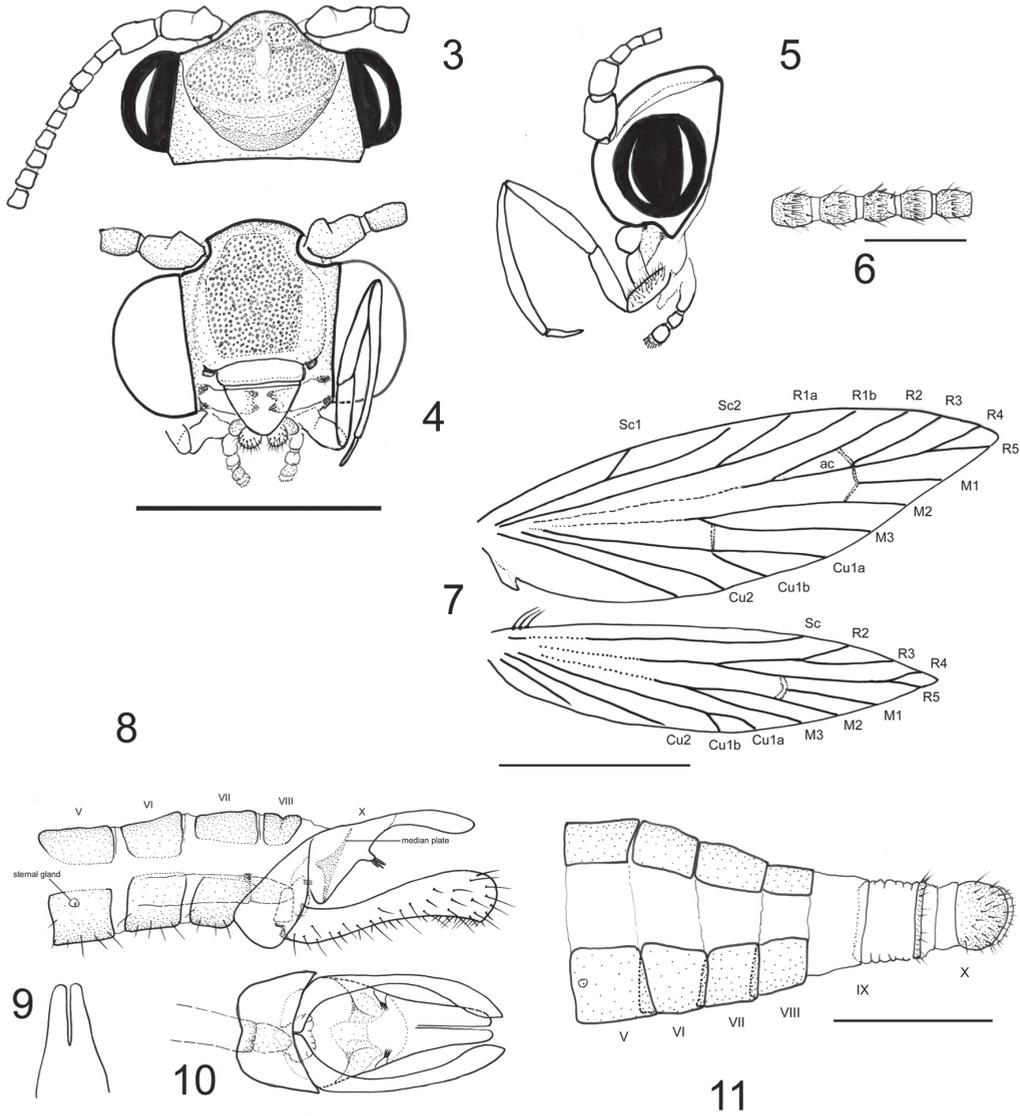


Figure 2. Adults of *Aureopterix bachmaensis* sp. nov. and their phylogenetic placement. **A.** Male, holotype; **B.** Female, paratype; **C.** Phylogenetic tree of *Aureopterix*. Best scoring RAXML-tree with node calibration in millions of years displayed above branches. *Sabatinka* branch not represented for visual convenience.



Figures 3–11. *Aureopterix bachmaensis* sp. nov.; **3–5.** Head, female; **3.** Dorsal view; **4.** Frontal view, right maxillary palpus omitted; **5.** Lateral view; **6.** Flagellomeres, mid-section; **7.** Wing venation, holotype; **8.** Male abdomen and genitalia, lateral view; **9.** Segment X, dorsal view; **10.** Male genitalia, ventral view; **11.** Female abdomen, lateral view. Scale bars: 0.25 mm (**3–5.**); 10 μ m (**6.**); 1 mm (**7.**); 0.5 mm (**8.**); 0.5 mm (**10., 11.**);

Male genitalia (Figs 8–10): segment IX bulbous, not forming a closed ring, anterior margin of ventral side slightly excavated, valvae very long, club-shaped, tips acute in ventral view; segment X shorter than length of valvae, narrowly cleft at apex for half of its length, paired apices rounded, lateral margin with a brush of 3–4 short setae on a short process directed ventro-medial; median plate weakly sclerotized, enclosed in basal part of segment X; phallic apparatus long and tubular, terminal part of phallocrypt with micro-spines on dorsal side, distal part of phallus membranous, cornuti absent.

Table 1. K2P distances between DNA barcode sequences of *Aureopterix* species. GenBank accession numbers are appended to each sample.

Species	MFNLEP41	MFNLEP42	MICOW073-09
MFNLEP41 <i>Aureopterix_bachmaensis</i> COI-5P LR961636			
MFNLEP42 <i>Aureopterix_bachmaensis</i> COI-5P LR961637	0.68%		
MICOW073-09 <i>Aureopterix_sterops</i> COI-5P HM431791	12.42%	11.79%	
MICOW398-10 <i>Aureopterix_micans</i> COI-5P HQ575019	12.77%	11.74%	14.44%

Female genitalia (Fig. 11): segment I to VIII with sclerotized terga and sterna, segment IX elongate, membranous and telescoping, with a continuous sclerotized ring on distal margin, segment X with rounded, lateral sclerites of paired and setose terminal papillae (= papillae anales). (The bursa was completely macerated during boiling in KOH).

Molecular results. (Fig. 2C, Table 1) We recovered only the COI-1a fragment (325bp) for both samples. In the best scoring RAXML-tree the genus *Aureopterix* is well supported as a monophylum with respect to *Zealandopterix* and *Tasmantrix* (BS = 97). Relationships among *A. bachmaensis* sp. nov., *A. micans* and *A. sterops* remain unclear.

Remarks. The locality in the Bach-Ma National Park will probably not remain the only record of this new species. Future field work will provide a more accurate picture of the species range, which is probably restricted to the Truong Son Mountain Range (= Annamite Range). This roughly north to south running mountain range along the Laos-Vietnam border is an area of endemism which gained global recognition in the early to mid-1990s with the discovery of six spectacular mammal species (Sterling and Hurley 2005) that are confined to this range. The report of *A. bachmaensis* sp. nov. in the National Park is an example from Lepidoptera underpinning the significance of the area.

Agathiphagidae

Agathiphagama gen. nov.

<http://zoobank.org/0BD622A5-835D-40E1-88EF-A179F51314FD>

Type species. *Agathiphagama perdita* sp. nov., Gender: feminine.

Etymology. Composed of the generic name *Agathiphaga* and the added syllable “ma”.

Diagnosis. Burmese amber, middle-sized species, terminal segments of maxillary palpi annulated, basal segment of labial palpi with dorsal hair-brush, tibial spurs 1.3.4., epiphysis present on short foretibia, forewings with R1 shortly branched into R1a and R1b, female with long, telescoping ovipositor, apophyses posteriores fused in apical half into a single apophysis extending in midline towards slender papillae anales.

The fossil genus differs from extant homoneurous moths of *Agathiphaga* Dumbleton, 1952 by differences in the morphology of the maxillary and labial palpi, the spur formula 1.3.4. (1.4.4. in *Agathiphaga*) and the long, fused terminal part of the apophyses posteriores (shorter in *Agathiphaga*).

The flexible form of the terminal segment of the maxillary palpi seems to be due to a mottled loss of sclerotization, which gives the segment an annulated appearance. In *Agathiphaga*, this segment is very short and not annulated (Dumbleton 1952).

The new genus is here assigned to Agathiphagidae. An alternative placement considered was the establishment of a new family as sister to Agathiphagidae in Agathiphagoidea. However, there is presently insufficient morphological basis to establish a new family.

Description. See description of *A. perdita* sp. nov. below.

***Agathiphagama perdita* sp. nov.**

<http://zoobank.org/0BDBAE24-209D-4838-84B9-CBE96944E77A>

Figs 12–17, 32–33

Type material. *Holotype* ♀, Burmese amber, NIGP 173715, (NIGP); *paratype* ♀, # 7095 (TF).

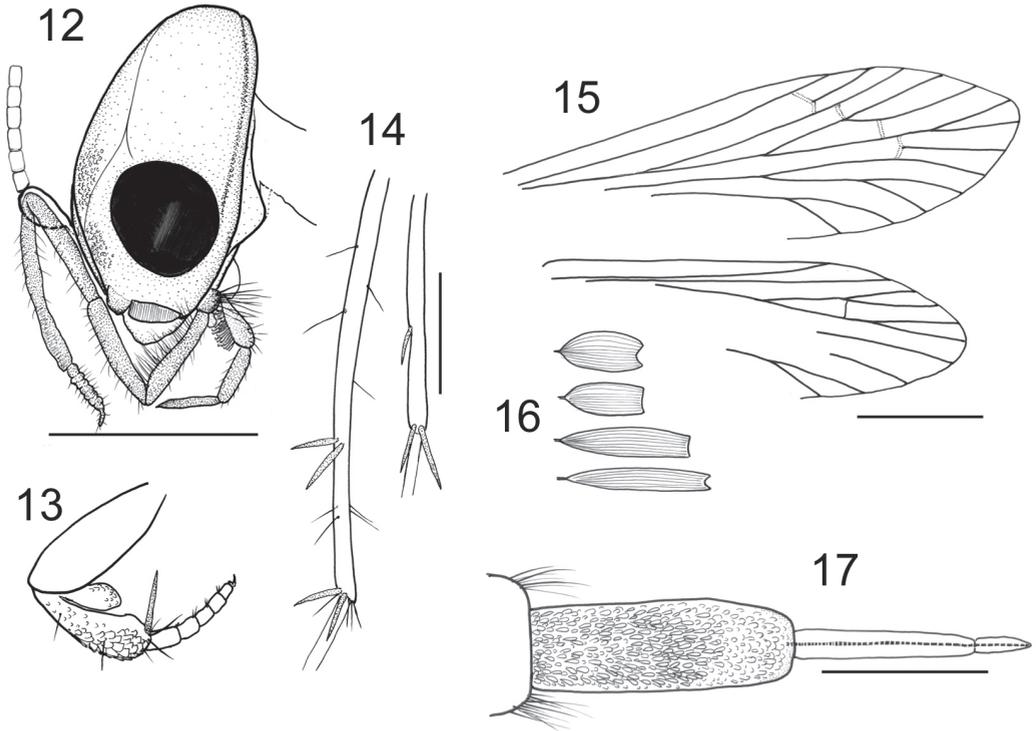
Etymology. The specific name is the Latin adjective “perditus”, lost, in singular, feminine nominative, referring to the species as an extinct taxon.

Preservation. The holotype is embedded in a large, polished and oval piece of amber (Fig. 32). The adult insect is nearly completely preserved, somewhat distorted and mainly visible in lateral view. The right side from head to thorax is macerated with right fore- and middle legs missing. The right head side is damaged forming a hole into the head capsule. The hindwings are partly covered by the forewings. One small, black Coleoptera species (3 mm length) is present.

Description. Length of forewings 10.2 mm, head capsule extending far above eyes (Fig. 12), ocelli absent; antennae filiform, longer than 0.5 of forewing length, more than 40 flagellomeres, clothed with small, lamellar scales, scape short, pedicel not larger than following flagellomeres. Maxillary palpi 5-segmented, basal segment with long bristles, terminal segment annulated, labial palpi 3-segmented, dorsal side of basal segment with short, erect, terminally hooked bristles. Foretibia with broad, scaled epiphysis and lateral and apical spines, spurs 1.3.4., meso- and metatibiae with lateral and apical spines (Figs 13, 14). Scales on wings of different shape and length, apical margins with serrations (Fig. 16). Wing venation (Fig. 15) in forewing with Sc simple, R1 shortly branched, accessory cell present, tips of R4 and R5 enclosing apex of forewing, M with four branches; hindwing with unbranched Sc and R1.

Female genitalia (Fig. 17): segment VIII dorso-ventrally flattened, densely covered by short, lamellar scales, segment IX and X forming a long, telescoping oviscapt with unpaired apophysis posterior, visible in the midline of the interior of segments IX and X.

Remarks. This is the first fossil species of the family. It is also the first evidence of the occurrence of the family Agathiphagidae in South-East Asia in the Mesozoic about 100 Ma ago. The morphological differences to *Agathiphaga* are significant and justify at least the establishment of a separate genus. According to Cruickshank and Ko (2003), the palynological record from the Burmese amber mines in northern Myanmar includes palynomorphs of Araucariaceae. Poinar et al. (2007) confirmed the araucarian source of the amber and suggested a species of the genus *Agathis* Salisbury as the resin-producing tree (Poinar 2019b). Extant species can secrete large quantities. Mechanical damage such as cutting into the bark of *A. dammara* (Chambert, 1803) results in large outpourings of resin (Fig. 38). This genus is present in South-East Asia with a number of species occurring in Malaysia and maritime South-East Asia (Michaux 2001). *Agathis* was considered by Morley (1998) as Gondwanan element which dispersed into South East Asia in the Tertiary. The seeds in the fe-



Figures 12–17. *Agathiphagama perdita* gen. nov., sp. nov., female holotype; **12.** Head, lateral view; **13.** Foreleg; **14.** Middle and hind leg; **15.** Wing venation; **16.** Forewing scales; **17.** Postabdomen and oviscapt. Scale bars: 1 mm.

male cones of the trees are the food resource of the two extant species of *Agathiphaga*, *A. vitiensis* Dumbleton, 1952 (Fidji, and further West Pacific Islands) and *A. queenslandensis* Dumbleton, 1952 (Australia, Queensland). The host-plant of *Agathiphagama perdita* sp. nov. could have been also a species of the gymnosperm family Araucariaceae. Judging from the fairly restricted range of *Agathiphaga* in the Australian Region (e.g. Dumbleton 1952) the species seems unlikely to have managed to disperse together with its host-plant into South East Asia. Discrepancy in the distribution of host plants and their associated Lepidoptera species is a frequently observed phenomenon. However, the distribution of herbivorous species is not only determined by the occurrence of the host plant but by the combined action of additional biotic and abiotic factors. Missing data, however, can account as well for a seeming absence in an area. The Microlepidoptera fauna of the region is inadequately researched and new records including surprising discoveries seem to be always possible.

The fossil *Agathiphagama* gen. nov. and the extant *Agathiphaga* are the only genera of Agathiphagidae. Both genera exhibit the characters of the family, but are probably not closely related due to the differences indicated in the diagnosis. The annulated terminal segments of the maxillary palpi of *Agathiphagama* gen. nov. seems to be a derived character. It resembles the terminal maxillary palpi of Annulipalpia and some Integripalpia genera (e.g. *Athripsodes* Billberg, 1820, *Ceraclea* Stephens, 1829) in Trichoptera. Kristensen (2003: 51) considered the annulated surface of the fourth segment as a lepidopteran ground plan character, but this character is not visible in the fossil specimens.

The Agathiphagidae are the only known family in extant Lepidoptera with four veins in the forewings including remarkable variation in branching pattern (Schachat and Gibbs 2016). This plesiomorphic character is, however, present in the Jurassic families Mesokristenseniidae and Ascololepidopterigidae. The former differs from *Agathiphagama* and Agathiphagidae in its spur formula 1.1.4 and in the absence of an epiphysis (Huang et al. 2010). The latter differs from Agathiphagidae and Mesokristenseniidae by lacking medial spurs on the metatibiae (Zhang et al. 2013).

Lophocoronidae

Acanthocorona gen. nov.

<http://zoobank.org/238DBF0F-58B8-41BF-B802-C398290772EA>

Type species. *Acanthocorona skalskii* sp. nov., Gender: feminine.

Etymology. A noun composed of the Latin “acanthus”, thorn and the Latin “corona”, crown, alluding to the name *Lophocorona* and to the long spikes at the bases of the valvae and the spine and denticules on its apical margins, forming a spiny crown when the tips of the valvae are held close together.

Diagnosis. Burmese amber, small-sized species, antennae short, basal flagellomeres broad, epiphysis present, homoneurous venation, forewings with accessory and median cells present, crossvein r1-r2 present, R5 running to termen (below apex) in both wings; valvae of male genitalia with one or more pairs of long, basal spikes and a terminal, short, rod-like ‘thorn’.

This fossil genus differs from extant homoneurous moths of *Lophocorona* by the presence of an epiphysis (absent in *Lophocorona*), the presence of crossvein r1-r2 and the joint presence of an accessory and median cell (accessory cell may be present or absent in *Lophocorona*). The valvae in the male genitalia carry a long, rod-like spine on the ventral tip together with numerous short denticules on the apical margin. In *Lophocorona* the spine on the ventral tip is small and blunt. The long spikes originating from the inner side of the base of the valvae can be regarded a synapomorphy of *Lophocorona* and *Acanthocorona* gen. nov.

Description. Forewing length 3–5 mm, eyes hemispherical, frons and vertex with tufts of long pili-form scales, ocelli absent; antennae short, about half the length of forewings, about 25–30 flagellomeres present, flagellomeres scaled on dorsal side, wider than long at base, becoming thinner and slender towards tip of antennae; proboscis present, dissociated into galea halves, maxillary palpi reduced in size, labial palpi upturned, terminal segment swollen, densely clothed by short bristles, tibial spurs 0.2.4., spurs covered by small scales, epiphysis present, legs slender (Fig. 26), with thin and strong spines on lateral and apical sides of tibiae, tips of tarsomeres with pair of short spines, ungues and arolium of praetarsus small; forewing venation (Figs 18, 30) with Sc1 and Sc2, simple R1, sectorial veins of R separate, originating from short accessory cell, R5 terminating to termen shortly below tip of forewing; medial cell present, M4 absent; hindwings (Figs 18, 30) with Sc and R1 unbranched, accessory and medial cell open, base of costa with a number of short bristles; scales of forewing short and spatulate, or long with apical margins serrated, scales of fringes long, lanceolate, rounded at apex (Fig. 29).

Male genitalia (Figs 19–27): valvae elongate, band-like, of species-specific shape, with an erect and protruding rod-like, blunt process on ventro-distal corner, directed dorso-mediad, inner side of apical portion or apical margin with short denticules, bases of valvae with one, two or three long spikes, originating from knob-like protuberances or papillae on the inner side; median plate short, of different shape; dorsal median lobe of segment X present or absent, simple or

bifid; phallic apparatus, if extruded, a long, slender tube, sometimes dilated on apex, gonopore in apical position.

Female genitalia (Fig. 31): sternum VIII with broad base and triangular ventral apex; segment IX fused with segment IX, oviscapt cone band-like, dorso-ventrally flattened, strongly sclerotized, fuscous to black, apex blunt, oviscapt saw usually hidden in oviscapt cone, sometimes protruding with its acute tip beyond cone margin.

Remarks. Diagnostic characters of *Lophocorona* Common, 1973 are: 1) absence of an epiphysis, and 2) the long stalk of R4 and R5 in the forewings encompassing the wing apex. These characters are in a plesiomorphic state in *Acanthocorona* gen. nov., with epiphysis present and R4 and R5 in the forewings always running as separate veins from accessory cell to wing margin. However, the structures of the male and female genitalia agree largely with those of *Lophocorona*. Especially the architecture of the female postabdomen is very similar to those of females of extant *Lophocorona* species (Nielsen and Kristensen 1996). The nearly complete correspondence of this character complex with *Lophocorona* Common, 1973 provided the clue for identifying specimens in Burmese amber as lophocoronids. A correct association of males and females in Burmese amber is, however, a difficult venture. There are no unique characters other than genitalia, which would permit combining sexes. The structures of the female postabdomen are described in the generic description, but without assigning female specimens to one of the described males.

Burmese amber contains a surprisingly high number of species attributable to *Acanthocorona* gen. nov. The individuals are in most cases embedded in an unfavourable position and exhibit only a reduced number of characters. But none of the externally visible traits contradict the diagnosis and description of the genus. Cross-veins are often difficult to see and they may appear to be absent in some individuals. This uncertainty makes the character unreliable and reduces its taxonomic weight. The following species are described and included in *Acanthocorona* gen. nov. essentially on the basis of the male genitalia. The morphology and arrangements of spines and denticles on apical parts of the valvae constitute the principal character complex, which exhibits a large variety allowing the separation and establishment of different species. The following descriptions of new species are short and concentrate on the male genitalia and their illustrations. The depicted features are diagnostic enough to distinguish the presented species and to identify new species in fresh, additional material of Burmese amber, which hopefully will continue to become available for scientific study in the future.

***Acanthocorona skalskii* sp. nov.**

<http://zoobank.org/207948F8-CA26-452C-A09D-D8C0D80F927B>

Figs 18–20, 34

Material. *Holotype* ♂, Burmese amber, NIGP 173716, (NIGP).

Etymology. The species is named in memory of Andrzej Skalski, who published the first record of a lophocoronid specimen from Asia (Skalski 1979), an interpretation later considered very tentative by Kristensen and Skalski (1998).

Preservation. Completely preserved in a nearly rectangular piece of amber, wings somewhat spread, but overlapping, head, legs and postabdomen clearly visible (Fig. 34).

Description. Length of forewings 4.1 mm, antennae dark brown, with 29 flagellomeres; wing venation (Fig. 18) with cross-veins r1-ac and m-cu present, hindwings without accessory- (ac) and median cell (mc).

Male genitalia (Figs 19, 20): segment IX with short, median prolongation in dorsal view, presumed median plate below this prolongation bilobed; rod-like spine on ventral apex of valvae long and straight, apical margin of valvae with denticules, and some additional denticules before margins; basal spikes of valvae paired, longer as length of valvae, sitting on elongate papillae from median side of valvae, a third median pair of bristles present, shorter than basal spikes. Phallus not visible.

***Acanthocorona muelleri* sp. nov.**

<http://zoobank.org/A81F6686-359F-4BCC-AF5E-A0480ABD4BEE>

Figs 21, 35, 36

Material. *Holotype* ♂, Burmese amber, BUB 1519, (PM).

Etymology. The species is named in honour of Patrick Müller, collector of amber inclusions, for providing material for scientific study.

Preservation. Completely preserved in a flat, oval piece of amber (Fig. 35), wings overlapping, legs and post-abdomen well visible in ventral view, air bubble on mouthparts and prosternum, additional insects present (two Hymenoptera, two Diptera, one Collembola).

Description. Length of forewings 3.0 mm, antennae brown, 23 flagellomeres.

Male genitalia (Figs 21, 36): rod-like spine on ventral apex of valvae long, straight and thickened, apical margin of valvae with three denticules of declining size, no denticles before margins; basal spikes of valvae paired, slightly shorter than length of valvae, arising on elongate papillae at median sides of valvae. Phallus long, tubular and gradually curved ventrad, tip with short, protruding vesica.

***Acanthocorona bowangi* sp. nov.**

<http://zoobank.org/0E56BB94-FB95-4A50-A086-5B9EB6451100>

Fig. 22

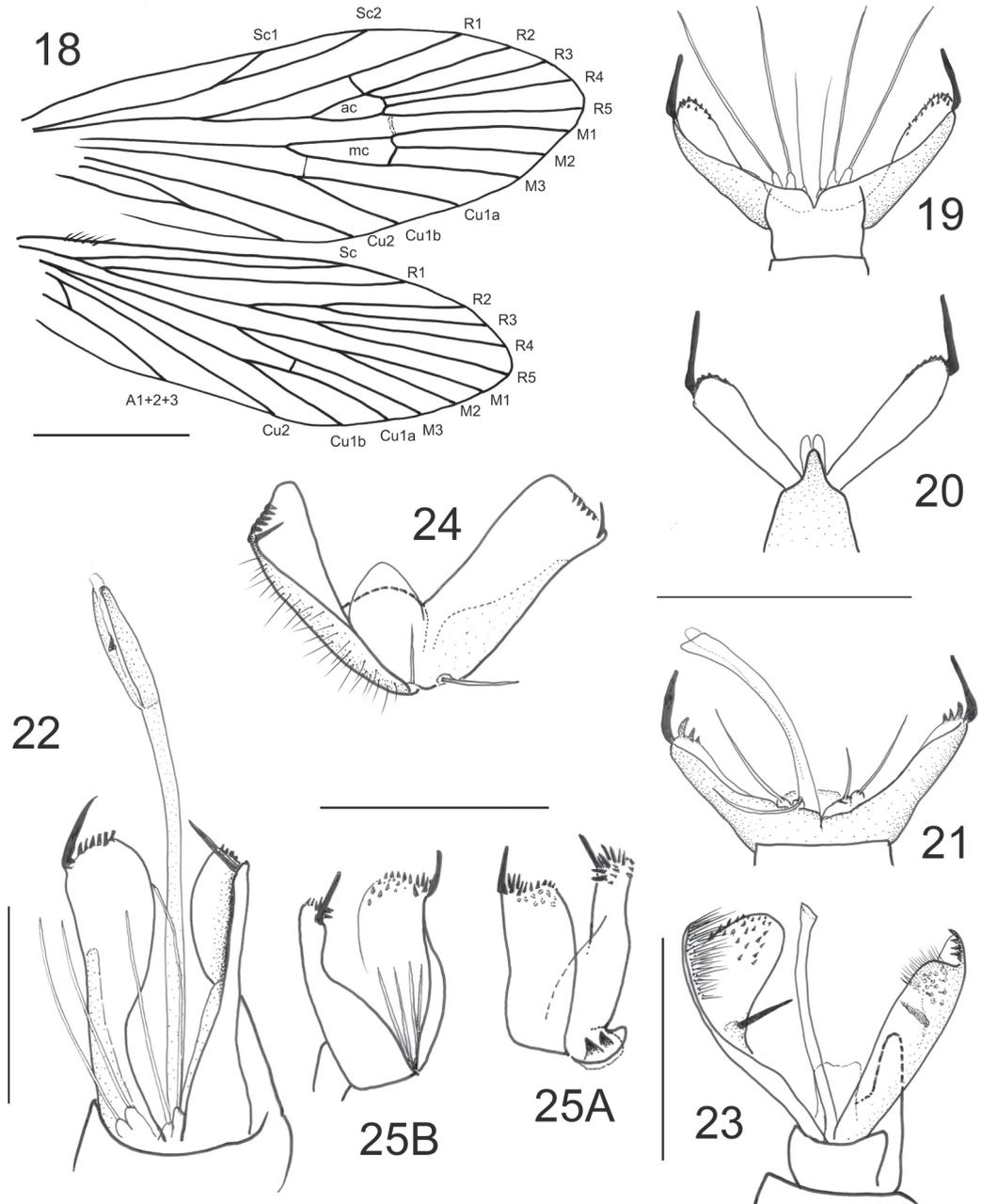
Material. *Holotype* ♂, Burmese amber, BUB 1519, (PM).

Etymology. The species is named in honour of Bo Wang for his efforts to make Burmese amber material available for scientific study.

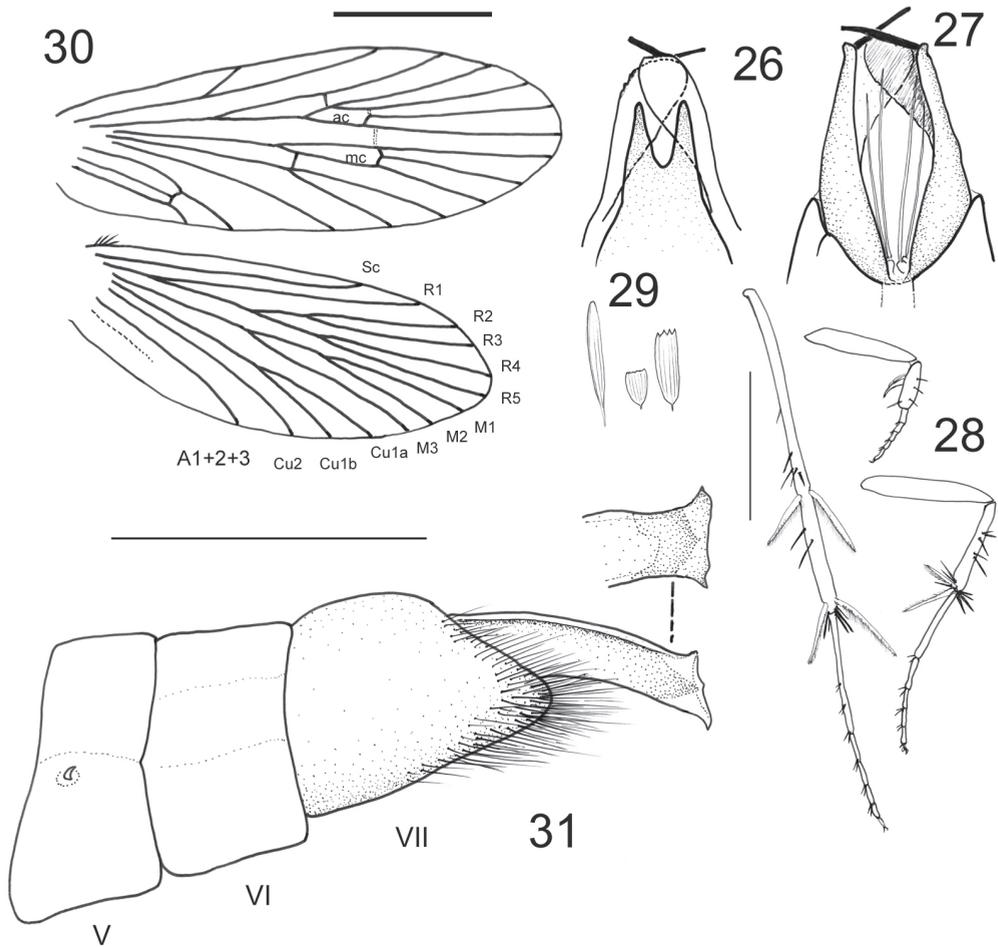
Preservation. Completely preserved on the margin in a large, drop-like piece of amber, wings somewhat overlapping, distorted, legs and post-abdomen clearly visible.

Description. Length of forewings 3.6 mm, antennae dark brown, 24 flagellomeres.

Male genitalia (Fig. 22): length of valvae as long as half the length of abdomen; rod-like spine on ventral apex of valvae long and straight, apical margin of valvae with row of denticules, no denticles before margins; basal spikes of valvae paired, slightly shorter than length of valvae, sitting on elongate papillae from median side of valvae. Phallus extremely long, slightly curved ventrad, ventral side of apex with elongate slit revealing short teeth.



Figures 18–25. *Acanthocorona* spp.: 18–20. *A. skalskii* sp. nov.: 18. Wing venation; 19. Male genitalia, ventral; 20. Male genitalia, dorsal; 21. *A. muelleri* sp. nov., male genitalia, ventral, 22. *A. bowangi* sp. nov., male genitalia, ventral; 23. *A. wichardi* sp. nov., ventral; 24. *A. kuranishi* sp. nov., ventro-caudal, 25. *A. sattleri* sp. nov., male genitalia; A – ventro-lateral, B – dorso-lateral. Scale bars: 1 mm (18.); 0.5 mm (20., 22., 23., 25.).



Figures 26–31. 26–30. *Acanthocorona spinifera* sp. nov.: 26. Male genitalia, dorsal; 27. Ventral; 28. Legs; 29. Forewing scales; 30. Wing venation; 31. *Acanthocorona* sp., female (NIGP 173719), postabdomen, ventro-lateral view, and oviscapt tip, dorsal view. Scale bars: 0.5 mm (28.); 1 mm (30.); 0.8 mm (31.).

***Acanthocorona wichardi* sp. nov.**

<http://zoobank.org/61FB43B8-BD57-4B52-83B1-6D50C4108B1C>

Fig. 23

Material. *Holotype* ♂, Burmese amber, NIGP 173717 (NIGP).

Etymology. The species is named in honour of Wilfried Wichard for providing material and taking photos of Microlepidoptera of Burmese amber.

Preservation. Completely preserved in an oval piece of amber with much particulate detritus particles and some air bubbles, wings overlapping, legs and post-abdomen clearly visible in ventral

view, one additional insect specimen present (one female of Hydroptilidae, Trichoptera, a single minute Coleoptera).

Description. Length of forewings 3.8 mm, antennae light brown, 24 flagellomeres, long spines on legs absent.

Male genitalia (Fig. 23): segment IX with median prolongation; rod-like spine on ventral apex of valvae absent, replaced by a bulbous area with short and long bristles, apical part of valvae enlarged forming an oval lobe with short denticules of on inner side, no denticles on margins, inner side of valvae with long spine, directed dorso-mediad; basal spikes of valvae absent; median plate short, rectangular in ventral view. Phallus long, tubular and curved ventrad.

Remarks. *A. wichardi* sp. nov. differs from the remaining species of the genus by lacking spines on the legs, absence of basal spikes and apical, rod-like spines of the valvae. The presence of a long spine on the median side of the valvae instead of emerging on the ventral corner is a unique character. The species is provisionally included in the genus until better preserved material becomes available which may lead to a different systematic placement.

***Acanthocorona kuranishii* sp. nov.**

<http://zoobank.org/2187398E-84B6-475A-B29D-A390C0062D61>

Fig. 24

Material. *Holotype* ♂, Burmese amber, MB.I. 5484, (MfN).

Etymology. The species is named in honour of Ryoichi Kuranishi (Chiba, Japan), who generously donated the amber piece with the inclusion to W. Mey and the MfN.

Preservation. Completely preserved in a round, polished piece of amber, but not clearly visible due to several fractures in the amber; numerous small bubbles of air present; wings overlapping, legs and postabdomen clearly visible.

Description. Length of forewings 4.0 mm, antennae light brown, 25 flagellomeres, legs with strong spines.

Male genitalia (Fig. 24): segment IX with short, triangular, median prolongation in ventro-caudal view; rod-like spine on ventral apex of valvae short, apical margin of valvae with row of five denticules, no denticules on inner side before margins; one pair of basal spikes of valvae present, about 1/3 the length of valvae. Phallus not visible.

***Acanthocorona sattleri* sp. nov.**

<http://zoobank.org/5638DDFF-C5C3-4592-B8CC-A5EEF7F1B935>

Fig. 25A, B

Material. *Holotype* ♂, Burmese amber, BUB 570, (PM); *paratype* ♂, Burmese amber, James Ziegras Collection, JZC – Bu 203 (AMNH).

Etymology. The species is named in honour of Klaus Sattler, London, specialist of Microlepidoptera in the Natural History Museum, London, for his support and help during many visits of the first author to the Microlepidoptera collection in London.



Figure 32. *Agathiphagama perdita* gen. nov., sp. nov., female holotype.



Figure 33. *Agathiphagama perdita* gen. nov., sp. nov., female holotype, photographed submerged in glycerine.



Figure 34. *Acanthocorona skalskii* sp. nov., male holotype, ventral view.



Figure 35. *Acanthocorona muelleri* sp. nov., male holotype, ventral view.

Preservation. Completely preserved in a flat, rounded and polished piece of amber, numerous small bubbles of air and two, minute midges (Diptera) present; wings overlapping, head, legs and postabdomen clearly visible in ventral view.

Description. Length of forewings 2.9 mm, antennae light brown, very short, about 0.3 of forewing length, with 21 flagellomeres.

Male genitalia (Fig. 25): segment IX rounded dorsally, segment X with short, bifid median prolongation in latero-dorsal view (Fig. 25A); rod-like spine long, accompanied by shorter spines on ventral apex of valvae, apical margin of valvae with row of denticules, additional denticules before margins; basal spikes of valvae paired, about half the length of valvae (Fig. 25B). Phallus not extruded.

Acanthocorona spinifera sp. nov.

<http://zoobank.org/F1BCDDB6-57DD-4486-8EC3-7B3D35A375F5>

Figs 18, 26–30, 37

Material. *Holotype* ♂, Burmese amber, NIGP 173718, (NIGP).

Etymology. The specific epithet is composed from Latin “spina”, spine, and “fero”, to carry, referring to the strong spines on tibiae of the adult moth.

Preservation. Completely preserved in a small, rounded, polished piece of amber, embedded in dorso-ventral position, with right wings spread out, some short fractures and few a bubbles of air present, legs and postabdomen well visible (Fig. 37).

Description. Length of forewings 4.8 mm, antennae dark brown, less than 0.5 of forewing length, with 30 flagellomeres; scales of forewing short and spatulate, or long with apical margin serrated, scales of fringes long, lanceolate, rounded at apex (Fig. 29).

Male genitalia (Figs 27, 28): segment X a large dorsal plate with deep, triangular excision of apical margin giving the structure a bifid form (Fig. 28); valvae broad, somewhat enlarged and rounded on apices; rod-like spine on ventral apex of valvae long, apically truncate, not accompanied by shorter spines, apical margin of valvae without denticules, basal spikes of valvae paired, about 0.8 the length of valvae (Fig. 27). Phallus not extruded.

Acanthocorona sp.

Fig. 31

Material. 1 ♀, Burmese amber, NIGP 173719, (NIGP); 1 ♀, # 7098 (TF).

Description. Length of forewings 3.4–4.2 mm, antennae pale brown, about 0.3 of forewing length, with 22–25 flat flagellomeres; labial palpi larger than maxillary palpi, terminal segment bulbous with long bristles, proboscis small; epiphysis present, legs with spines and scaled spurs; wing venation homoneurous, R5 to termen.

Female genitalia (Fig. 31): sternum VIII with broad base and triangular ventral apex; segment IX fused with segment IX, oviscapt cone band-like, dorso-ventrally flattened, strongly sclerotized,

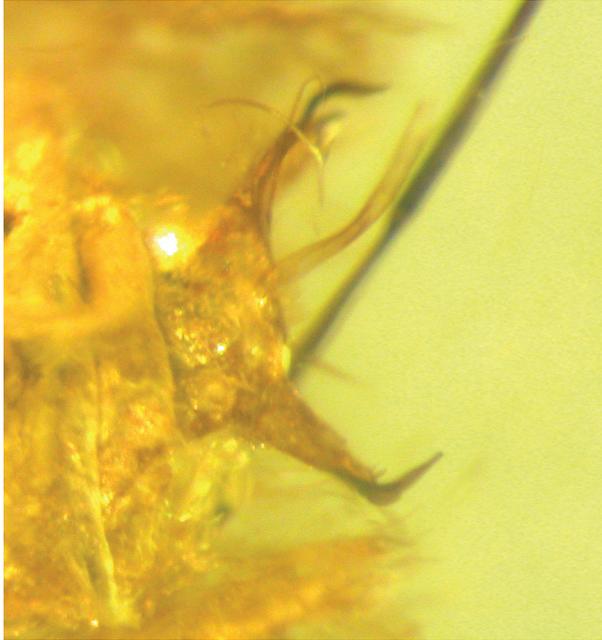


Figure 36. *Acanthocorona muelleri* sp. nov., close-up of male genitalia, ventral view.



Figure 37. *Acanthocorona spinifera* sp. nov., male holotype, ventral view.



Figure 38. Old tree of *Agathis dammara* (Chambert, 1803) in the forest of Mt. Salak-Halimun National Park (Java) with resin secretion; **A.** Basal trunk with several outpourings; **B.** Close-up of an outpouring caused by mechanical damage (photo: W. Mey).

fuscous to black, apex blunt, oviscapt saw usually hidden in oviscapt cone, sometimes protruding with its acute tip beyond cone margin.

Remarks. These female specimens cannot be assigned to any of the named species at the moment (see under remarks in the genus description). Since the female genitalia is an important character complex for the recognition of the family, the genitalia of one individual (NIGP 173719) was illustrated. The genitalia of the second species are difficult to see but are identifiable as those of a female.

Discussion

This paper aims to complete the picture of the distribution and diversity of past and recent primitive moths. A formal biogeographic analysis or providing a comprehensive review of recent and past distributions was beyond the scope of this study. The following discussion aims to guide any future biogeographical studies on primitive moths of South-East Asia, as well as to foster further works on Lepidoptera fossils.

1. *Aureopterix bachmaensis* sp. nov.

Wagner and Davis (2014) discovered Neotropical taxa of Micropterigidae occurring in Costa Rica and reported the first example of a genus range in the family stretching over both sides of the Equator (*Squamicornia*). *Aureopterix* is now another example of a micropterigid genus with records from the Northern and Southern Hemisphere, but in this case, oceans divide the disjunct parts of the generic range. The distance between the disjunct ranges of *A. bachmaensis* and the other two known species is about 6000 km on a northwest-southeast axis. Knowledge of the microlepidopteran fauna of the Larger and Smaller Sunda Islands as well as of New Guinea is poor, and thus we cannot exclude the possible occurrence of Micropterigidae in these regions. The notion of a continuous distribution of *Aureopterix* in the Indo-Australian Archipelago, today or in the past was our initial hypothesis, considering the many documented examples of this distribution type in Lepidoptera (Holloway 1998; Holloway and Nielsen 1998; Holloway *et al.* 2001; De Jong 2001).

Dispersal and colonization processes are closely related to the tectonic structure and geological and climate history in South East Asia, Melanesia and the Southwest Pacific. Kitching *et al.* (2001) and De Jong (2001) analysed the distribution pattern of butterflies and suggested a number of hypotheses which are synthetical explanations including tectonic, evolutionary and ecological processes with dispersal as important mechanism. In contrast to butterflies, thought to have originated around 119 Ma ago (Espeland *et al.* 2018) primitive homoneurous families of Lepidoptera are much older and have already existed during periods of tectonic movements 180 Ma ago in the Early Jurassic (Ansorge 2002; Grimaldi and Engel 2005). The basal splitting event among known extant Lepidoptera is presumed to have given rise to the Micropterigidae (Kristensen and Skalski 1998; Wahlberg *et al.* 2013; Regier *et al.* 2015; Kawahara *et al.* 2019) and its sister group, the bulk of the Lepidoptera. The family has a widely scattered cosmopolitan distribution, which might suggest a Pangaeian origin. In a continental drift scenario and/or any relevant independent dating, disjunct distribution patterns in this family can also be explained by providing vicariance-driven scenarios based on tectonic history reaching back into the Mesozoic. Recently, for example, Grehan and Mielke (2018, 2020) proposed such a vicariance model for explaining the distribution of the homoneurous Hepialoidea in the Southwest Pacific area.

In a molecular study of the radiation of the micropterigid genus *Sabatinca* Walker, 1863 in New Caledonia and New Zealand using COI-5P, both species of *Aureopterix* known for the Australian region were included (Gibbs and Lees 2014). According to the dating analysis of these authors based also on fossil calibrations, the Australia-New Caledonia split in *Aureopterix* is ca. 54 Ma old (95% interval: 40–74 Ma) and the branching of *Aureopterix* and *Zealandopterix* in their chronogram was estimated at ca. 83 Ma (95% confidence interval: 62–102 Ma). These dates substantially postdate the timing of the breakup of East Gondwana into Madagascar+India and into Australia, New Zealand and Antarctica at ca. 130 Ma based on palaeomagnetic dates (McIntyre et al. 2017), after the presumed detachment of terranes from northern Gondwana predicted from its geology at ca. 120 Ma (Metcalf 2001, 2017). Thus, the vicariance scenarios are not in agreement with the age and phylogeny-based divergence times of *Aureopterix* and related taxa as documented in Gibbs and Lees (2014), who also noted such a conflict in the split of *A. micans* and *A. sterops*. If this phylogenetic dating is accurate, we have to consider alternative, dispersal processes as the main driver in shaping the disjunct range of *Aureopterix*, rather than passive transport on continental terranes or vicariance via submerged parts of ancient continents. The recovering of *Aureopterix* within a clade including the strictly Australasian genera *Tasmantrix* and *Zealandopterix* suggests an Australasian origin of *Aureopterix*, with a long-distance dispersal for *A. bachmaensis* being the most probable scenario. The discovery of this genus in Vietnam is remarkable since the overseas dispersal scenario is rather hard to imagine because these taxa are moist forest dwellers, essentially confined to the substratum with larvae and adults highly prone to desiccation when leaving their habitats (Lorenz 1961). The biology of *Aureopterix* is not known yet, but host plants were shown to be strictly conserved in Micropterigidae of Japan, all feeding on the liverwort *Conocephalum conicum*. Gibbs and Lees (2014) also acknowledged a weak dispersal power in Micropterigidae. There might be other dispersal mechanisms we are unaware of, or the geological history of continental terranes, including the context with neighbouring oceanic islands or island arcs seem to be imperfectly known to date (for example geological uncertainties about submerged continents such as in the Australian region Zealandia), or both.

2. Agathiphagidae, Lophocoronidae

The stunning discovery of extinct taxa of primitive Lepidoptera in Myanmar, which were thought to be restricted in their distribution to the Australian Region, substantially revises present notions on the historical biogeography of Lepidoptera groups. In the absence of fossil distributions, Agathiphagidae and Lophocoronidae seem like classic cases of endemism in the Australian Region. *Agathiphaga* has two known species and stretches across the Pacific to Solomons, Vanuatu and Fiji and is thought to have benefitted from the possibility of long diapause in drifting *Agathis* seeds (Upton 1994). The biology of *Lophocorona*, by contrast, is still unknown. The fossil species of Agathiphagidae and Lophocoronidae found in Myanmar might alternatively provide evidence of a wider ancestral distribution of the two families, if such oceanic dispersal mechanisms do not prove to be a significant transport mechanism. The hypothesis that their extant ranges in the southern Hemisphere are relicts of a previous intercontinental distribution encompassing Asia and Australia has not yet been tested.

The time of divergence for lineages leading to the families Agathiphagidae and Eriocraniidae+Lophocoronidae was estimated by Wahlberg et al. (2013) at around 160 Ma (Agathiphagidae) and at around 180 Ma (Eriocraniidae+Lophocoronidae). At this time, in the Early to Late Jurassic, the distribution and positions of continents were quite different from their configuration today. The increasing

separation of Laurasia and Gondwana by the Tethys ocean occurred in the Jurassic and was completed in the Cretaceous (Metcalf 2017). This long period in earth history allows for proposing hypotheses which explain present distribution patterns in terms of passive transport on continental plates.

From a historical perspective, the Oriental fauna is a mixture of tropical Laurasian and Gondwanan taxa, over which is overlaid the results of dispersal processes. The collision of the Indian subcontinent into Asia in the early Eocene brought elements of the Gondwana fauna to the north and resulted in a pronounced enrichment of the biota (Morley 1998). Long before the accretion of India, several terranes were detached from the margin of North-East Gondwana and were shifted to the north during the Jurassic. They arrived at Laurasia and became part of the Asian continent during the Cretaceous (Metcalf 2017). With the movement of these continental terranes, ancient biota could have been transported, and given permanent over-water conditions of the terranes during the passage, arrived in Asia and immigrated into the resident biota. Based on this geological scenario, the extant occurrence and distribution of the Gondwanan caddisfly family Hydrobiosidae (Trichoptera) in Asia were explained by a vicariance/dispersal model (Mey 1998). Further examples of this terrane transport from angiosperms and invertebrate groups with disjunct ranges in Asia and Australia were provided by Poinar (2019b), underpinning the explanatory value of this model of shifting terranes. The occurrences of Agathiphagidae and Lophocoronidae during the Mesozoic in Asia can be explained likewise as a result of a transport by northward drifting Gondwana terranes. So far there have been practically no molecular or other analyses that might seriously test such models.

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Faunistic and taxonomic notes on *Phalacropterix apiformis* (Rossi, 1790) and *P. restonicae* (Fiumi & Govi, 2015) from Corsica, France (Lepidoptera, Psychidae, Oiketinae)

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Abstract. Records of the psychid species *Phalacropterix apiformis* (Rossi, 1790) from Corsica, France are mapped. Information about biology and phenology is also given, as well as a description of the morphological characteristics of this species. We combine this with DNA barcoding results. *P. apiformis* is compared with *P. restonicae*, described in 2015 by Fiumi & Govi from Corsica. We conclude on the basis of this evidence that both taxa are conspecific: we propose *Phalacropterix restonicae* **syn. nov.**

Samenvatting. Faunistische und taxonomische Bemerkungen über *Phalacropterix apiformis* (Rossi, 1790) und *P. restonicae* Fiumi & Govi, 2015 aus Korsika, Frankreich. Nachweise der Psychidae-Art *Phalacropterix apiformis* (Rossi, 1790), von der Insel Korsika, Frankreich, werden auf einer Karte dokumentiert. Ferner werden Informationen über die Biologie und Phänologie gegeben, sowie eine Beschreibung der morphologischen Merkmale dieser Art. Diese verbinden wir mit den Ergebnissen des DNA Barcodings. *P. apiformis* wird mit *P. restonicae* verglichen, die 2015 von Fiumi & Govi von Korsika beschrieben wurde. Auf der Grundlage dieser Ergebnisse kommen wir zu dem Schluss, dass beide Taxa artgleich sind: *Phalacropterix restonicae* **syn. nov.**

Introduction

Phalacropterix apiformis was first described by Rossi (1790) from “Etrusca”, Italy. It was placed in the genus “*Bombyx*” and considered as the genotype of *Phalacropterix* (Hübner, 1825) by subsequent designation in Kirby (1892). According to present knowledge, the genus *Phalacropterix* is composed of eight species, which are distributed exclusively throughout the Palaearctic Region (Arnscheid and Weidlich 2017). Apart from *P. graslinella*, which is widespread over large areas of temperate Europe as far as Siberia, the other *Phalacropterix* species show restricted distribution patterns. They occur in southern and south-eastern Europe and through the Anatolian Peninsula to the Middle East. Most species are found in the Mediterranean area (five species in total).

Material and methods

The images of the male genitalia (using the procedure described in Arnscheid and Weidlich 2017) were taken with an Olympus OMD EM10 Mark II digital camera, alongside an Olympus stereo microscope equipped with a photo adapter, and stacked with Combine ZP using Soft Stack, then sharpened and

focused with Neat Image V8 and post-processed with PhotoScape V.37. The DNA barcode sequences published in BOLD (Barcode of Life Data System) are based on a fragment of the mitochondrial COI gene (cytochrome c oxidase 1). DNA extraction, amplification, and sequencing of the barcode region of the mitochondrial cytochrome oxidase I (COI) gene (658 base pairs at the 5' terminus) were carried out following the protocols of deWaard et al. (2008). Levels of interspecific variation of the DNA barcode fragments were evaluated under the Kimura 2 parameter model of nucleotide substitution (Kimura, 1980). Taxonomic and collection data, voucher images, COI sequences and/or GenBank accession numbers are available for all specimens in the BOLD database (<http://www.boldsystems.org>). The Neighbour-Joining tree as recommended in the barcoding protocol (Ratnasingham and Hebert 2007, 2013) was generated using MEGA 7 (Kumar et al. 2016). The Barcode Identification Number (BIN) BOLD:ABV5577 in the BOLD database comprises the following sequences numbers for *P. apiformis*: GWORB3908-14, TIPSY509-12, GWORB4255-15, TIPSY257-12, GBLAD336-14 and TIPSY233-12. The sequence numbers LEFIA1290-10 and TIPSY047-08 representing the outgroup species *P. graslinella* are accessible by querying BIN BOLD:AAI4339.

Abbreviations

- CMW Private collection of Michael Weidlich
CWA Private collection of Wilfried R. Arnscheid
e. o. ex ovum
e. p. ex pupa
e. l. ex larva

The distribution of *P. apiformis* in Corsica

P. apiformis is distributed in the western Mediterranean area. In Italy *P. apiformis* occurs not only on the mainland, but also on the islands of Sardinia and Sicily (Parenzan and Porcelli 2006; Weidlich 2015) as well as on the Island of Capraia in the Tuscan archipelago (Dapporto et al. 2003; Parenzan and Porcelli 2006). In addition the species has also been recorded in Malta, the French mainland and on Corsica. The first author visited Corsica in 1999 sampling Psychidae for one week. In 2010, the second author spent ten days on Corsica, also searching for psychids. Besides *Banksia montanella* Walsingham, 1899, which is endemic to the island, larval cases of *P. apiformis* were also collected, and several caterpillars were reared to adults. The species was found to be widespread along the coast, up to the high montane region. In addition to their results from fieldwork, the authors searched the literature for hints to the occurrence of *P. apiformis* on Corsica. We excluded general mentions such as “Corse”, or “Corsica”, in monographs or check-lists. Fig. 1 shows the localities numbered from north to south with records colour-coded according to the time of sampling.

Biology and phenology

P. apiformis is found on Corsica from sea level up to 1800 m (Fig. 3). Records from even higher elevations, e.g. at Col de Vergio, Monte Renoso and Monte Incudine we consider to be imprecise. The caterpillars are polyphagous on different herbs and grasses. When pupating they commence spinning exposed on rocks, but also in cracks and clefts on boulders (Fig. 3c). Their period of flight is mainly at the beginning of May but occurred from 24.iv.1999 under laboratory conditions.

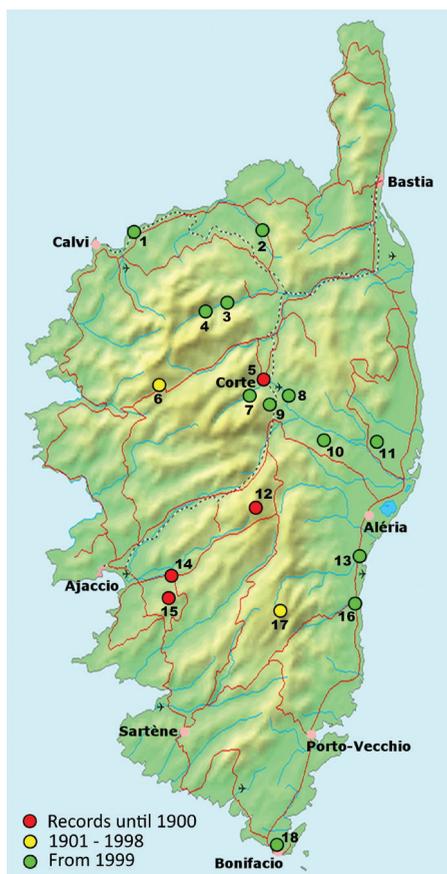


Figure 1. Distributional localities of *Phalacropterix apiformis* on Corsica (France) (https://upload.wikimedia.org/wikipedia/commons/3/3e/Corsica_Map.png, modified). **1.** 1 case, near Calvi NE, Marine di St. Ambrogio, 20 m, 13.iv.1999, leg. Weidlich. **2.** 6 cases, near Bastia SW, Urtaca 4 km NW, 150 m, 9.iv.1999, 1 ♂ e. l. 15.v.1999, leg. Weidlich. **3.** 12 cases, Parc naturel régional de la Corse, Gorges de l’Asco, 330 m, 9.iv.1999, 2 ♂♂ e. l. 5.v.1999, 1 ♂ e. l. 6.v.1999, 1 ♂ e. o. 23.v.2000, 4 ♂♂ e. o. v.2000, leg. Weidlich. **4.** 3 cases, Parc naturel régional de la Corse, near Asco 3 km SW, 950 m, 10.ix.2010, leg. Arnscheid. **5.** Parc naturel régional de la Corse, Corte: “den Case” (Mabille, 1867: 553). **6.** Parc naturel régional de la Corse, near Evisa NE, Col de Vergio: 1 ♀ Case, leg. Reisser (Reisser and Kautz, 1927: 20, Schawerda, 1927: 218). **7.** Parc naturel régional de la Corse, Gorges de la Restonica, cases, leg. Pfister (Pfister, 1982: 86); 7 cases 12.iv.1999, 550 m, 1 ♂ e. l. 7.v.1999, 1 ♂ e. l. 11.v.1999, 1 ♂ e. l. 15.v.1999, leg. Weidlich; 8 ♂♂ e. l. 25.iv.–5.vi.2014, 1400 m (Fiumi and Govi, 2015: 36). **8.** 7 cases, 11.iv.1999, 1 case, 13.iv.1999, Parc naturel régional de la Corse, near Corte, 6 km SE, 300 m, 1 ♂ e. p. 03.v.1999, 1 ♂ e. l. 11.v.1999, leg. Weidlich. **9.** 1 case, Parc naturel régional de la Corse, near Corte S, Casanova 1 km N, 600 m, 10.iv.1999, leg. Weidlich. **10.** 1 case, Pedicorte di Gaggio, 710 m, 11.iv.1999, leg. Weidlich. **11.** 1 case, near Linguizzetta 2 km S, 250 m, 13.ix.2010, leg. Arnscheid. **12.** Parc naturel régional de la Corse, near Ghisoni SW, Monte Renoso (Mabille, 1868: 638). **13.** 8 cases, near Solenzara, Vix S, 50 m, 10.iv.1999, 1 ♂ e. p. 24.iv.1999, 1 ♂ e. l. 8.v.1999, 1 ♂ e. l. 14.v.1999, 2 ♂♂ e. l. 28.v.1999, leg. Weidlich. **14.** near Ajaccio E, Cavro (= Cauro): cases and e. l. specimen (Mann, 1855: 539). **15.** near Ajaccio E, Pozzo di Borgo: cases and e. l. specimen (Mann, 1855: 539). **16.** 12 cases, River Solenzara, 5 m, 11.iv.1999, 4 ♂♂ e. l. 10.v.1999, 1 ♂ e. l. 15.v.1999, leg. Weidlich. **17.** Parc naturel régional de la Corse, Monte Incudine: 1 case, leg. Schawerda (Schawerda, 1928: 48). **18.** Bonifacio: Kollmorgen (1899: 327); 1 case, 10.iv.1999, leg. Weidlich.

Table 1. The morphological differences between *P. apiformis* and *P. restonicae*, as mentioned by Fiumi and Govi (2015).

Character	<i>P. restonicae</i>	<i>P. apiformis</i>
wingspan	15–16 mm	15–19 mm
color of abdomen	brownish	brownish and black
forewing veins m2 & m3	one-point-rising	divided
shape of tegumen	more hollow	?
shape of vinculum	triangle-shaped	oval-shaped
saccus	sharp and bent	?
shape of anellus	rounder distally	less round distally
phallus	bent, of genital length	?
sclerite	smaller in size and shape	somewhat broader
cases	smaller	somewhat larger

Morphological diagnosis of *P. restonicae*

As already explained, the existence of *P. apiformis* on Corsica has already been known for a long time (e.g. Mann 1855). Kollmorgen (1899) reported the occurrence of this species as “very common, from the coast (Bonifacio) up to 1800 m.” Therefore, it was very surprising that in 2015 Fiumi and Govi described a new *Phalacropterix* species from Corsica, based on the total of eight specimens, which they had collected in 2014 in the area of “Gorges de la Restonica” which is near Corte and an area well researched by lepidopterists for decades. *P. restonicae* was named after this, its type locality. According to Fiumi and Govi (2015), the two taxa differ in the characteristics displayed and compared in Table 1.

Based on a larger number of specimens of both taxa, the authors cannot confirm a significant difference in the wingspan. The males show a wingspan of 15–18 mm, which is in the normal range of wingspan variation of the entire *P. apiformis* population. Nevertheless, the forewing length is more informative than the wingspan because wingspan depends largely on how the specimen has been spread. When compared, these measured values show that there is no significant statistical difference. Even the abdominal colouration of both taxa varies considerably, the observed colouration ranging from a medium brown-yellowish to completely being black (Fig. 2, a–c). The venation was also variable between the two taxa, and was sometimes commonly asymmetric, due to the fact that most taxa of the subfamily Oiketinae show this characteristic, especially species of the genera *Ptilocephala* and *Oiketicoides* (Arnscheid, unpublished). We found the forewing venation of the *Phalacropterix* population on Corse shows M2 and M3 from one point rising, shortly stalked, or completely divided.

Description of the male genitalia of *P. apiformis* compared with *P. restonicae*

The tegumen of *P. apiformis* is slightly indented medially and show a small pointed process directed downwardly. Valvae short, of one-third of genitalia length, stout, cucullus roundish, distally with short spines. Clasper of sacculus elongate, narrower in the distal half, covered with short spines apically. Anellus short, semicircular and covered with short spines. Vinculum nearly triangular, occasionally slightly vaulted laterally. Saccus of half genitalia length, broad, spatulate caudally. Phallus as long as genitalia, dark sclerotized medially, somewhat enlarged caudally, covered irregularly with fields of short cornuti. Looking closer to the genitalia of *P. restonicae* it appears slightly more compact in general view. The distal end of the tegumen is slightly more elongated in some specimen.

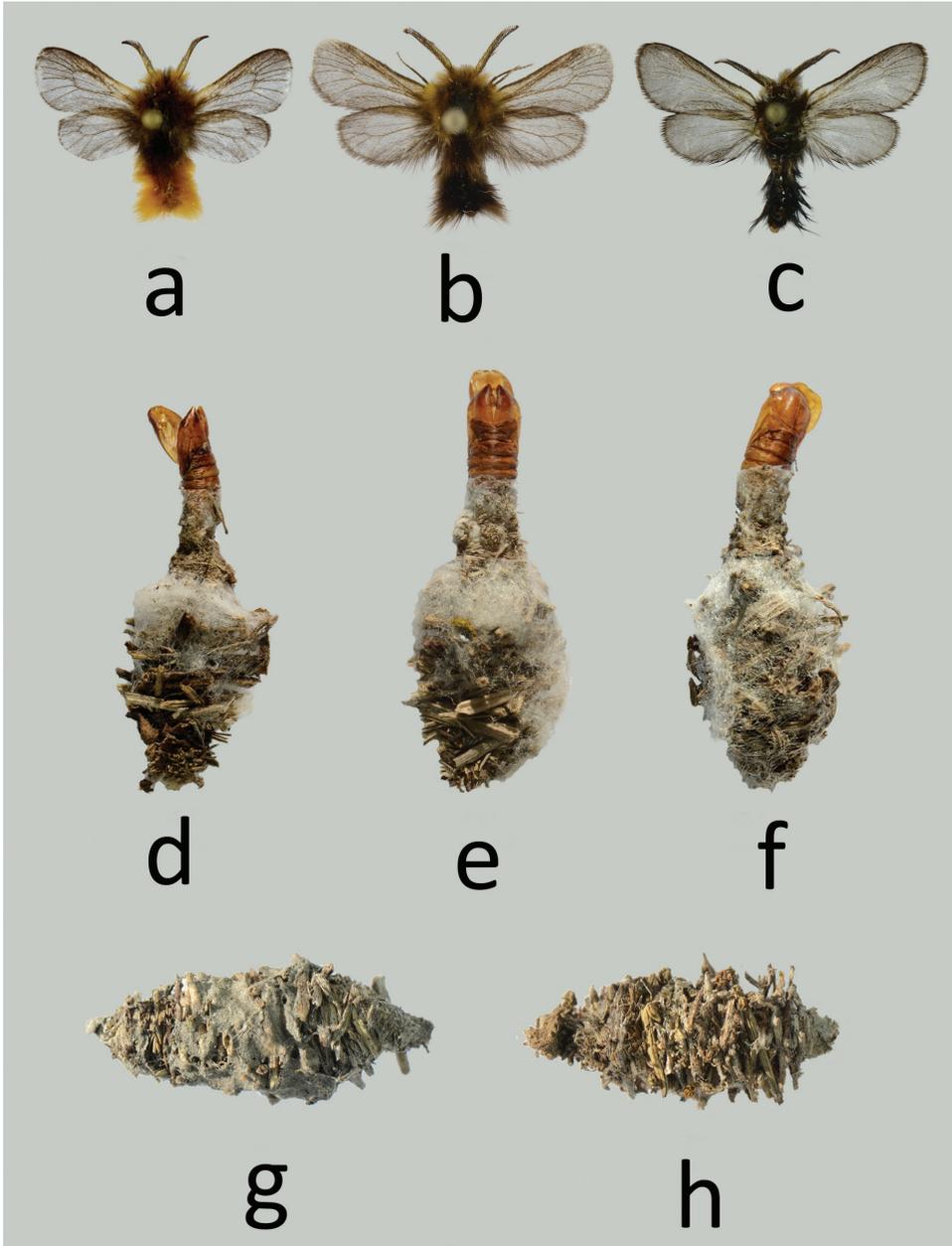


Figure 2. Male adults and larval cases of *P. apiformis* from Corsica. **2a.** ♂ e. l. 14.v.1999, near Solenzara, near Vix S, 50 m, leg. Weidlich (wingspan 14 mm). **2b.** ♂ e. l. 10.v.1999, Solenzara - river, 5 m, leg. Weidlich (wingspan 16.5 mm). **2c.** ♂ e. l. 9.v.1999, near Solenzara, near Vix S, 50 m, leg. Weidlich (wingspan 16 mm). **2d.** ♂ case, e. l. 14.v.1999, near Solenzara, near Vix S, 50 m, leg. Weidlich (length with exuvia: 21 mm). **2e.** ♂ case, e. l. 10.v.1999, Solenzara - river, 5 m, leg. Weidlich (length with exuvia: 23 mm). **2f.** ♂ case e. l. 9.v.1999, near Solenzara, near Vix S, 50 m, leg. Weidlich (length with exuvia: 22.5 mm). **2g.** ♀ case, 13.iv.1999, near Calvi NE, Marine di St. Ambrogio, 20 m, leg. Weidlich (length 19 mm). **2h.** ♀ case, 9.iv.1999, Parc naturel régional de la Corse, Gorges de l' Asco, 330 m, leg. Weidlich (length 17 mm) (all CMW). Photo: M. Weidlich.

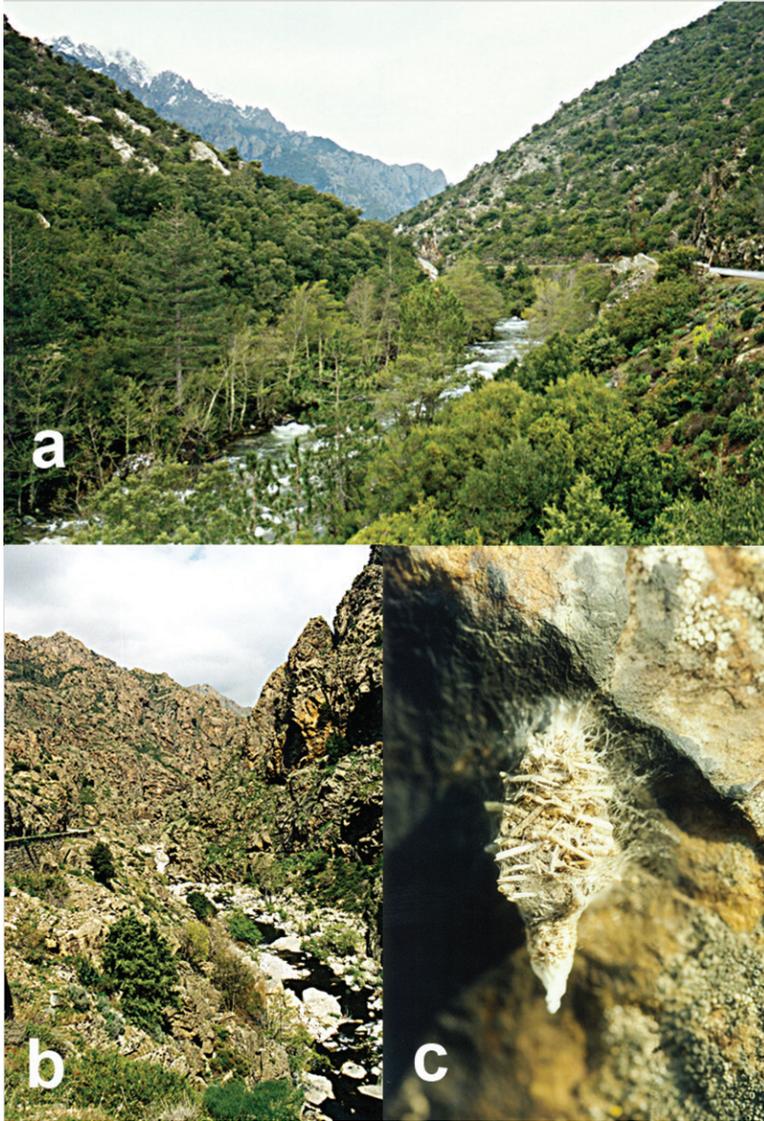


Figure 3. Habitat of *Phalacropterix apiformis* on Corsica. **a.** Landscape in “Parc naturel régional de la Corse”, Gorges de l’ Asco, 330 m (10.iv.1999). **b.** Habitat of *Phalacropterix apiformis*, “Parc naturel régional de la Corse”, Gorges de la Restonica, 550 m (12.iv.1999). **c.** ♂ Case of *Phalacropterix apiformis* in “Parc naturel régional de la Corse”, near Corte 6 km SE, 300 m (11.iv.1999). Photos: M. Weidlich.

The valva length in both taxa is variable, sometimes reaching the distal end of the tegumen or protruding slightly above it. Distally, the anellus of *P. restonicae* appears slightly rounded and somewhat more pointed in *P. apiformis* (Figs 4, 5). Whether this is statistically significant, however, is unclear.

There is no doubt that the variability of the male genitalia in Psychidae is great. This has in the past even led to the (however wrong) assumption that in contrast to most Heterocera the structure of the genitalia plays no part or a very minor role in taxonomic evaluation. As a result, the authors

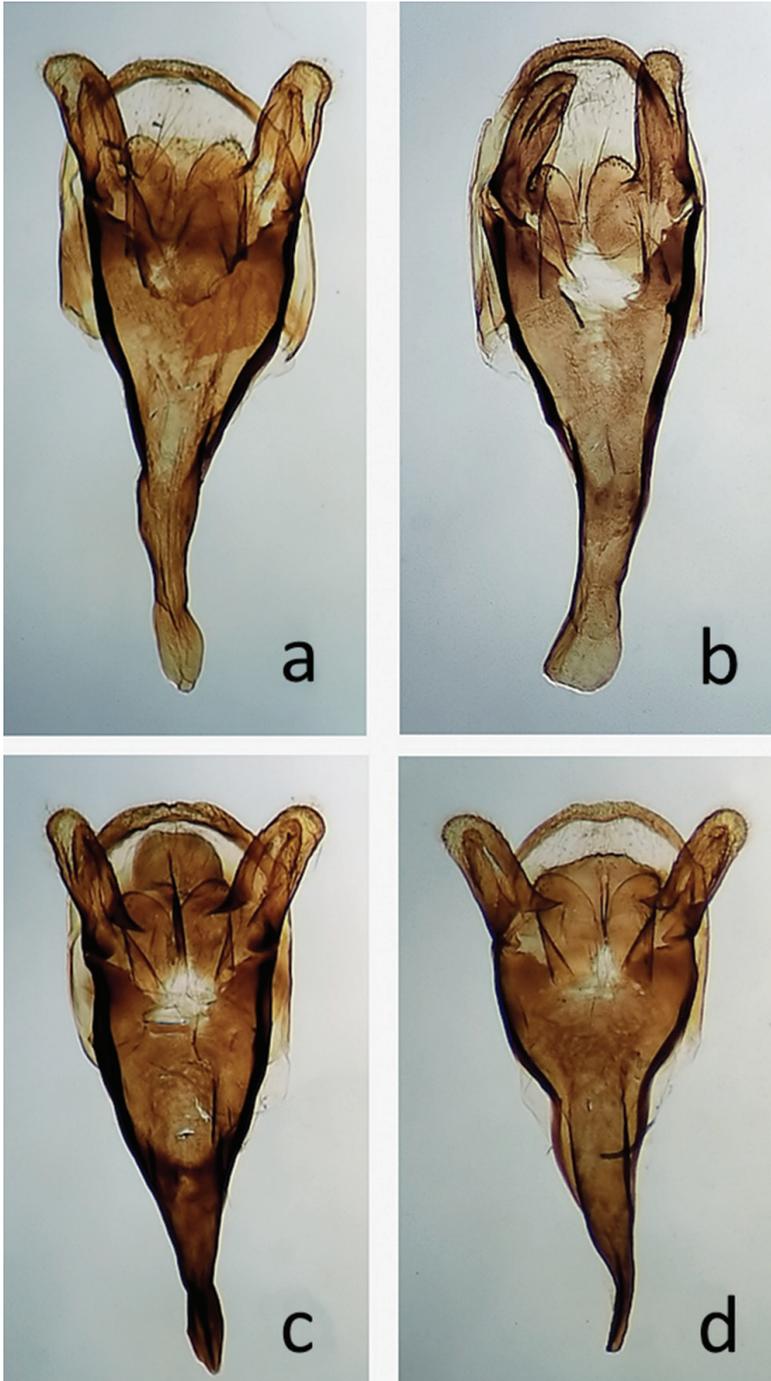


Figure 4. Variability of male genitalia of *P. apiformis* from Corsica and Italy. **4a.** Italy, Liguria, Ville S. Pietro (IM), e. p. 4.v.2006, genital slide 4102. **4b.** Ditto, e. p. 14.v.2002, leg. Arnscheid, genital slide 4103 (CWA). **4c.** Corsica, near Solenzara, Vix S, e. l.1999, leg. Weidlich, genital slide 4100 (CWA). **4d.** Corsica, near Corte, 6 km SE, genital slide 4101 (CWA). Photo: W.R. Arnscheid.

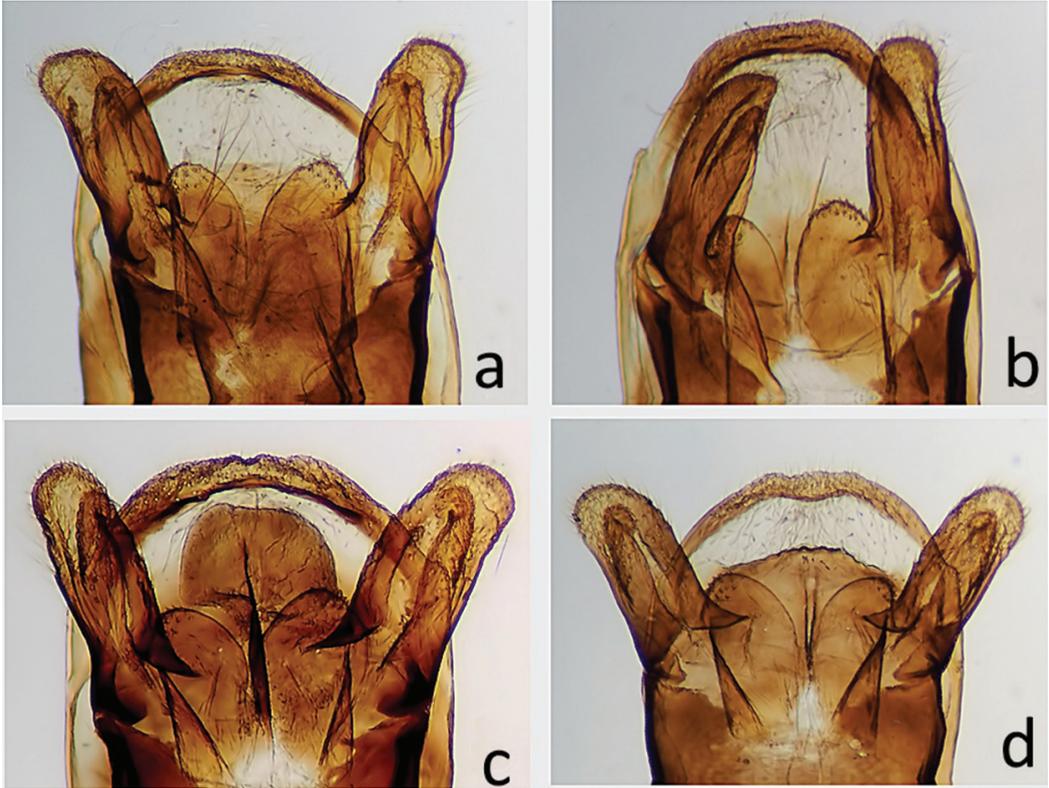


Figure 5. Variability of male genitalia of *P. apiformis* from Corsica and Italy (in detail). **5a.** Italy, Liguria, Ville S. Pietro (IM), e. p. 4.v.2006, genital slide 4102. **5b.** Ditto, e. p. 14.v.2002, leg. Arnscheid, genital slide 4103 (CWA). **5c.** Corse, near Solenzara, Vix S, e. l.1999, leg. Weidlich, genital slide 4100 (CWA). **5d.** Corsica, Corte, genital slide 4101 (CWA). Photo: W.R. Arnscheid.

have concluded that *P. restonicae* is in no way morphologically significantly different from *P. apiformis*, as stated previously by Fiumi and Govi (2015). The morphological diagnostic characteristics of species have exhibit little correlation with their genetic characteristics. Altogether, we have to accept that taxonomy based on morphological diagnostic characters is limited in its value for the study of evolution in this group. Therefore, whenever possible, we have also used for our studies molecular data.

Genetic divergences

In the BOLD database a total of six publicly accessible samples forming two BINs were considered, which are identified as *P. apiformis* and *P. restonicae*. The intraspecific pairwise genetic divergence of the samples reaches a maximum of 1.3%. In the absence of other data, this value seems too small for the establishment of a distinct species. Even within the outgroup-species *Phalacropterix graslinella* (Boisduval, 1852) with its widely dispersed populations, intraspecific divergence equals only about 1 %. In contrast, the inter-specific divergence between *P. apiformis*/*P. restonicae* and *P. graslinella* equals 11 % (Fig. 6, Tab. 2).

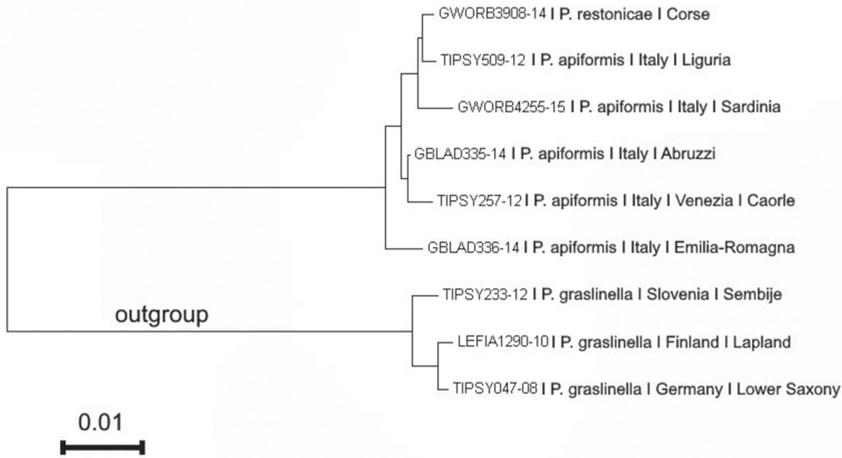


Figure 6. Neighbor-joining tree of DNA barcodes of *P. apiformis*.

Table 2. Matrix of pairwise genetic divergences of several *Phalacropterix* species.

Taxon	Origin	Pairwise divergence (p)							
<i>P. restonicae</i>	France, Corsica								
<i>P. apiformis</i>	Italy, Liguria	0.003							
	Italy, Sardinia	0.007	0.007						
	Italy, Abruzzi	0.005	0.005	0.008					
	Italy, Friuli	0.008	0.008	0.011	0.003				
	Italy, Emilia-Romagna	0.011	0.011	0.015	0.007	0.010			
<i>P. grasinella</i>	Slovenia, Sembije	0.121	0.123	0.121	0.121	0.121	0.121		
	Finland, Lapland	0.123	0.125	0.123	0.123	0.123	0.123	0.008	
	Germany, Lower Saxony	0.123	0.125	0.123	0.123	0.123	0.119	0.008	0.003

Conclusion

Traditionally, taxonomists have used morphological diagnostic characters to determine species, but meanwhile, it is now obvious that speciation and establishment of morphological diagnostic characteristics are not often correlated directly especially in allopatry. This is the case here. Because speciation is not always accompanied by morphological change, the true number of biological species is likely to be greater than the current tally of nominal species, most of which are delineated on purely morphological grounds.

Unexpected genetic diversity within species throughout the tree of life prompts several questions about possible regional and taxonomic biases in our estimates of diversity (Bickford et al. 2007). It is typical for island faunas in particular to develop local forms. The extent to which species have evolved apart is assumed to primarily be a matter of time especially in the case of allopatry. In any case, the period of isolation on the island of Corsica for the species *P. apiformis* has likely not been sufficient to allow full speciation on Corsica. Both morphological and genetic characteristics within the framework of the usual variability in these psychids do not provide evidence of such complete speciation. Hence, comparing the similarities both in morphological and molecular characteristics, we do not consider the taxon *P. restonicae* as a separate species but one conspecific with *Phalacropterix apiformis*: *Phalacropterix restonicae* syn. nov.

Acknowledgements

Our special thanks goes to Luisa Böttner (Spring, Texas, USA) for her critical comments and linguistic corrections and to two reviewers, and to David Lees for editorial comments and changes.

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On the date of publication of Linnaeus' second edition of "Fauna Svecica"

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<http://zoobank.org/54535A85-4A2E-4744-B484-0A9D1971607F>

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Abstract. It is shown that the correct year of publication of the 2nd edition of Linnaeus' "Fauna Svecica" is 1761, not [1760].

Taxonomists may have noticed that the date of publication of the second edition of Linnaeus' "Fauna Svecica", a work traditionally dated as 1761 in agreement with the date printed on its front cover (Linnaeus 1761a), is increasingly being recorded as "[1760]" (e.g., Evenhuis 1997; Bousquet 2016; Wiemers et al. 2018). Rationale for this interpretation has been summarised by Evenhuis (1997) with the following evidence:

1. Presence in the British Museum library of a copy purchased on 22nd December 1769 with a fly-leaf bearing the annotation "Ex libris M. Maty. 1759. Presented Novr. 14, 1760", as recalled by Soulsby (1933: 91).
2. Mention of the publication in Gronovius' (1760: 169) compendium of natural history publications.

Evenhuis thus concluded that copies of the second edition were already circulating in 1760 and that the final dating as 1761 can be explained if the title page and preface have been printed subsequently and then bound with the main text.

The first piece of evidence is highly suspicious, as the date of the annotation would imply that Matthew Maty, who became principal librarian of the British Museum in 1772, would have already had that copy in hand in 1759. The second one is instead clearly erroneous, indeed as Gronovius listed "Fauna Svecica" on page 169 of his bibliographic compendium, but referred only to the first edition of Linnaeus' work: "Fauna Suecica sistens Animalia Sueciae regni. – * Lugduni Batavorum 1746. in 8°. cum tabulis aeneis". It may be noted that Gronovius recorded the pirated version issued in Leiden of the first edition of "Fauna Svecica" (Linnaeus 1746a) as being issued one year in advance of the Stockholm one (Linnaeus 1746b) as being issued one year in advance of the Stockholm one (Linnaeus 1746b), but he made no mention of the second edition.

It may be noted that in the main text of the second edition, Linnaeus (1761a: 4, 250) mentions an article issued in 1760 (Gmelin 1760) and adds a biological observation dated 1760. However, in order to clarify the issue, which has bearing on the dating of numerous taxa described in this work it

is fair to assume that there is no more reliable source of information than Linnaeus himself, who can posthumously be ‘queried’ after his massive correspondence and manuscripts he left over to posterity.

In a letter dated 24 October 1760 to Carl Christoffer Gjørwell, the Swedish naturalist mentioned that his “Fauna Svecica”, i.e. the first edition (Linnaeus 1746b), was out of print and needed to be re-published, but he did not know which among his plethora of projects to prioritise (Linnaeus 1760). If, on 24th October 1760, Linnaeus did not know how to cope with a re-edition of the book, it seems impossible that just 20 days later (on 14th November 1760), such a work could already have been in circulation. Clearly also, Matthew Maty could not have annotated his copy in 1759.

Further to this, in the letter dated 2 March 1761 to Abraham Bäck, Linnaeus (1761b) told his friend that what was left of his time besides other commitments was taken up by the new edition of the *Fauna [Svecica]*, which now imposed on him a huge investment in effort. Importantly, in a letter of 3 April 1761 to the same correspondent, Linnaeus (1761c) said that on “*martis et veneris*” (Tuesdays and Fridays) he worked three hours each afternoon to correct the *Fauna*, stressing that such time was barely sufficient to write the additions.

In the letter of 2 July 1761 to Johannes Burman, Linnaeus (1761d) said he had eventually brought to completion “Fauna Svecica” *altera editio*, which exhausted him, and in a letter on 5 August 1761 to Nicolaas Laurens Burman, he reported that the work had then been published (Linnaeus 1761e). The very same information was also expressed in another letter dated 10 September 1761 that was addressed to the Italian botanist Carlo Allioni (Linnaeus 1761f).

All this first-hand information by Linnaeus is evidently compatible only with an actual printing date of the book between 3rd April 1761 and 5th August 1761. This interval may further be restricted as starting from 2nd July 1761, if by ‘completion’, written literally as “now I have brought to end” (“*jam ad finem perduxi*”), he meant conclusion of the manuscript and not its printing. In either case, these time spans are perfectly consistent with the date of 28 July 1761 that is stated in the dedication of the book.

It is also worthy to recall an undated *curriculum vitae* (“Memorial”) by Linnaeus, deposited at what was then the Königlichen Bibliothek in Berlin, in which the Swedish naturalist listed his publications and attributed the date of 1761 to the second edition of “Fauna Svecica” (Fries 1907: 37).

It is therefore recommended to reinstate ‘1761’ as the correct year of publication of the second edition of “Fauna Svecica”, adopting [5th August] 1761 as the best fit for the precise date of publication. Meanwhile, the annotation on the copy mentioned by Soulsby (1933) must be regarded as a clerical error by Matthew Maty that was likely introduced while recording subsequently lots being itemised from his library.

References

Note: alternative spellings (Latin/Swedish) for Carolus Linnaeus have been streamlined to the latinised form of this author’s name without the ligature for the diphthong ‘ae’.

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Long-distance dispersal of migrant butterflies to the Arctic Ocean islands, with a record of *Nymphalis xanthomelas* at the northern edge of Novaya Zemlya (76.95°N)

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Abstract. Although migrant butterflies are rare (or sporadically seen) guests on the Arctic Ocean islands, there is a slowly growing dataset on repeated occurrences of these insects in insular tundra and polar deserts. Altogether six long-distance migrant butterfly species were found to cross wide marine barriers north of the Arctic Circle (66.56°N), i.e. *Vanessa atalanta*, *V. cardui*, *Nymphalis antiopa*, *N. xanthomelas*, *Aporia crataegi*, and *Pieris napi*. Migrant individuals of *V. cardui* discovered on Svalbard (up to 78.27°N in 1978) reflect the farthest dispersal event of butterflies to the Arctic ever reported. Our record of *N. xanthomelas* at the northern margin of Novaya Zemlya (76.95°N) represents the northernmost finding of this species globally, reflecting the world's second farthest record of northern poleward immigration of butterflies. This occurrence coincides with an exceptionally warm summer season, when the third highest July and second highest August air temperature occurred (since global records began in 1880). Furthermore, the immigration into Novaya Zemlya coincides with a population explosion and massive expansion of *N. xanthomelas* in Siberia in 2019–2020. Our air current reconstructions indicate that this species most likely immigrated into Novaya Zemlya from mainland regions situated south-southeast (Polar Urals, Yugorsky Peninsula, and western Yamal) and east (Taymyr) of the archipelago. Overall, our findings reveal that long-distance dispersal events of butterflies to the Arctic islands are always linked to massive expansions of the corresponding species in mainland areas.

Introduction

It was shown that the faunas of Lepidoptera in Arctic polar deserts are characterised by low species richness and largely contain cold-tolerant, highly specialised species (Wolff 1964; Downes 1966; Tatarinov and Chernov 2006; Makarova et al. 2013; Coulson et al. 2014; Bolotov et al. 2015a; Kullberg et al. 2018). However, various long-distance migrant butterfly and moth species may also reach the High Arctic but could not establish permanent populations there, e.g. *Vanessa cardui* (Linnaeus, 1758), *V. atalanta* (Linnaeus, 1758), and *Plutella xylostella* (Linnaeus, 1758)

(Trybom 1877; Poppius 1906; Lokki *et al.* 1978; Korshunov *et al.* 1982, 1985; Chernov and Tatarinov 2006; Kozlov *et al.* 2006; Coulson *et al.* 2002, 2014). Studies on the immigration of southern insect species into the polar regions is a topic of great importance for further understanding of more general issues related to the patterns and pathways of global animal migrations (Williams 1925; Coulson *et al.* 2002; Hodkinson 2018).

A large body of historical and recent literature describes regular occurrences of migrant butterflies on subarctic islands situated in the North Atlantic such as Iceland (Wolff 1929, 1971; Downes 1966; Sømme 1993) and Faroes (Jacobson 1898; Jensen and Sivertsen 2010). Although many of these records were found to originate from human-mediated introductions with ships, goods, and plants, e.g. those of *Aglais io* (Linnaeus, 1758), *A. urticae* (Linnaeus, 1758), *Nymphalis antiopa* (Linnaeus, 1758), and *Pieris rapae* (Linnaeus, 1758) (Wolff 1971; Ólafsson and Björnsson 1997), several other species such as *Vanessa cardui* and *V. atalanta* arrived to the islands via natural dispersal events (Wolff 1929, 1971; Ólafsson and Björnsson 1997; Jensen 2001).

Individuals of a few migrant butterfly species repeatedly occurred even in extremely cold insular areas in the Arctic Ocean such as Greenland (Scott 1986; Karsholt *et al.* 2015), Svalbard (Lokki *et al.* 1978; Laarsonen 1985; Coulson 2015), Kolguev (Bolotov 2012), Vaygach (Vlasova *et al.* 2014), and Dolgiy (Kullberg *et al.* 2018). To the best of our knowledge, there were no reliable records of migrant butterflies from other Arctic islands and large archipelagoes, e.g. Novaya Zemlya, Franz Josef Land, Severnaya Zemlya, New Siberian Islands, Wrangel Island, and the Canadian Arctic Archipelago (Jacobson 1898; Wolff 1964; Scott 1986; Antonova and Khruleva 1987; Rydell *et al.* 2001; Makarova *et al.* 2013; Coulson *et al.* 2014). It is still unclear how many species of butterflies could reach the Arctic Ocean islands through natural migration events and how far north they can migrate globally.

This study (1) reports on the first occurrence of a migrant butterfly species on the Northern Island of Novaya Zemlya; (2) presents the most northern record of migrant specimens of *Nymphalis xanthomelas* (Esper, 1781) globally; (3) summarises available occurrences of long-distance migrant butterflies from the Arctic Ocean Islands; and (4) discusses possible causes and patterns of butterfly migrations to the High Arctic in a broader climate warming context.

Material and methods

Sampling of migrant butterfly occurrences on the Arctic Ocean islands

A body of available literature was collected via Google Scholar and Web of Science using keywords “migrant butterflies” and “migrant Lepidoptera” in combination with geographic names such as “Arctic islands”, “Svalbard”, “Vaygach”, “Greenland”, and “Iceland”. From these references, we collected the data on occurrences of migrant butterflies on the Arctic Ocean islands: species, sampling/observation locality, date, and number of recorded specimens. We selectively sampled records of migrant butterflies associated with natural long-distance dispersal events. Data on human-mediated introductions of butterflies to the Arctic islands and migrant butterfly occurrences on subarctic islands (e.g. Iceland and Faroes) were not included to the final dataset but used for the discussion.

All the selected occurrences were georeferenced using Google Maps and Google Earth v. 7.3.3 tools (Table 1). The estimated uncertainty of the co-ordinates was low ($\pm 1-2$ km), because most of records were precisely linked to certain geographic locations. The shortest distance from a given locality to the mainland (km) was estimated with ESRI ArcGIS 10 software (www.esri.com/arcgis).

Table 1. Occurrences of long-distance migrant butterflies on the Arctic Ocean islands. Human-mediated introductions and data on subarctic islands (e.g. Iceland and Faroes) were not included. N/A – not available. †Dead specimen was found.

Family	Species	Locality	Latitude and Longitude	Shortest distance from the locality to the mainland (km)	Date	N	Reference
Nymphalidae	<i>Nymphalis xanthomelas</i> (Esper, 1781)	Russia: Cape Zhelaniya, Northern Island, Novaya Zemlya Archipelago	76.9481, 68.5400	450	23.vii.2020	1	This study
Nymphalidae	<i>N. xanthomelas</i> (Esper, 1781)	Russia: Cape Zhelaniya, Northern Island, Novaya Zemlya Archipelago	76.9481, 68.5400	450	23.viii.2020	1	This study
Nymphalidae	<i>N. antiopa</i> (Linnaeus, 1758)	Russia: shore of Lake Yangoto, Vaygach Island	70.2511, 59.0922	80	19.viii.2010	1†	Vlasova et al. (2014)
Nymphalidae	<i>Vanessa cardui</i> (Linnaeus, 1758)	Norway: NE slope of the Kolberget Mount at Grumantbyen, Svalbard	78.1667, 15.1167	850	02.vii.1978	1	Lokki et al. (1978)
Nymphalidae	<i>V. cardui</i> (Linnaeus, 1758)	Norway: Sassendalen Valley, Svalbard	78.2728, 17.1323	850	02.vii.1978	1	Lokki et al. (1978)
Nymphalidae	<i>V. cardui</i> (Linnaeus, 1758)	Russia: 1 km west of Bugrino village, Kolguev Island	68.7861, 49.3401	75	07.vii.2009	1	Bolotov (2012); this study
Nymphalidae	<i>V. cardui</i> (Linnaeus, 1758)	Russia: Dolgiy Island	69.2730, 59.1010	30	2004	N/A	Kullberg et al. (2018)
Nymphalidae	<i>V. cardui</i> (Linnaeus, 1758)	Greenland: Qaqortoq (formerly Julianehåb)	60.7222, -46.0403	970	20.vii.1991	1	Karsholt et al. (2015)
Nymphalidae	<i>V. cardui</i> (Linnaeus, 1758)	Greenland: Upernaviarsuk	60.7493, -45.8902	970	20.vii.1991	1	Karsholt et al. (2015)
Nymphalidae	<i>V. cardui</i> (Linnaeus, 1758)	Greenland	N/A	N/A	7.vii–14.viii.1991	>2	Karsholt et al. (2015)
Nymphalidae	<i>V. cardui</i> (Linnaeus, 1758)	Southern Greenland	N/A	N/A	1992	>2	Karsholt et al. (2015)
Nymphalidae	<i>V. atalanta</i> (Linnaeus, 1758)	Greenland: Aasiaat (formerly Egedesminde)	68.7097, -52.8694	1,090	ix.1967	1	Karsholt et al. (2015)
Pieridae	<i>Aporia crataegi</i> (Linnaeus, 1758)	Russia: Cape Bolvanskij Nos, Vaygach Island	70.4464, 59.0900	90	09.vii.2013	1	Vlasova et al. (2014)
Pieridae	<i>A. crataegi</i> (Linnaeus, 1758)	Russia: Dolgiy Island	69.2730, 59.1010	30	2004	N/A	Kullberg et al. (2018)
Pieridae	<i>Pieris napi</i> (Linnaeus, 1758)	Russia: 5 km north of Bugrino village, Kolguev Island	68.8247, 49.2930	80	24.vii.2009	1	Bolotov (2012); this study

Field observations on adult migrant butterflies

The field observations on Novaya Zemlya were made around the research station “Cape Zhelaniya” of the Russian Arctic National Park [76.9481°N, 68.5400°E] during the period from 05 July to 18 October 2020 (observers: Vadim Zakhariin and Oleg Valkov, rangers of the National Park). This site is situated at the northern margin of the Northern Island of the Novaya Zemlya Archipelago (Fig. 1) and represents a flat polar desert area surrounded by a low mountain ridge with glaciers and perennial snowfields (Fig. 2A).

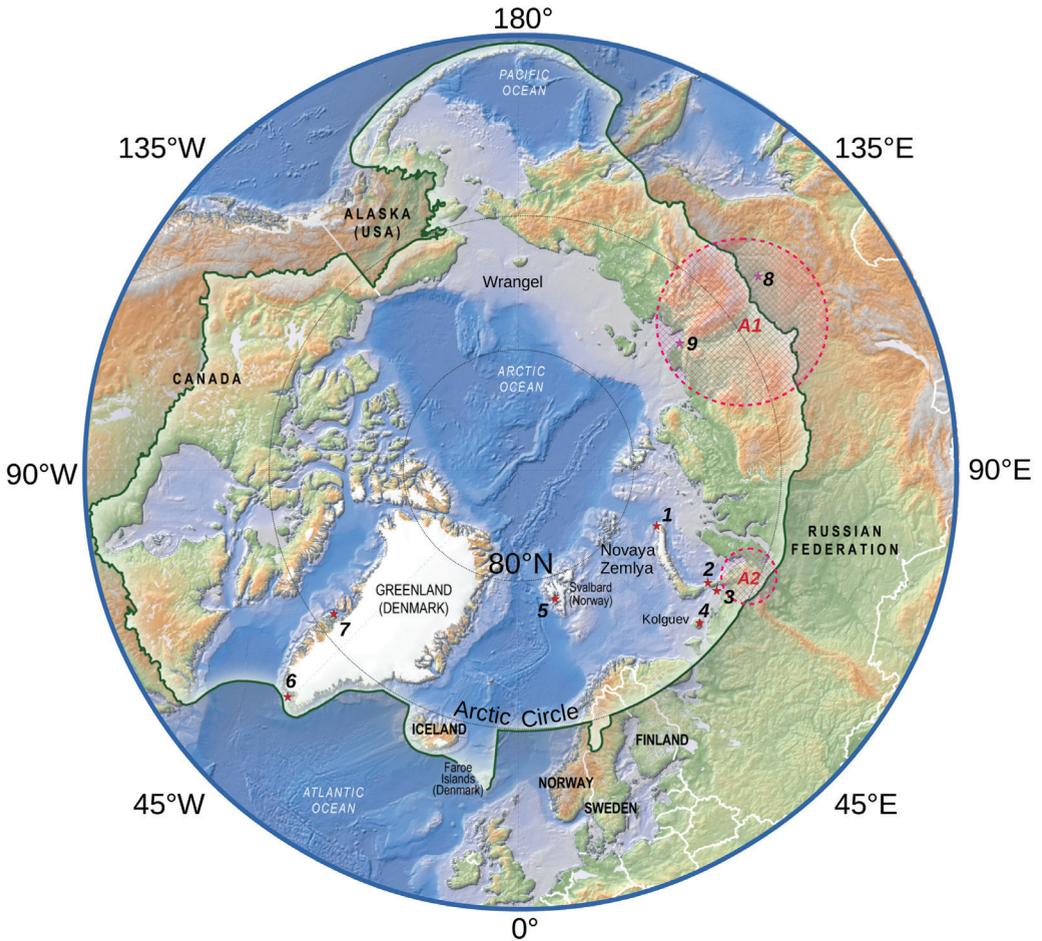


Figure 1. Occurrences of long-distance migrant butterflies on the Arctic Ocean Islands. The red stars indicate insular occurrences of migrant butterflies: 1 – Cape Zhelaniya, Northern Island, Novaya Zemlya, Russia (*Nymphalis xanthomelas*, 2020); 2 – north of Vaygach Island [shore of Lake Yangoto and Cape Bolvanskij Nos], Russia (*Nymphalis antiopa*, 2010, and *Aporia crataegi*, 2013); 3 – Dolgiy Island, Russia (*Vanessa cardui* and *A. crataegi*, 2004); 4 – Bugrino village, Kolguev Island (*V. cardui* and *Pieris napi*, 2009); 5 – Svalbard [Grumantbyen and Sassendalen], Norway (*V. cardui*, 1978); 6 – Southern Greenland [Qaqortoq and Upernaviarsuk] (*V. cardui*, 1991); 7 – Aasiaat, Greenland (*V. atalanta*, 1967). The pink stars indicate localities in mainland Eastern Siberia (Yakutia), in which a population explosion of *N. xanthomelas* was registered in 2020: 8 – Yakutsk; and 9 – Tiksi, east of the Lena River delta. The circles hatched with pink lines indicate approximate areas of massive expansion of *N. xanthomelas* throughout Eastern Siberia in 2020 (A1) and of regular occurrence of this species in the Polar Urals and adjacent areas since 1970s (A2) (see discussion section for detail). The CAFF Map No. 14 (Arctic Council; <http://library.arcticportal.org/id/eprint/1336>) was used as the topographic base of this image.

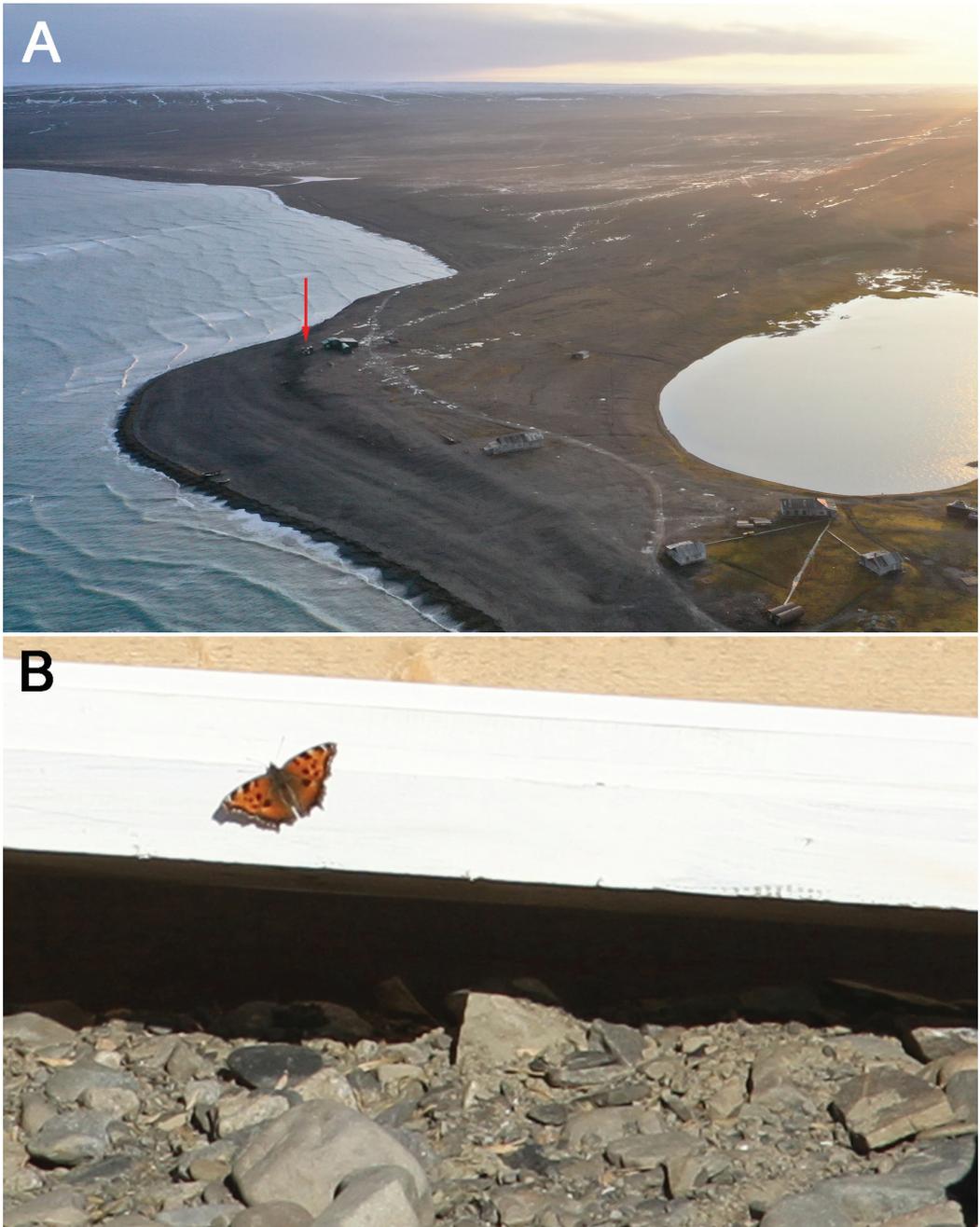


Figure 2. Scarce Tortoiseshell *Nymphalis xanthomelas* on Cape Zhelaniya, Northern Island, Novaya Zemlya. (A) General view of the northern extremity of Novaya Zemlya. The red arrow indicates the field observation site [76.9481°N, 68.5400°E]. In the front is the research station “Cape Zhelaniya” of the Russian Arctic National Park. In the background is a mountain range covered by glaciers and perennial snowfields. (Photo: Steffen Graupner). (B) Living butterfly near the research station on 23 August 2020. (Photo: Vadim Zakhariin).

Additional field observations were performed in Eastern Siberia (Yakutia Republic), i.e. in the vicinity of Yakutsk [62.0371°N, 129.6131°E; 26.vii and 07.viii.2020] and near Tiksi airport [71.7064°N, 128.8843°E; 30.vii–05.viii.2020] (Fig. 3A) (observer: Olga Aksenova).

Climate data and air current reconstruction

The data on mean air temperature anomalies for the summer season of 2020 was obtained from free open sources such as the NOAA GlobalTemp v.5.0.0 database and NOAA's Global Climate Reports (NOAA/OAR/ESRL PSL, Boulder, Colorado, USA; <https://www.ncdc.noaa.gov>; Vose *et al.* 2012). The Ventusky web application (<https://www.ventusky.com>; InMeteo, Pilsen, Czech Republic) was used to reconstruct air currents and weather conditions in Northern Siberia and Novaya Zemlya at the dates corresponding to the butterfly migrations.

Results

Occurrences of long-distance migrant butterflies on the Arctic Ocean islands

Overall, our dataset contains 15 occurrences of long-distance migrant butterflies on six Arctic Ocean islands, i.e. Svalbard, Kolguev, Vaygach, Dolgiy, Novaya Zemlya (Northern Island), and Greenland (Table 1). The occurrence covers the period from 1967 to 2020. In most cases, two migrant butterfly species per island were recorded, while on Svalbard and Novaya Zemlya only one species was discovered so far. These occurrences correspond to six species belonging to two families: *Vanessa atalanta*, *V. cardui*, *Nymphalis antiopa*, *N. xanthomelas* (Nymphalidae), *Aporia crataegi* (Linnaeus, 1758), and *Pieris napi* (Linnaeus, 1758) (Pieridae). The most northern record of migrant butterflies (*Vanessa cardui*) in the world was made on Svalbard (up to 78.27°N). Our occurrences of *N. xanthomelas* on Novaya Zemlya are the world's second farthest record of migrant butterflies on the Arctic islands (76.95°N). Furthermore, it seems to be the most northern finding of this species globally. The shortest distance from an insular butterfly occurrence to the mainland shoreline in our dataset varies from 30 (Dolgiy) to 1,090 km (Greenland) (Table 1).

Records of *Nymphalis xanthomelas* north of the Arctic Circle in 2020

The first imago of *N. xanthomelas* was recorded at Cape Zhelaniya near the research station of the Russian Arctic National Park [76.9481°N, 68.5400°E] (Fig. 1) on 23 July 2020 (visual observation by Oleg Valkov) (Table 1). The second butterfly was photographed there on 23 August 2020 by the park ranger Vadim Zakhariin (Fig. 2A, B). These findings are representing natural migration events, because the butterfly occurrences do not correspond to the dates of ship calls and aircraft arrivals. There were five ship calls at Cape Zhelaniya: 05 and 28 July, 04, 21, and 24 August 2020. Additionally, a helicopter from the town of Naryan-Mar (Nenets Autonomous Okrug) arrived on 13 July 2020.

In mainland Siberia (Yakutia), *N. xanthomelas* was found to be abundant around the city of Yakutsk [62.0371°N, 129.6131°E] on 26 July and 07 August 2020 and near the Tiksi settlement [71.7064°N, 128.8843°E] on 30 July–05 August 2020 (Fig. 3A, B).

The occurrences of *N. xanthomelas* in the High Arctic in 2020 coincide with an extremely warm summer season. Based on the NOAA GlobalTemp v.5.0.0 database and NOAA's Global Climate Reports, the third highest July and second highest August air temperature since global records began in 1880 were registered during this period. Our reconstructions revealed that a warm air

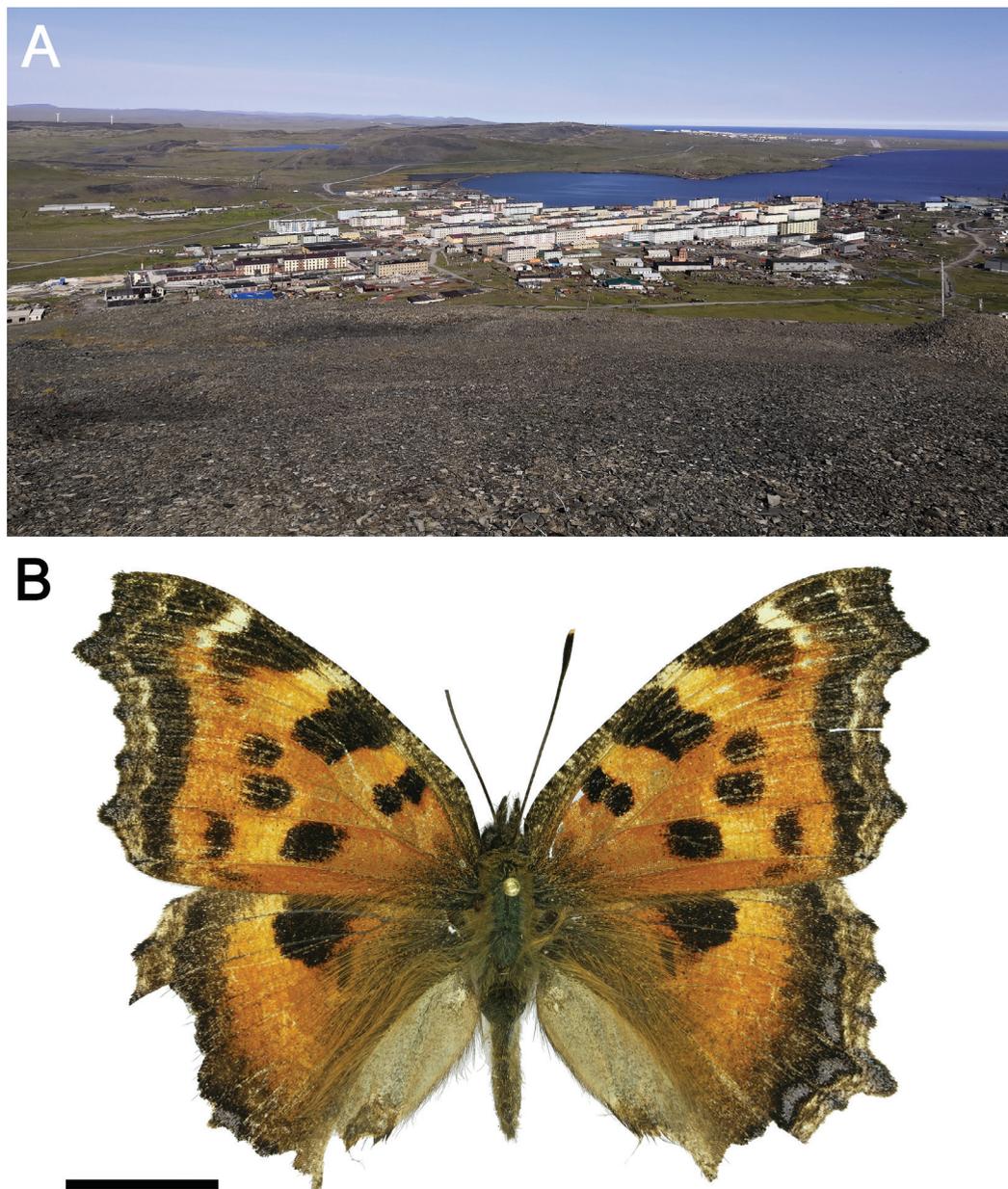


Figure 3. Scarce Tortoiseshell *Nymphalis xanthomelas* on the coast of Tiksi Bay of the Laptev Sea, east of the Lena River Delta, Yakutia Republic, Eastern Siberia. (A) General view of the Tiksi settlement (Photo: Olga V. Aksenova). (B) Specimen collected near Tiksi on 05 August 2020. Scale bar: 10 mm. (Photo: Vitaly M. Spitsyn).

mass from the Polar Urals, Yugorsky Peninsula, and western Yamal moved along the eastern coast of Novaya Zemlya to the northern edge of the archipelago during the period of 21–23 July 2020 (approximate direct distance 650 km) (Fig. 4A). Furthermore, there was an intense movement of

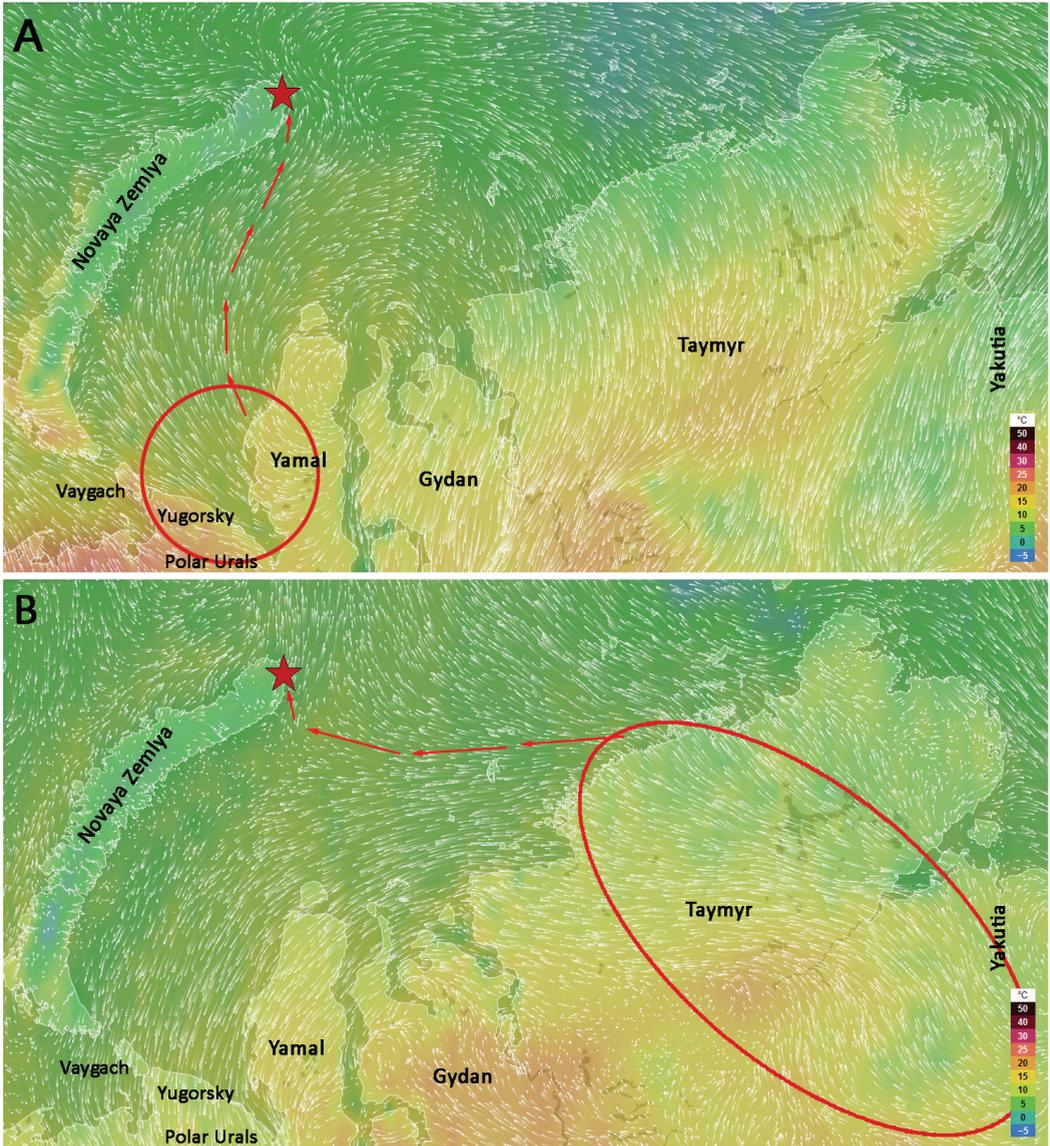


Figure 4. Reconstruction of air currents and air temperatures throughout Northern Siberia and Novaya Zemlya at the dates corresponding to *Nymphalis xanthomelas* migrations in 2020. In each case, the weather conditions were reconstructed on a day before the butterfly occurrence on Novaya Zemlya. The white arrows indicate air mass movements. The red stars indicate the butterfly occurrences. The red contours indicate possible source mainland areas for the butterfly immigration into Novaya Zemlya. The red arrows indicate possible migration routes of the butterflies on moving warm air masses from the mainland areas. The images were created using the Ventusky web application (<https://www.ventusky.com>; InMeteo, Pilsen, Czech Republic). (A) 22 July 2020, 12:00 PM (this pattern was constant during the period of 21–23 July 2020). (B) 22 August 2020, 12:00 PM (this pattern was constant during the period of 17–23 August 2020).

warm air mass from Taymyr towards Novaya Zemlya during the period of 17–23 August 2020 (approximate direct distance 580 km) (Fig. 4B). Because the daily patterns of air current movements and temperatures were similar within each period, we illustrated the situation on 22 July and 22 August 2020 (both at 12:00 PM, i.e. on a day before the butterfly occurrence on Novaya Zemlya) (Fig. 4A and 4B, respectively) as examples.

Discussion

Occurrences of migrant butterflies on the Arctic Ocean Islands are linked to regional expansions in the mainland

In total, six migrant butterfly species were recorded on the Arctic Ocean islands (Svalbard, Kolguev, Vaygach, Dolgiy, Novaya Zemlya, and Greenland) so far (see Table 1). Records of *N. xanthomelas* from Novaya Zemlya correspond to the recent expansion of this species throughout mainland Siberia and Europe, the patterns and timing of which are discussed in a special section (see below). We show that this species crossed 580–650 km wide marine barriers on warm air currents from the mainland (see Fig. 4).

Nymphalis antiopa is a widespread forest species, with occasional migrations to subarctic areas (Bogacheva and Olschwang 1978; Olschwang 1980; Korshunov et al. 1985; Chernov and Tatarinov 2006) and the British Isles (Williams 1935; Van Swaay et al. 2008). A dead specimen of this species was found on the shore of Lake Yangoto in the northern part of Vaygach Island [70.2511°N, 59.0922°E] (Vlasova et al. 2014) that appears to be the most northern occurrence of this species globally. This record coincides with expansion of *N. antiopa* towards the Polar Urals (Kara River basin) in 2010 (Tatarinov and Kulakova 2017), where it can sometimes establish temporary local populations (Chernov and Tatarinov 2006). Its imago was recorded in the Amderma settlement at the northern edge of the Yugorsky Peninsula [69.76°N, 61.66°E; 06.viii.2012] (Vlasova et al. 2014). Conversely, a single visual observation of *N. antiopa* on Svalbard (Sømme 1993; Coulson 2015) reflects rather a human-mediated introduction event with imported wood than a natural expansion event, as those in Iceland (Ólafsson and Björnsson 1997).

Vanessa atalanta and *V. cardui* are well-known seasonal long-distance migrant species that may successfully breed in boreal and subarctic areas (Bolotov 2002, 2004; Bolotov et al. 2013; Brattström et al. 2018) with a subsequent backward autumnal migration of newly emerged adults to the lower latitudes (Williams 1935; Stefanescu 2001; Mikkola 2003a, b; Stefanescu et al. 2017). *V. cardui* appears to be one of the most widespread and mobile butterflies globally (Shields 1992; Talavera and Vila 2017), which shows low genetic diversity and no clear phylogeographic structure (Pfeiler and Markow 2017). The African continent seems to be both the starting and the final area for its seasonal circulating migrations to Europe and back (Stefanescu et al. 2011, 2012, 2017). Migrations of both species regularly reached subarctic islands such as Faroes and Iceland (Wolff 1929, 1971; Ólafsson and Björnsson 1997; Jensen 2001). Among the Arctic Ocean islands, *V. atalanta* was found only on Greenland (Karsholt et al. 2015), while migrant individuals of *V. cardui* were recorded from Svalbard, Kolguev, Dolgiy, and Greenland (Lokki et al. 1978; Laarsonen 1985; Bolotov 2012; Karsholt et al. 2015; Kullberg et al. 2018). Exact source areas for the immigration of *V. atalanta* and *V. cardui* into Greenland are unclear, although these arrivals can clearly be linked to massive expansions and population dynamics in more southern continental regions of North America (Scott 1992, 2020; Swanson and Monge-Nájera 2000; Vandenbosch 2003). Records of *V. cardui*

from Svalbard in 1978, Dolgiy in 2004, and Kolguev in 2009 coincide with its massive migrations to the North (Korshunov *et al.* 1982; Bolotov and Tikhomirov 2000; Tatarinov and Kulakova 2005, 2010, 2013; Bolotov *et al.* 2013; Stefanescu *et al.* 2013). In 1978, this species was recorded across Finland up to Lapland (Lokki *et al.* 1978), as well as from Northern European Russia (Bolotov and Tikhomirov 2000) and Taymyr (Korshunov *et al.* 1982). In 2004, it commonly occurred in the eastern part of the Bolshezemelskaya Tundra (Tatarinov and Kulakova 2005). In 2009, there was an enormous expansion event of *V. cardui* from North Africa and the Mediterranean Region towards northern Europe and the Urals (Stefanescu *et al.* 2011, 2013; Bolotov *et al.* 2013; Tatarinov and Kulakova 2010, 2013; Tatarinov 2016). For example, this butterfly was found on 87.5% of observation sites surveyed around the Padimey Lakes in the eastern part of the Bolshezemelskaya Tundra [67.5711°N, 62.1616°E; 24.vi–17.vii.2009] (Tatarinov and Kulakova 2010). Some number of migrant individuals arrived to Iceland [07.vi–02.vii.2009] (Elzerman 2009; Goethals 2009).

The record of *Aporia crataegi* on Vaygach Island coincides with a population explosion and intense expansion of this species in European Russia and Western Siberia in 2012–2013 (Tatarinov and Kulakova 2013; Vlasova *et al.* 2014). In 2012, this butterfly was abundant around Amderma settlement at the northern edge of the Yugorsky Peninsula [69.76°N, 61.66°E; 17–20.vii.2012] (Vlasova *et al.* 2014), and in the Pechora River delta relatively close to Kolguev (Tatarinov and Kulakova 2013). Although successful development of *A. crataegi* larvae on creeping willows, the dwarf birch, and blueberry were observed in the Polar Urals (Kara River basin) (Chernov and Tatarinov 2006) and on the Kanin Peninsula (Bolotov 2012), its breeding on the Arctic Ocean islands such as Vaygach is next to impossible. Our records from Vaygach and Amderma seem to be the farthest northern occurrences of this species globally. Other examples of *A. crataegi* observations beyond the Arctic Circle are as follows: near Igarka, Taymyr [67.4594°N, 86.6119°E; 15.vii.1955] (Korshunov *et al.* 1982), Khadyta River valley, southern Yamal [67.0°N, 69.5°E; 1976–1979] (Olschwang 1980), and several records throughout the Bolshezemelskaya Tundra [up to 68.17°N; 1997–2004] (Tatarinov and Kulakova 2005). This migrant species shares a shallow phylogeographic structure throughout Northern Eurasia, including extinct populations in the United Kingdom and Korea (Todisco *et al.* 2020).

Pieris napi commonly occurred in subarctic and arctic areas of Eurasia such as the Finnish Lapland (Marttila *et al.* 2001), Bolshezemelskaya Tundra (Tatarinov and Kulakova 2005), Polar Urals (Korshunov *et al.* 1985; Bogacheva 1986; Tatarinov and Kulakova 2005), Yamal (Korshunov *et al.* 1985), and Taymyr (Korshunov *et al.* 1982). However, its native long-distance dispersal events to the Arctic Ocean islands are rather rare, with a single available occurrence from Kolguev (Bolotov 2012). A *P. napi* specimen recorded from Svalbard was accidentally imported (Kaisila 1973; Lokki *et al.* 1978).

Usually, air currents support long-distance dispersal in insects (Mikkola 1986; Stefanescu *et al.* 2007; Chapman *et al.* 2015). Wind-borne dispersal processes could explain cases of extremely long migrations such as the arrivals of the American Painted Lady butterfly *Vanessa virginiensis* (Drury, 1773) to the Azores, Canary Islands, Madeira, mainland Spain and Portugal, France, and Britain (Vieira 2017). It was shown that lepidopterans could be carried to the Arctic and Sub-Antarctic islands by air masses (Lokki *et al.* 1978; Sømme 1993; Coulson *et al.* 2002; Convey 2004; Hawes and Greenslade 2013). For example, the immigration of *Plutella xylostella* into Svalbard in 2000 was associated with a warm southeasterly air mass movement from Russia (Coulson *et al.* 2002). This invasion coincides with the arrival of multiple dipteran and lepidopteran species to the Faroes and Iceland (Jensen 2001), revealing a possible concatenated aerial dispersal of various inverte-

brates from continental Europe through the North Atlantic-Arctic Ocean marine barriers. Similar observations on weather-dependent aerial arrivals of migrant butterflies and moths were made on Svalbard (Lokki et al. 1978) and in Iceland (Wolff 1971). In the present study, we show that *N. xanthomelas* migrated to the northern margin of Novaya Zemlya on warm air masses moving from the mainland (see Fig. 4 and discussion below).

The recent expansion of *Nymphalis xanthomelas*: timing, geographic coverage, and success

The distribution of *N. xanthomelas* covered Central and Eastern Europe and temperate Asia up to Korea and Japan (Kudrna et al. 2011). The most northern findings of this species in Europe were from southern Finland (Kaisila 1962; Kudrna et al. 2011). In European Russia, it was seen rarely as far north as the Kirov, Vologda, and Saint Petersburg provinces (Ershov 1884; Tatarinov and Kulakova 2013). There were a few more northern records, e.g. near Kotlas [61.25°N, 46.64°E; vi.1906] (Krulikovsky 1909), Ukhta [63.67°N, 53.32°E; 1998] (Tatarinov and Kulakova 2013), and Petrozavodsk [61.78°N, 34.33°E; 25.iv.2005] (Kutenkova 2006; Gorbach 2013). In contrast, *N. xanthomelas* was more widespread and common throughout the Ural Mountains (Gorbunov and Olschwang 1997; Tatarinov 2016), where it occurred up to the Polar Urals, e.g. in the Kara River basin [68.87°N, 64.57°E; vii.2010] (Tatarinov and Dolgin 1999; Tatarinov and Kulakova 2013). Additionally, there were multiple occurrences from the eastern part of the Bolshezemelskaya Tundra, i.e. Vorkuta [67.49°N, 64.05°E; 1970s], Chum Station [67.0914°N, 63.1831°E; 23.vi.2001], Shapkina River [67.0°N, 55.0°E; 5–29.vii.2003], and Khalmer-Yu River [68.1654°N, 64.5783°E; 7–9.vii.2004] (Tatarinov and Kulakova 2005, 2007, 2013). In the Polar Urals, successful development of this species on dwarf willows (e.g. *Salix reticulata* L.) was registered (Tatarinov 2016).

It was also known to occur throughout the forest zone of Siberia, with a few records in forest-tundra and tundra of the Taymyr Peninsula (Korshunov et al. 1982, 1985; Kozlov et al. 2006). The downstream of the Verkhnyaya Taymyra River [74.15°N, 99.40°E; 17.viii.1983] appears to be the most northern locality in Asia, in which a migrant specimen of this species was collected (Korshunov et al. 1985). There were additional earlier findings on Taymyr, i.e. from Dudinka [69.40°N, 86.18°E; 1–12.vii.1915], Talnakh [69.48°N, 88.40°E; 5–6.viii.2001], Lake Lama [69.42°N, 90.71°E; 28.vii.2002] (Kozlov et al. 2006), and the middle reaches of the Rybnaya River [55.77°N, 94.80°E; 12.vii.1976] (Korshunov et al. 1982). Massive population explosions of *N. xanthomelas* were registered in Eastern Siberia (Yakutia) in 1958, 1967–1968, 1994, and 2002 (Ammosov 1971; Kaymuk et al. 2005).

Overall, this butterfly was seen rarely throughout Europe before the 2010s, i.e. for over one and a half centuries (Ershov 1884; Kaisila 1962; Anikin et al. 1993; Manil and Cuvelier 2014; Dennis and Hardy 2018). In Russia, the recent massive expansion of *N. xanthomelas* started in the 2010s. An extensive migration of *N. xanthomelas* (mean counts = 900–2700 individuals per hour) was observed on 24–25.vi.2012 in the Chuvashia and Mary-El republics (Lastukhin et al. 2016). The butterflies flying westward were recorded along the road from the Yakanzasy village [57.2947°N, 65.0805°E] to Lake Karas' [56.3996°N, 47.7974°E] (Lastukhin et al. 2016). The species became abundant throughout the boreal zone of European Russia (Arkhangelsk Region and Komi Republic), the Urals, and Western Siberia (Tyumen Region) (Tatarinov and Kulakova 2013; Vlasova et al. 2014; Bolotov et al. 2015b; Tatarinov 2016). In the Arctic, it was common in the Amderma settlement at the northern edge of the Yugorsky Peninsula [69.76°N, 61.66°E; 18–19.vii.2012] (Vlasova et al. 2014), as was in several other localities of the Nenets Autonomous Okrug, including the town of Naryan-Mar

[67.63°N, 53.05°E] (Tatarinov 2016; Kozlov *et al.* 2019). Successfully overwintered adults were recorded in Arkhangelsk [64.5308°N, 40.6264°E] in April 2014 (Bolotov *et al.* 2015b), and in the Subpolar and Polar Urals in 2013–2017 (Tatarinov 2016; Morgun 2017; Vlasova and Potapov 2018).

In 2019–2020, another population explosion of *N. xanthomelas* was recorded in Yakutia, Eastern Siberia. In 2019, the abundance of this species had increased so much that its massive expansion throughout Yakutia attracted full attention of regional mass media (News.Ykt.Ru 2019). Vagrant individuals of this species occurred east of the Lena River delta (Tiksi settlement; 71.6995°N, 128.8791°E) in late July-early August 2020. These data indicate that the arrival of migrants to Novaya Zemlya coincided with a massive expansion of *N. xanthomelas* in Eastern Siberia. Based on our air current reconstructions, we propose that the butterflies migrated to Novaya Zemlya from two source areas, i.e. the Polar Urals, Yugorsky Peninsula, and western Yamal (the occurrence on 23 July), and Taymyr (the occurrence on 23 August) (see Fig. 4A and 4B, respectively).

In European countries, the range of *N. xanthomelas* shifted northward since 2009–2010, and its settlements appeared in Finland and southeastern Sweden in 2011–2013 (Manil and Cuvelier 2014). In 2012–2013, this species was found to be highly abundant throughout Ukraine (Martynov and Plushtsch 2013). In Estonia, a series of striking immigration events of *N. xanthomelas* was registered in 2012–2015 (Tiitsaar *et al.* 2019). In July 2014, the butterfly was abundant throughout Scandinavia, northern Germany, the Netherlands and northern Belgium, while a flock of migrants crossed the Channel and immigrated into eastern England (Manil and Cuvelier 2014; Fox *et al.* 2015; Hensle and Seizmair 2015; Dennis and Hardy 2018). These observations coincide with intense dispersal processes in Western Siberia, the Urals, and European Russia (Tatarinov and Kulakova 2013; Vlasova *et al.* 2014; Bolotov *et al.* 2015b; Lastukhin *et al.* 2016; Tatarinov 2016). It is clear that its expansion in Western Europe resulted from the population explosion and massive westward migration of *N. xanthomelas* in Russia (Tatarinov and Kulakova 2013; Vlasova *et al.* 2014; Bolotov *et al.* 2015b; Lastukhin *et al.* 2016) and Ukraine (Martynov and Plushtsch 2013). The abundance of *N. xanthomelas* in mainland Western Europe and the United Kingdom during the summer of 2015 decreased abruptly, most likely due to very scarce offspring of overwintered migrant butterflies caused by unfavourable weather conditions (Manil and Cuvelier 2015). Conversely, in Estonia it was still a common species in 2016–2017 (Tiitsaar *et al.* 2019).

Finally, we assume that the recent expansion of *N. xanthomelas* to Western Europe and to the Arctic areas in Siberia and Europe was triggered by global climate warming during the period of 2012–2020. The European distribution of this species can be explained well by climatic variables, while its range shift to Scandinavia was predicted under climate warming scenarios (Settele *et al.* 2008). It was shown that the long-term trends in the range shifts, abundance, and phenology of migrant butterflies in continental Europe and Britain correlate with seasonal weather conditions and rising air temperatures (Mikkola 1986; Parmesan *et al.* 1999; Warren *et al.* 2001; Burton and Sparks 2003; Sparks *et al.* 2005, 2007; Dennis and Hardy 2018).

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Carried with the wind: mass occurrence of *Zeiraphera griseana* (Hübner, 1799) (Lepidoptera, Tortricidae) on Vize Island (Russian High Arctic)

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Abstract. Vize Island, located in the northern part of the Kara Sea (79°30'N, 76°59'E), is one of the least studied islands of the Russian High Arctic in terms of its biota. Hundreds of live and freshly dead individuals of Larch Budmoth *Zeiraphera griseana* (Hübner, 1799) were observed on this island from 16 July–2 August 2020. This is the first and the only terrestrial invertebrate ever discovered on Vize Island. The moths were likely transported to the island by air currents from the northern part of the Krasnoyarsk region, where an outbreak of *Z. griseana* was reported on over 75,000 ha. The distance travelled by moths approached 1200 km. Thus, the high Arctic islands are less isolated from insect migrants than was commonly thought. These islands will be colonised by boreal insects as soon as changing environmental conditions allow the establishment of local populations.

Introduction

Arctic habitats have fascinated biologists for centuries. Nevertheless, their species-poor insect faunas provide little reward for entomologists to justify spending several weeks or even months in the hostile environments of tundra or polar deserts. Consequently, the data on insects from the high Arctic islands, excepting the Svalbard Archipelago, are based only on occasional collecting and therefore remain scarce. This is particularly true for moths and butterflies: ten Lepidoptera species (three residents and seven migrants) were discovered in Svalbard (Coulson et al. 2014), eight species are known from the Northern Island of Novaya Zemlya (Kullberg et al. 2019), no species were reported from Franz Josef Land (Coulson et al. 2014) and four species (two residents and two migrants) were collected on Bolshevik Island in the Severnaya Zemlya Archipelago (Makarova et al. 2013).

This scarcity of data prompts entomologists to appreciate any observation on insects made in the high Arctic and to carefully collect information on occasional migrants (e.g. Kaisila 1973; Lokki et al. 1978). The current climatic changes have given additional weight to studies of insect migration to high latitudes, because the rapid warming of the Arctic (Walsh 2014) increases the susceptibility of species-poor polar faunas to invasion by more southerly species—provided the insects can reach the high Arctic islands and survive there (Coulson et al. 2002). In this paper, we report a mass occurrence of Larch Budmoth *Zeiraphera griseana* (Hübner, 1799) on Vize Island.

Methods

Vize Island (discovered in 1932) is located in the northern part of the Kara Sea (79°30'N, 76°59'E), 575 km from the mainland and 275 km from the Severnaya Zemlya Archipelago (Fig. 1). This small (288 km²) ice-free and hilly lowland island (the highest elevation is 22 m above sea level) has many rivers and streams (Figs 2, 3). The mean air temperatures are positive only in July and August (0.5 °C and 0.1 °C, respectively). The uniform landscapes are dominated by forb and cryptogam high-Arctic tundra (classification follows Walker *et al.* 2005). Vascular plants and lichens cover 5–10% and 10–15% of the ground surface, respectively. The most common of 20 species of vascular plants known from this island (Safronova and Khodachek 1989; M. Gavriilo personal observations), listed in decreasing order of importance, are *Saxifraga oppositifolia* L., *S. cespitosa* L., *Papaver radicum* Rottb., *Cochlearia groenlandica* L., *Cerastium regelii* Ostenf., *Saxifraga cernua* L., *S. hyperborea* R.Br., *S. foliolosa* R.Br., and *Cerastium bialynickii* Tolm. This island also hosts 31 species of mosses (Afonina 2015), 10 species of liverworts (Potemkin 2014),

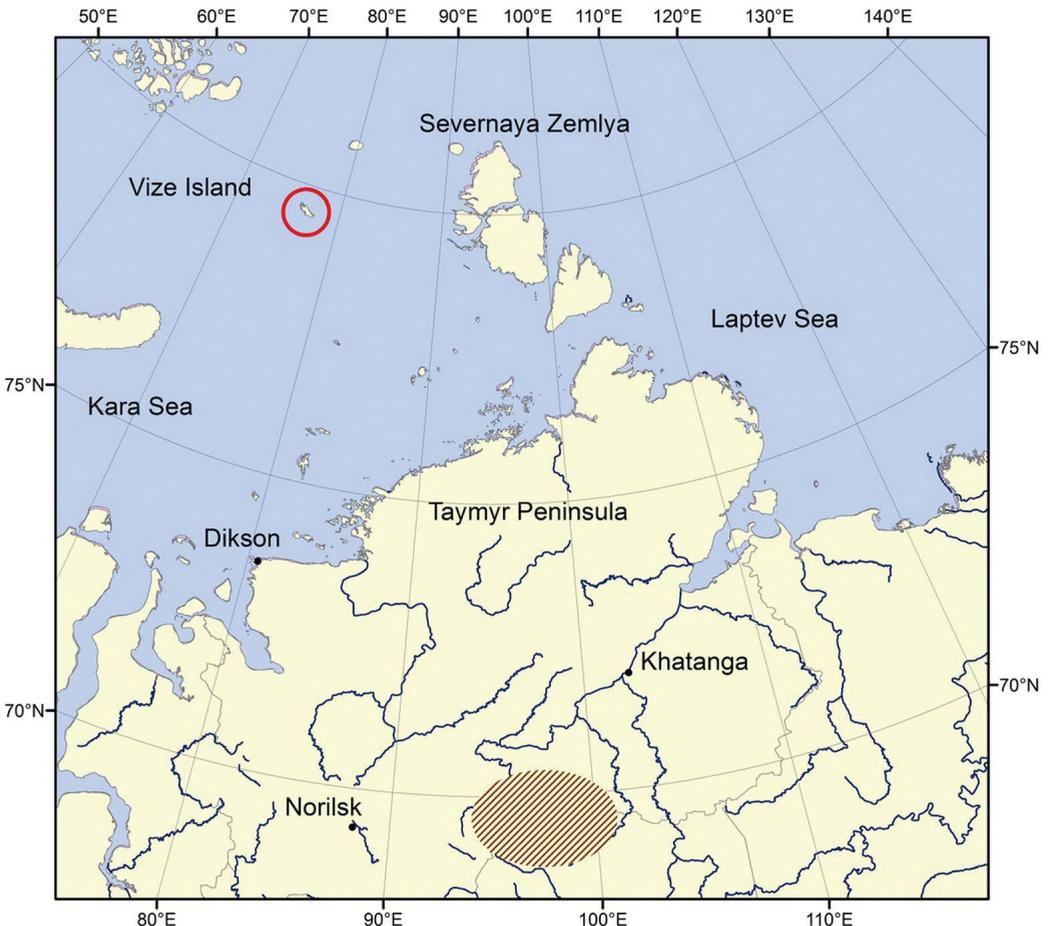
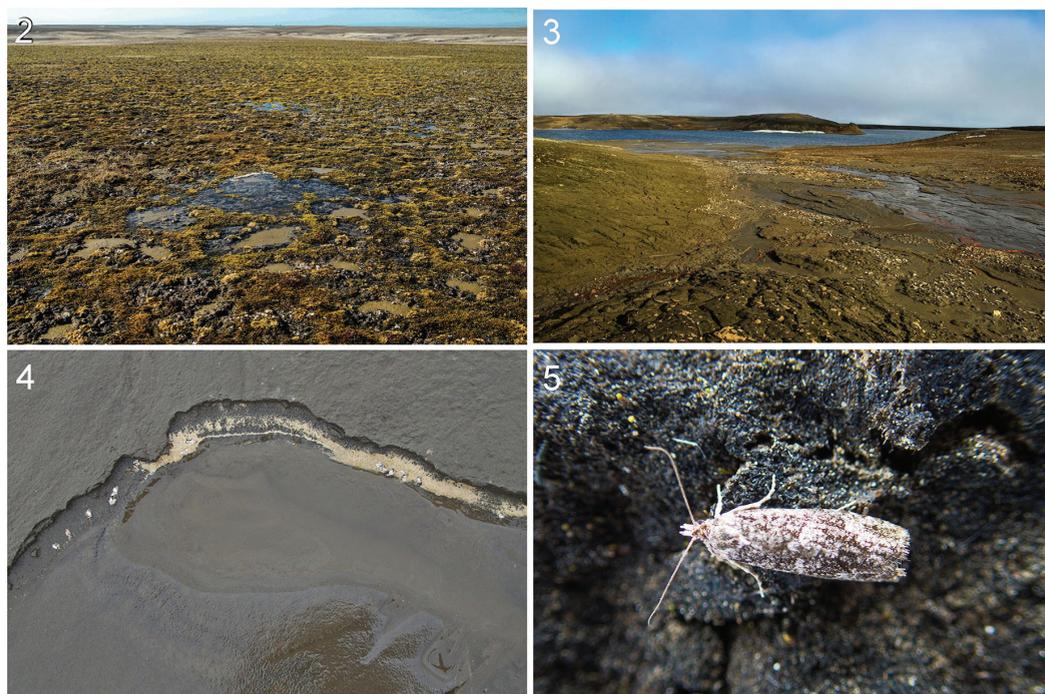


Figure 1. Location of Vize Island (red circle) and of an outbreak of *Zeiraphera griseana* (Hübner, 1799) recorded in 2020 (shaded area).



Figures 2–5. Examples of habitats on Vize Island and moths *Zeiraphera griseana* (Hübner, 1799). **2.** The typical landscape: forb and cryptogam high-Arctic tundra. **3.** Shallow river valley, at the sandy banks of which dead moths were observed. **4.** Dead moths at the stream bank. **5.** Live moth sitting on the ground.

41 species of ground lichens (Zhurbenko and Konareva 2015) and 5 species of lichenicolous fungi (Zhurbenko 2015). No terrestrial invertebrates have been recorded on Vize Island so far.

The expedition by the Arctic and Antarctic Research Institute (Russia) visited Vize Island from 9.vii.–30.viii.2020. Its aim was the exploration of Ivory Gull, *Pagophila eburnea* (Phipps, 1774) ecology, but the researchers used their stay on the island to perform the first systematic study of its biodiversity. Insects were searched by sweeping entomological nets over plants and by visual examination of flowers and moss carpets; they were also recorded during general faunistic surveys. The collected moths were preserved in paper envelopes; their identification was confirmed by examination of the male genitalia. Several specimens were relaxed, pinned and donated to the Zoological Institute (St. Petersburg) and to the Finnish Museum of Natural History (Helsinki). Weather data were downloaded from an open access web source (rp5.ru).

Results

Weather conditions

The persistent transition of daily air temperature through zero occurred on 30.vi.2020. The summer of 2020 was exceptionally warm, with mean air temperatures of 1.98 °C and 4.45 °C in July and August, respectively (Fig. 6). A moderate breeze (9–10 m/s with gusts up to 15 m/s) blowing from southeast (i.e., from the nearest continental landmass) was observed on 12–14.vii.2020 (Fig. 6). This was the only weather event of its kind during July-August, 2020.

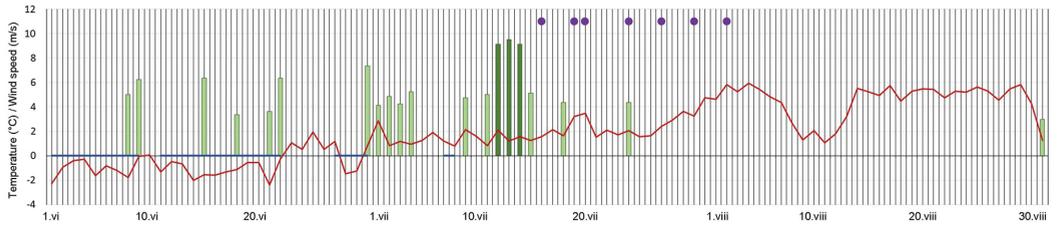


Figure 6. Weather conditions on Vize Island in summer of 2020. Red line: mean daily air temperature (°C); bars: mean daily wind speed blowing from south-east quarter (m/s; days with winds 9–10 m/s are shown by dark green bars); blue line: days with negative minimum air temperature; purple circles: days when live *Zeiraphera griseana* (Hübner, 1799) moths were observed.

Observations on moths

The live and freshly dead *Z. griseana* moths were first observed on 16.vii.2020 on the sandy banks of a pond near the meteorological station. On 19.vii, multiple freshly dead moths were discovered on sandy banks of rivers and streams along the 6 km route across the tundra north-east from the station. A total of 215 dead moths were counted within a 5×112 m area at the sandy bottom of a river valley with shallow (10–15 cm depth) streams, resulting in one moth per 2.6 m². Moths, single or in groups, were mostly found at the water's edge, along with some fine floating debris (Fig. 4). The flying moths (one at each date) were then spotted at/near the station on 20.vii, 24.vii, 27.vii and 2.viii; one moth was observed walking over the grass-lichen-moss vegetation on 30.vii (Fig. 5). Finally, multiple dead moths were seen on the sandy banks of 16 rivers or streams crossed by an 18 km route within the island on 2.viii.2020. However, no moths were seen on the same day along a 1 km part of the sandy beach at the northern coast of Vize Island. No other terrestrial invertebrates were observed or collected during this expedition, despite all reasonable efforts.

Discussion

The Larch Budmoth is widely distributed across Palearctic, reaching or approaching the northern distribution limit of coniferous forests in Finland (<http://www.laji.fi>), the Kola Peninsula in northwestern Russia (Kozlov and Jalava 1994) and the Taymyr Peninsula in Siberia (Kozlov *et al.* 2006). Its larvae feed on the needles of different conifers (Galkin 1992; Wermelinger *et al.* 2018); therefore, the migratory origin of the *Z. griseana* moths observed on Vize Island is without doubt.

Migratory behaviour is typical for *Z. griseana*, but the active migrations generally occur at the regional scale and are associated with severe defoliation of their host plant (Baltensweiler and Fischlin 1979). In Europe, periodic outbreaks of the Larch Budmoth are typical in the Alps (Baltensweiler and Fischlin 1979; Wermelinger *et al.* 2018), whereas outbreaks of *Z. griseana* in northern Europe are rare: we are aware of only two outbreaks in the northern part of the Arkhangelsk oblast (in 1984 and 1989; Selikhovkin 2009) and one outbreak in the Murmansk oblast of Russia (in 1980; Kozlov 1981). Both these regions are located 1200–1800 km from Svalbard, Franz Josef Land and Novaya Zemlya; nevertheless, migration of *Z. griseana* to any of the European Arctic islands has not been recorded yet (Coulson *et al.* 2014; Kullberg *et al.* 2019).

By contrast, outbreaks of *Z. griseana* in Siberia, resulting in severe damage of larch forests, have been documented since 1966 (Pleshanov and Raigorodskaya 1972), although they also likely

occurred prior to that date (Florov 1952). The northernmost outbreaks in the 1960s were reported from the Putorana Mountains (approx. 69°N; Galkin 1992) and the Nizhnaya Tunguska River (approx. 66°N; Galkin 1992). Large numbers of *Z. griseana* moths, probably originating from these regions, were observed in July of 1969 in tundra near Ust-Tareya (73°15'N, 90°36'E), some 250 km north of the northernmost larch records and some 500 km away from the continuous larch forest (Pleshanov and Raigorodskaya 1972; Chernov 1978). Even more exciting was the observation on 13–17.viii.1946 of dozens of live *Z. griseana* moths on ice in the East Siberian Sea, at a location 250–300 km from the continent and 800 km from the larch distribution limit (Andriyashev 1947; Florov 1952).

Thus, our observation of the mass occurrence of *Z. griseana* moths on Vize Island confirms that the poleward migration of this species is a sporadic but relatively frequent event. We suggest that moths were transported to this island on 12–14.vii.2020 by strong winds directed from the continent. The nearest potential source population was located in the northern part of the Krasnoyarsk region (Fig. 1), where an outbreak of this species was reported on over 75,000 ha (<http://www.xn--80aanigoucolcq3g.xn--p1ai/news-filials/23578.html>). Thus, the minimum travel distance of the moths was ca. 1200 km.

The dispersing insects generally require warm and dry conditions for take-off (Coulson et al. 2002). These conditions occurred near Norilsk in the Taymyr Peninsula on 13.vii, during the only day between 7.vii and 14.vii when the winds in this region blow from the south. Assuming that the wind speed along the entire route was the same as that recorded at Vize Island (i.e. 9–10 m/s), the travel time of the moths from Taymyr to Vize Island was 34–38 hours, i.e. shorter than the estimated travel time of the Diamond-back moth *Plutella xylostella* (Linnaeus, 1758) to Svalbard in 2000 (Coulson et al. 2002). Importantly, some *Z. griseana* moths remained alive and active for at least 20 days after their arrival, indicating that long-distance travel did not critically deplete resources stored in their bodies. This long activity period is somewhat surprising because, despite the exceptionally warm summer, with air temperatures exceeding the climatic norm by 2.4 °C (Anonymous 2020), the weather (Fig. 6) was still unfavourable for this boreal species.

We conclude that the high Arctic islands are less isolated from insect migrants than is commonly thought. The successful arrival of a large number of live moths from continental Siberian forests to Vize Island has once more demonstrated the absence of insurmountable physiological barriers to initial colonisation of high-Arctic islands by boreal insects.

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Antispilina ludwigi Hering, 1941 (Lepidoptera, Heliozelidae) a rare but overlooked European leaf miner of *Bistorta officinalis* (Polygonaceae): new records, redescription, biology and conservation

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Abstract. We record *Antispilina ludwigi* Hering, 1941 newly for France: Massif Central and Jura, Belgium: Ardennes and Switzerland: Jura and Alps, from many localities at middle elevations. All records were based on leafmines, often with larvae, in Snake-root, *Bistorta officinalis* Delarbre (Polygonaceae) and adults were reared from several localities. The species inhabits poor grasslands, moor habitats and heathland with relatively large hostplants. As the habitat is declining, and also other lepidopteran species feeding on this host are in decline, we expect that despite the new findings, this species is also declining and should preferably be monitored together with host specialist butterflies, such as *Boloria eunomia* (Esper, 1799) and *Lycaena helle* (Denis & Schiffermüller, 1775). During the period that the mines are present, the species is easy to record, even after the larvae have left the mines. The species is redescribed and diagnosed.

Introduction

The small leafmining family Heliozelidae has recently been the subject of several papers, including papers on phylogeny and classification (van Nieukerken and Geertsema 2015; Milla et al. 2017, 2019; van Nieukerken and Eiseman 2020), records of three new invasive species in Europe (Bernardo et al. 2011, 2015; van Nieukerken et al. 2012; Takács et al. 2020) and treatments of difficult species pairs that were previously considered single species (Mutanen et al. 2007; van Nieukerken et al. 2018). Of the thirteen known European species, nine of which are native (van Nieukerken et al. 2018; Takács et al. 2020), the small *Antispilina ludwigi* Hering, 1941, the only one feeding on a herbaceous plant, remains relatively poorly known.

Hering (1941) described the species and genus on the basis of moths reared from leafmines on Snake-root (or Common Bistort), *Bistorta officinalis* Delarbre (also known as *Polygonum bistorta* L. or *Persicaria bistorta* (L.) Samp.), collected from Hessen, Germany by A. Ludwig, a record several times repeated in literature (Grabe 1944; Skala 1949; Ludwig 1952). After that there have been only a few published faunistic records based on leafmines from Germany: Nordrhein-Westfalen (Ludwig 1952), Sachsen (Buhr 1964), Poland (Borkowski 2003b; Buszko and Pałka 2016), the

Czech Republic (Liška *et al.* 2000) and Lithuania (Ivinskis 2004), all with relatively little information. Several of these records have been overlooked subsequently, e.g. the German checklists did not cite it for Sachsen (Gaedike and Heinicke 1999; Gaedike *et al.* 2017), but the first version did cite Baden-Württemberg, a record later removed as no original sources could be found (Gaedike 2010).

When working on the family Heliozelidae the first author received ample material from Poland for molecular work. He then realised that it should be possible to find the species in other European mountains by focused searching of the hostplant for mines. In 2009 he encountered many mines during a hike on the Mont Mézenc in the Massif Central of France. This success led to a more focussed search in July 2017 in Auvergne and prompted him to encourage SW and RB to search for *Antispilina ludwigi* in the Belgian and Swiss mountains. To our surprise we all succeeded, and here formally record the species as new for Belgium, France and Switzerland. The records for Belgium and Switzerland were already available in a rather cryptic form online (Lepiforum e.V. 2008–2021; Wullaert 2021), and material from France and Belgium was used in our published DNA barcode and phylogenetic analyses (van Nieuwerkerken *et al.* 2012; van Nieuwerkerken and Geertsema 2015; Milla *et al.* 2017, 2019).

We redescribe the species, for which no full descriptions were available, provide information on its biology, and discuss conservation issues concerning this rare but overlooked insect.

Material and methods

Collecting

Most of the material treated here was collected by three of the authors as larvae and leafmines. Leafmines were searched by checking the hostplants. Samples of leaves with mines were taken home in plastic bags. Where needed some larvae were removed from their mines for molecular and morphological study and stored in 96% ethanol. Samples of leafmines were dried in a plant press and are stored in glassine envelopes. Additionally, larvae from Poland were sent to EvN by Anna Mazurkiewicz as preserved specimens in ethanol 96% in individual vials.

Rearing

Collected leaves were kept in small jars or polyethylene bags, with some moss and/or paper tissue added, until the larvae had prepared their leaf-epidermis-shield cases in the fourth instar. It was often necessary to remove the cut-out cases manually from the leaves, when they failed to detach probably due to loss of turgor in the leaves, after which the leaves were taken from the rearing jars and dried as vouchers. Adults were reared after hibernation under low temperatures, either in a fridge at ca. 4° C (French material in Leiden) or outdoors (Switzerland). Adults were reared successfully after the containers were taken indoors in early March (EvN) or left out of doors under natural conditions (RB). Larvae brought indoors on 29 January in Switzerland failed to pupate and died prematurely. However, a few parasitoids did emerge from these (see below). No adults emerged from Belgian larvae that were kept in a cool room.

Material

In Leiden all larval specimens, samples of leafmines and the majority of adults received a registry number in the form RMNH.INS.#####. As all material was either reared from leafmining larvae or collected as leafmines, all on the same hostplant *Bistorta officinalis*, we do not cite the hostplant

in the material lists. Numbers of larvae and mines for Belgian collection records refer to observed numbers, of which a sample was taken for rearing (that unfortunately failed) and some mines are stored in the collection.

We list only observations for new records, not those that duplicate the collections records. A detailed dataset of material, all observations and literature records was uploaded via NLBIF to GBIF (<https://doi.org/10.15468/be5dvw>).

To find additional records, hundreds of photographs of live and herbarium specimens of *Bistorta officinalis* were examined from several web portals (<https://bioportal.naturalis.nl/>; <http://www.botanicalcollections.be/#/en/home>; http://vh.gbif.de/vh/static/en_startpage.html; <https://www.gbif.org/>). This, however, did not provide any additional records.

Abbreviations

- MfN** Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions und Biodiversitätsforschung an der Humboldt-Universität, Berlin;
- RBC** Bryner, R., personal collection, Biel, Switzerland;
- RMNH** Naturalis Biodiversity Center, Leiden, Netherlands;
- SWC** Wullaert, S., personal collection, Houthalen, Belgium;
- WB** Werkgroep Bladmineerders [leafmine working group Belgium].

Morphology

Methods for preparation of the genitalia, other body parts and larval pelts follow our earlier work (van Nieukerken et al. 2012, 2018). Morphological terminology for adults and larvae follows recent Heliozelidae treatments (van Nieukerken and Geertsema 2015; van Nieukerken et al. 2018; van Nieukerken and Eiseman 2020).

Illustrations

Photographs of moths, leafmines, genitalia slides and larval slides in Leiden were taken with a Zeiss AxioCam digital camera attached, respectively, to a Zeiss Stemi SV11 stereo-microscope, a motorized Zeiss SteREO Discovery.V20 or a Zeiss Axioskop H, using Carl Zeiss AxioVision software version 4.8 or 4.9. Full depth views of male genitalia were made by stacking individual photographs with Zerene Stacker 1.04.

Field photographs by EvN were taken with a Canon EOS 350D or EOS 600D, all photographs by RB were taken with a Canon EOS 5D, Mark II with a Canon MP-E 65mm lens and those by SW with a Nikon D5100, AF-S Micro Nikkor 105mm lens.

Line drawings were prepared by BWL from genitalia in glycerin, using pieces of tissue and pins to fix the parts in position under the microscope, while the drawing was prepared.

The distribution map was prepared with QGIS 3.10.14.

DNA barcoding

All nine available DNA barcodes were generated for our earlier studies, and six of these were published (van Nieukerken et al. 2012, 2018; Milla et al. 2017, 2019). Three more are here presented for the first time. All data, including GenBank accession numbers are available in Barcode of Life Dataset DS-ANTILUDWI (<https://doi.org/10.5883/DS-ANTILUDW>). Procedures are detailed in the cited papers.

Taxonomy

Antispilina ludwigi Hering

Common names: Knöterich-Erzglanzfalter (German), Adderwortelgaatjesmaker (Dutch)

Antispilina ludwigi Hering, 1941:19. Holotype ♂, **Germany**: [Hessen] “Dillkreis, Im Feuerhack bei Waldaubach”, emerged 20 March 1941. Mines 29 July 1940, *Polygonum bistorta* [MfN] [examined]

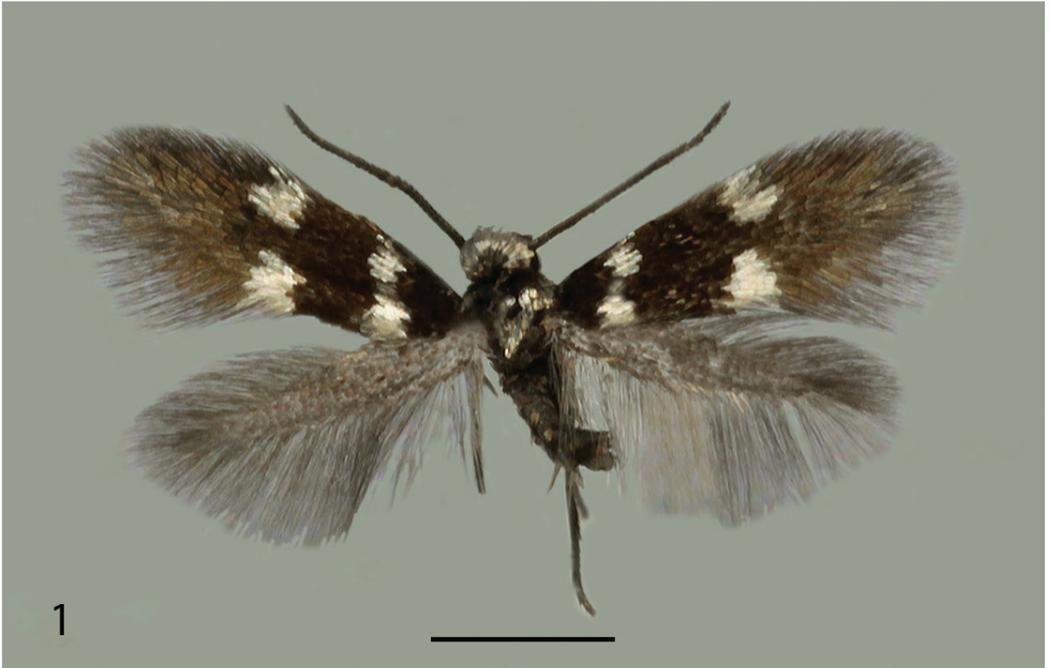
Antispilina ludwigi; Ludwig 1952: 24; Grabe 1955: 100; Buhr 1964: 37 [Sachsen]; Wojtusiak 1976: 9 [Poland, key, description, genitalia + adult ill.]; Razowski 1978: 91. [Poland, redescription, ill]; Laštůvka 1998: 17 [Czech Republic, checklist]; Gaedike and Heinicke 1999: 43 [Germany, catalogue]; Liška *et al.* 2000: [Czech Republic]; Borkowski 2003a: 88 [Poland]; Borkowski 2003b: 113 [Poland, photographs adults and mines]; Ivinskis 2004: 36 [Lithuania]; Buszko and Pałka 2016: 245 [Poland]; Gaedike *et al.* 2017: 24 [Germany, catalogue]; Buszko and Nowacki 2017: 17 [Poland, catalogue]; van Nieukerken 2018: https://fauna-eu.org/cdm_dataportal/taxon/6b71a06e-5ecb-48b6-84f0-45462a9d4604 [Europe, catalogue]; Laštůvka *et al.* 2018: 121–122 [Czech Republic, colour illustrations]; Bryner in Lepiforum 2003–2021: http://www.lepiforum.de/lepiwiki.pl?Antispilina_Ludwigi [Switzerland, photographs all stages, genitalia and mines]; Werkgroep Bladmineerders 2020: <http://www.bladmineerders.be/nl/content/antispilina-ludwigi-m-hering-1941> [Belgium, photographs mines, larvae], De Prins and Steeman 2003–2021: <https://projects.biodiversity.be/lepidoptera/species/5448/> [Belgium, catalogue].

Diagnosis. *Antispilina ludwigi* is a small completely dark grey-black moth, including the forewing fringe, with a narrow silver fascia at one-third and two opposite silver spots at two-thirds, resembling *Antispila* species. The small size (4–5 mm wingspan) and the dark colour separate *A. ludwigi* from the larger *Antispila* species (4.8–9 mm), that also have a distinct fringe line and white forewing fringe. *Holocacista rivillei* (Stainton, 1855) is about the same size, but the fascia is usually divided, it has also a white fringe, and the male foretibia bears a small epiphysis and it is not so dark. The latter species occurs in Mediterranean habitats with wild or cultivated grapevine (*Vitis vinifera* L.), whereas *A. ludwigi* is confined to poor grasslands and moors, mostly in mountains. A key was provided by van Nieukerken *et al.* (2018). The leafmine is the only blotch mine known on *Bistorta officinalis*, but early mines may sometimes be confused with the reddish circular patches caused by the fungus *Ramularia bistortae* Fuckel (Mycosphaerellaceae, Ascomycota) (Ellis 2020) (e.g. Fig. 26).

Description. Male (Figs 1, 24, 25). Forewing length 2.1–2.4 mm, wingspan ca. 4.5–5.0 mm. Head (Figs 3–5): frons with smooth scaling, bronzy-fuscous with brassy reflection; vertex bronzy-fuscous. Antenna reaching 2/3 of forewing, with 18–19 segments, basally covered with fuscous scales; scape pale brown ventrally with pecten consisting of 3 or 4 hairs. Labial palpus pale fuscous, comprising 2 palpomeres; maxillar palpi minute, 1-articled. Haustellum as long as head capsule. Thorax and tegulae brassy with metallic reflections, may appear silvery in some lighting. Legs dark grey, no white spots, epiphysis absent. Forewing almost jet-black, apically with brassy reflections, a silvery white, narrow outwardly oblique fascia at 1/5 to 1/4, usually constricted in middle; a silvery white small triangular dorsal spot at 1/2, and a squarish costal spot slightly beyond dorsal one; fringe grey with brassy reflection, fringe line absent. Hindwing and fringe dark grey. Abdomen greyish black.

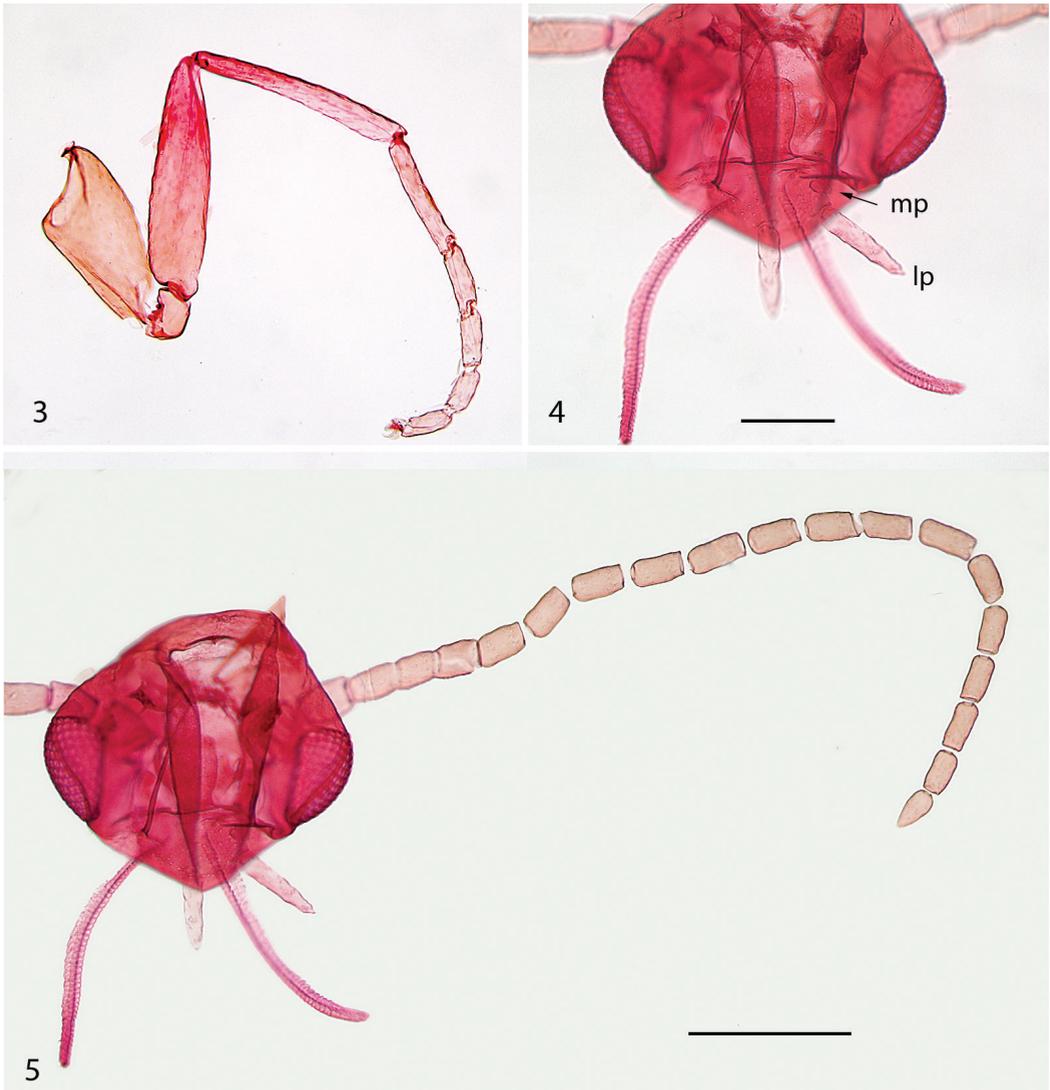
Female (Fig. 2). Forewing length 2.0–2.3 mm, wingspan ca. 4.2–5.0 mm. Abdomen apically pointed.

Venation (Fig. 6). Forewing: Sc poorly visible. R unbranched, a separate vein, to costa, but a persistent trachea connecting R with Rs+M+CuA. Rs+M+CuA ending in 4 rather indistinct branches, Rs1+2 to costa, Rs3+4 to termen, M and CuA to dorsum. Hindwing with Sc+R to costa, poorly visible, Rs+M with 3 branches, Rs indistinct, to costa, 2 branches of M to termen and dorsum; CuA a separate vein to dorsum; no visible Anal vein.



Figures 1, 2. *Antispilina ludwigi*, male and female. Switzerland, Bern, Rüeggisberg. Scale bar 1 mm. Photographs R. Bryner.

Male genitalia (Figs 7–13). Total length ca 530 μ m. Vinculum well sclerotized, long, narrowest in middle, as long as valva or longer. Tegumen bilobed. Valva subtriangular with blunt apex, length twice width, stalked pecten ca. $2/3$ from base of valva, with ca. 12–13 blunt sensilla, the number



Figures 3–5. *Antispilina ludwigi*, male adult, morphological details, whole body slide EvN4448. **3.** Foreleg. **4.** Head and mouthparts, lp: labial palp with 2 palpomeres; mp: maxillary palp, 1-articled. **5.** Head and antenna with 19 segments. Scale bars: 100 μ m (1, 2), 200 μ m (3). Photographs E.J. van Nieukerken.

on each valva may differ. Transtilla with long sublateral processes and slightly bilobed posterior process. Juxta weakly sclerotized, three-pronged anteriorly. Phallus cylindrical, ca. 400 μ m long, without cornuti, distal part slightly swollen, about as long as vinculum; phallocrypt spinose.

Female genitalia (Figs 14–17). Tip of oviscapt dorsoventrally flattened, with five cusps in total. Posterior apophyses slightly longer than anterior apophyses. Eighth sternum membranous, except narrow sclerotized region in distal part. Eighth tergite sclerotized, posterior part dorsally elevated, anterior end crooked, middle part projected anteriorly. Guy wire arising from middle part of vestibulum, as long as vestibulum. Vestibulum membranous with a pair of sclerotized rods.

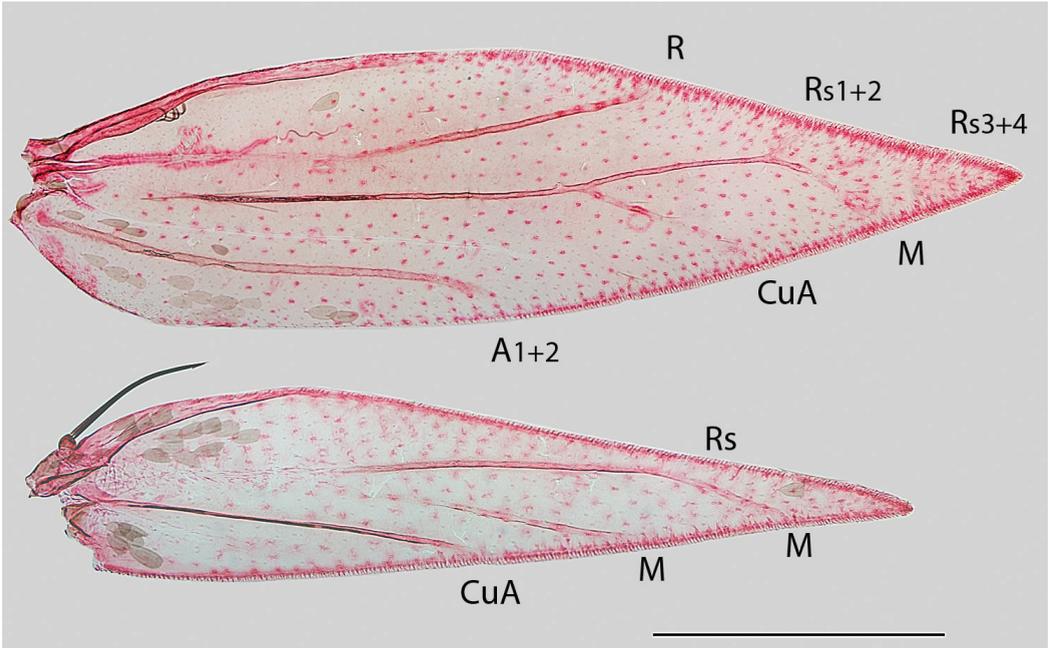
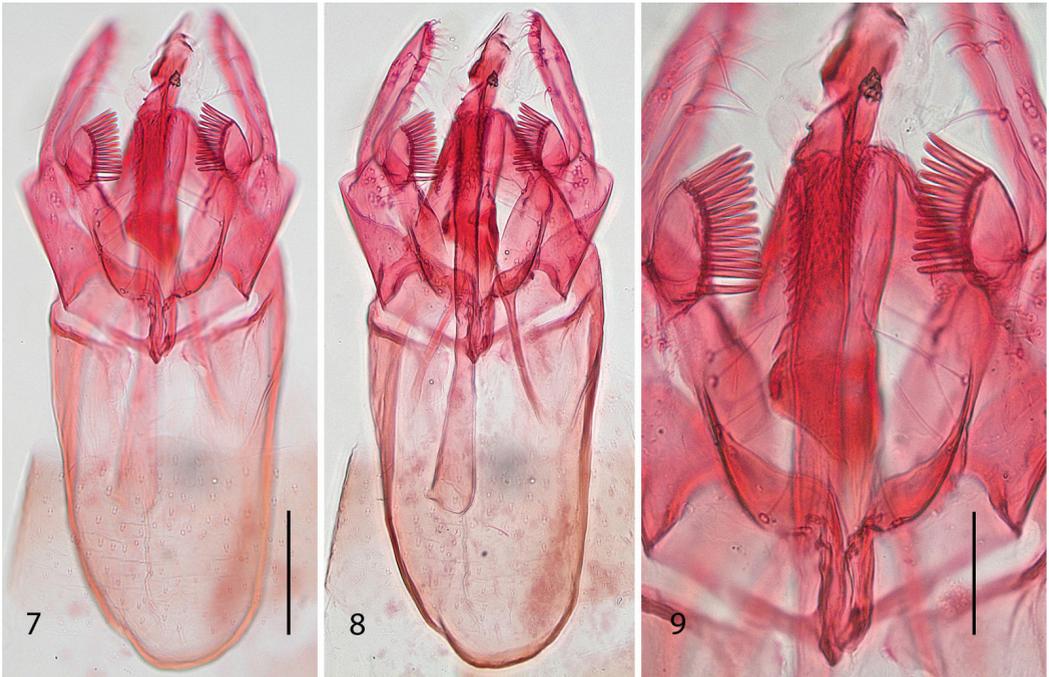
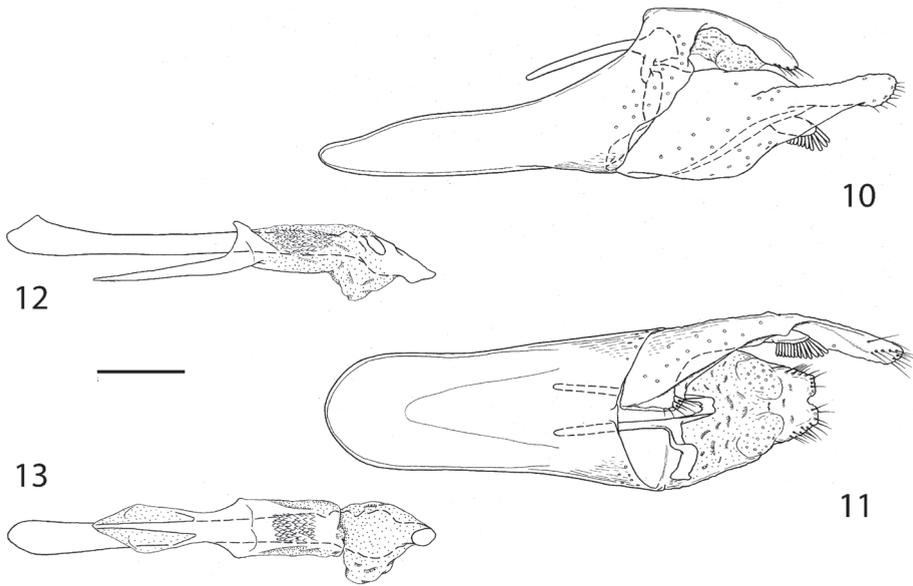


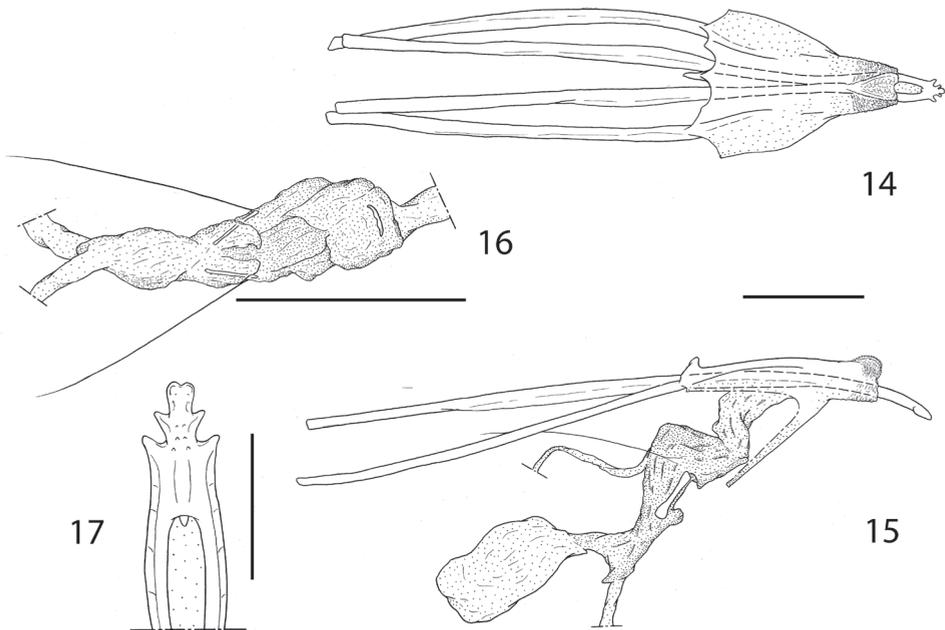
Figure 6. *Antispilina ludwigi*, male venation, slide EvN4676. Photograph E.J. van Nieukerken.



Figures 7–9. *Antispilina ludwigi*, male genitalia, slide EvN4448. **7.** Ventral view, single exposure. **8.** Stacked image from four individual exposures. **9.** Detail, stack from two exposures. Scale bars 100 μm (7, 8), 50 μm (9). Photographs E.J. van Nieukerken.



Figures 10–13. *Antispilina ludwigi*, male genitalia, Germany, Hessen: Dillkreis. Drawn in glycerin. **10, 11.** whole genitalia, phallus removed, lateral and ventral view. **12, 13.** phallus, lateral and ventral view. Scale bar 100 μm . Art work Bong-Woo Lee.



Figures 14–17. *Antispilina ludwigi*, female genitalia, Germany, Hessen: Dillkreis. Drawn in glycerin. **14, 15.** whole genitalia, lateral and ventral view. **16.** vestibulum, ventral view. **17.** Oviscapt, detail. Scale bars 200 μm , 50 μm (17). Art work Bong-Woo Lee.

Larva (Figs 18–22, 35). Body white, prothoracic plates and head pale brown. Prosternum and pronotum with ovate plates (sclerites) in what we assume are the 4th and 5th instars (see van Nieukerken and Eiseman 2020); earlier instars not examined in detail), other segments and prothorax outside the plates as well covered with small transverse swellings. Head width 4th instar ca 400 µm. Legs and prolegs absent. The 4th instar cuts out the flat cocoon or shield from pieces of the leafmine.

Pupa (Fig. 23). Not studied in detail.

Biology. Host plant. Snake-root (or Common Bistort), *Bistorta officinalis* Delarbre (= *Polygonum bistorta* L., *Persicaria bistorta* (L.) Samp., *Bistorta major* Gray) (Polygonaceae).

Leafmine (Figs 26–35). The exact oviposition site has not been determined, but in most cases this must be close to the midrib (87% of the French mines, n=251), or close to another large vein. The larva first makes a circular blotch close to the vein with the frass glued to the upper and under epidermis, resulting in a round red-brownish spot on both leaf surfaces. From there the mine enlarges into an elongated blotch mine, usually between lateral veins towards leaf margin; the blotch is further transparent and whitish in colour. From there the frass is more scattered, blackish, partly in clumps and no longer concentrated throughout the rest of the mine. The outer edges of the mine are irregularly eaten out and do not contain any frass. In many cases the mine is not larger than ca 1 cm, in thin leaves this can be larger. At the end the caterpillar returns to the round spot and makes there an elongate to circular leaf cut from both epidermal layers (reinforced by the frass) of ca. 3 mm long (Fig. 32). There are often several mines per leaf, and mines regularly occur as “twins” at both sides of the midrib (e.g. Fig. 31). In some cases several mines converge into large communal mines, where several larvae may feed next to each other (Fig. 35). Leaves with many mines are very conspicuous, even from a distance.

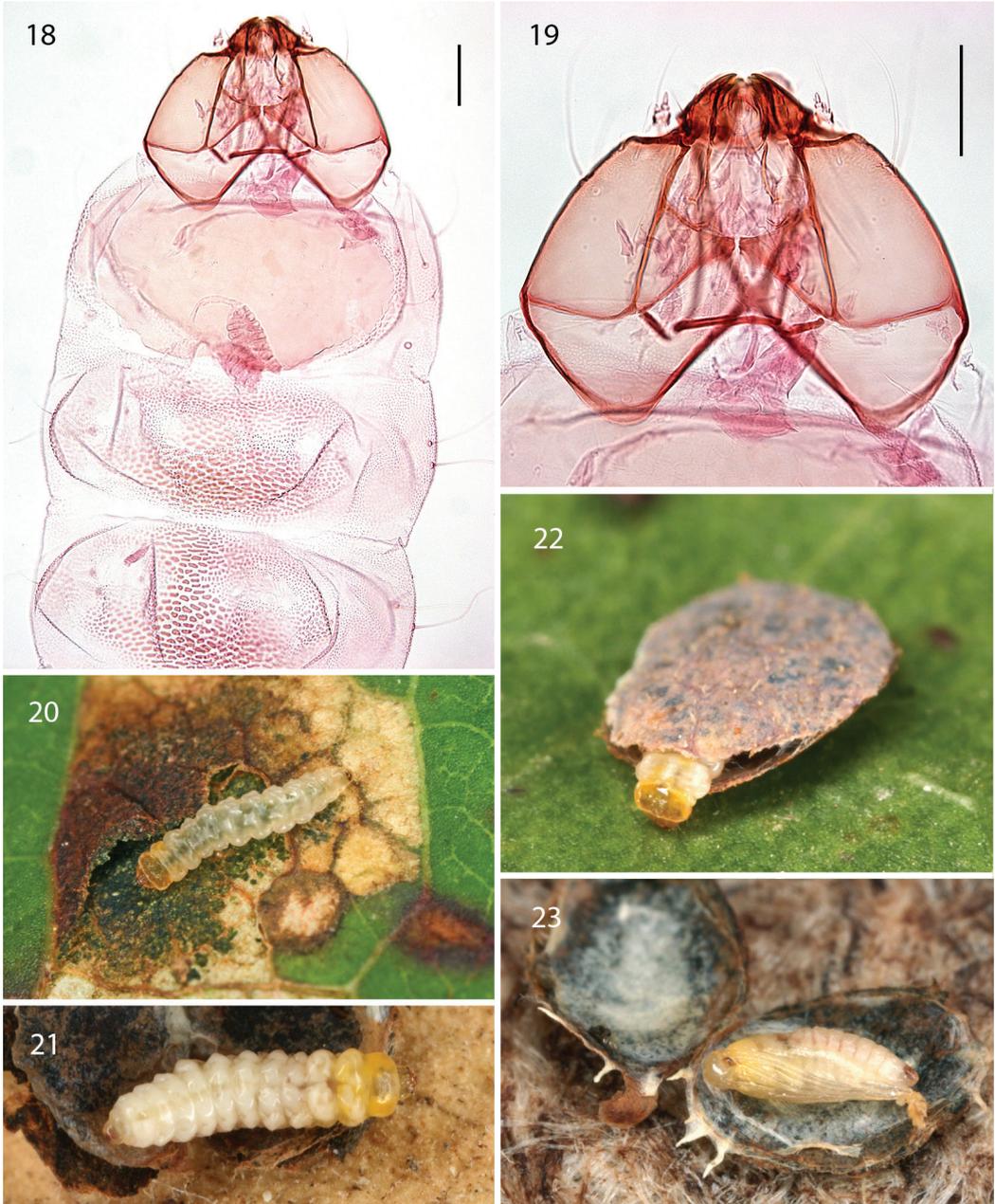
The larva crawls away with the shield (Fig. 22) and seeks a shelter, where it will moult inside the shield into the non-feeding 5th instar and later pupate. The larva probably attaches the shield to some plant material (Fig. 36) as in the other genera in the *Holocacista*-group (van Nieukerken and Eiseman 2020).

Larvae were found from June to September (own data; Liška et al. 2000; Borkowski 2003b; Buszko and Pałka 2016), earlier at lower altitudes, in the mountains most larvae were active in July. Reared adults always emerged after hibernation the next spring between March and June; one adult was swept from the hostplant on 27.v.2020 in the locality St. Imier at 1095 m (Switzerland). We assume that there is only one generation, with an extended period of larval feeding, and adults flying from April to June depending on altitude.

Parasitoids. We only reared three specimens of *Pnigalio* sp. (Eulophidae, identified by Hannes Baur) and one Chalcidoidea, unidentified to lower taxon (identified by Seraina Klopffstein). All emerged in February from cocoons that were taken indoors in January (locality Saignelégier, Jura, Switzerland). No parasitoids emerged from the extensive breedings of French material.

Distribution (Fig. 40). Central Europe: recorded from Belgium, France, Switzerland, Germany, the Czech Republic, Poland and Lithuania.

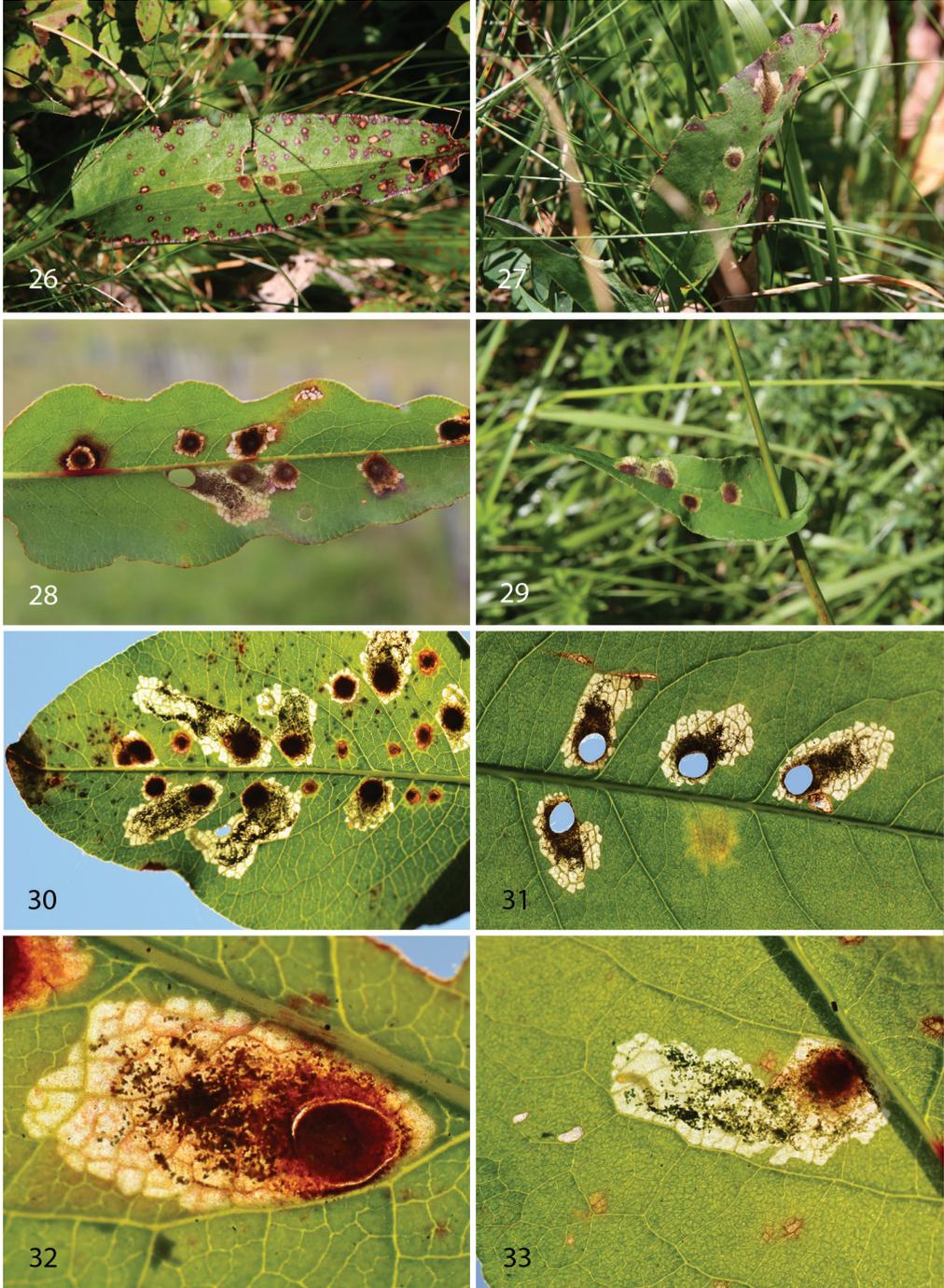
The species has previously only been found a few times: in Germany in a small area in Hessen and Nordrhein-Westfalen (Hering 1941; Ludwig 1952; Grabe 1955) and Sachsen (Buhr 1964); in Poland it was known from the Sudety mountains (Wojtusiak 1976; Razowski 1978; Buszko and Nowacki 2000; Borkowski 2003a, b), but later also found in the lowlands in the South-East (Buszko and Pałka 2016), one record from the Czech Republic, also from the Sudety range (Liška et al. 2000) and from southern Lithuania (Ivinskis 2004). Here we report its occurrence for the first time from France (Mas-



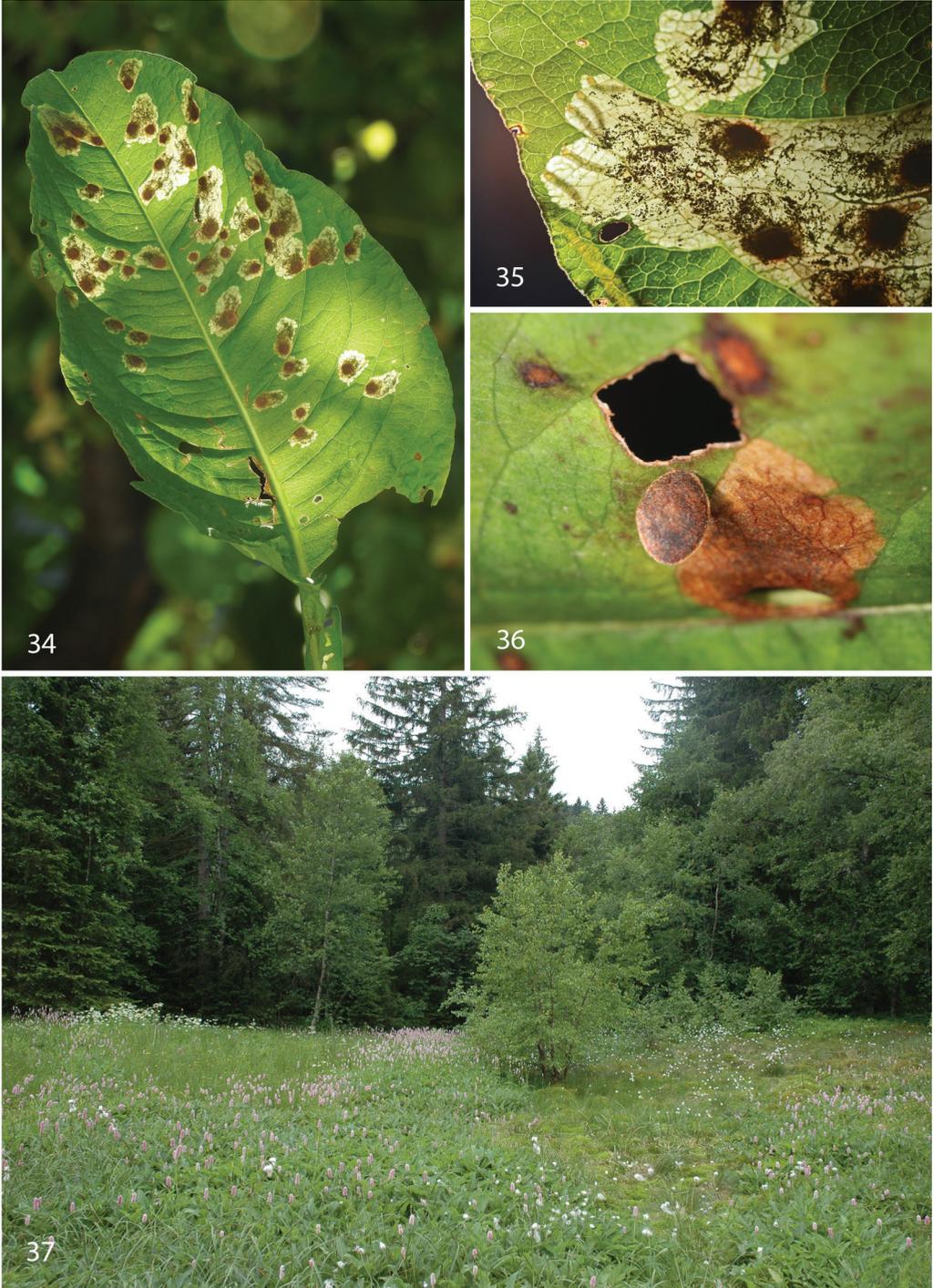
Figures 18–23. *Antispilina ludwigi*, immature stages. **18, 19.** Details of slide mounted caterpillar, probably 4th instar, Poland, RMNH.INS.12423; scale bars 100 μ m. **20.** Caterpillar, final feeding instar (4th) in opened mine, Switzerland, St-Imier, 2.viii.2017. **21.** Non feeding instar (5th) from opened shield, Switzerland, Saignelégier, 5.ii.2018. **22.** Caterpillar walking with shield, Switzerland, St-Imier, 3.viii.2017. **23.** Pupa in opened cocoon, Switzerland, Saignelégier, 4.v.2018. Photographs E.J. van Nieukerken (18, 19), R. Bryner.



Figures 24–25. *Antispilina ludwigi*, live male, Switzerland, Saignelégier, 4.v.2018. Photographs R. Bryner.



Figures 26–33. *Antispilina ludwigi*, leafmines and larvae on *Bistorta officinalis*. **26, 27.** France, Mt. Mézenc, 29.vii.2009. **28, 29.** France, Puy-de-Dôme, Res. Nat. Chastreix-Sancy, resp. Roc de Courlande and Fontaine Salée, 13.vii.2017. **30–33.** Belgium, Rocherath, Naturschutzgebiet der Holzwarche, 23.vi.2017. Photographs E.J. van Nieukerken (26–29), S. Wullaert (30–33).



Figures 34–37. *Antispilina ludwigi*, leafmines and larvae on *Bistorta officinalis* and habitat. **34–36.** Switzerland, Saignelégier, 4.viii.2017. **37.** Habitat in Switzerland, Jura, St-Imier, probably in flying time of *Antispilina ludwigi*, taken 21.vi.2009. Photographs R. Bryner.

sif Central: Auvergne, Cevennes and Jura), Switzerland (Jura and Alps) and Belgium (Ardennes). It is very likely that *A. ludwigi* also occurs further east in Belarus, Ukraine or Russia, where Microlepidoptera and especially leafmining Lepidoptera have only been collected very sparsely.

Habitat (Figs 37–39). Most of our own records were obtained in mountainous bogs, poor wet meadows, often along streams and montane heathland where the host is abundant. This is often patchy habitat with shrubs and sometimes scattered larger trees. The attacked hostplants often are relatively large and leaves with mines are usually hidden among the vegetation. Smaller plants in mowed grasslands rarely had mines. The following plants were common in many of the localities in the Massif Centrale: *Arnica montana* L., *Betula pubescens* Ehrh., *Calluna vulgaris* (L.) Hull, *Cicerbita alpina* (L.) Wallr., *Cytisus oromediterraneus* Rivas Mart. et al., *Dianthus gratianopolitanus* Vill., *Genista pilosa* L., *G. tinctoria* L., *Gentiana lutea* L., *G. pneumonanthe* L., *Meum athamanticum* Jacq., *Potentilla erecta* (L.) Rausch., *Rumex acetosa* L., *Sanguisorba officinalis* L., *Succisa pratensis* Moench, *Trollius europaeus* L., *Vaccinium myrtillus* L., and *V. uliginosum* L.

Buszko and Palka (2016) found the species in lowland habitats in ‘*Molinietum-caeruleae*’ meadows, between 170 and 215 m. Our records are from mountains between 450 and 1650 m elevation and also most published records are from mountains in similar elevational range.

DNA barcodes. Nine specimens were barcoded, representing populations in Poland, France and Belgium. All cluster within Barcode Identification Number BOLD:AAW5935, with an average distance of 0.36% and a maximum distance of 0.81%. (BOLD:AAW5935; dataset <https://doi.org/10.5883/DS-ANTILUDW>). The nearest neighbour, at a distance of 9.38%, is an unnamed heliozelid from Costa Rica.

Remark. There are several specimens in collections with paratype labels, such as the three cited here (and see Lepiforum e.V. (2008–2021)), but as Hering (1941) cited a single specimen in the description, the type material consists only of a holotype, and no paratypes.

Material examined. 21 ♂♂ 19 ♀♀, cocoons. All specimens are reared from *Bistorta officinalis*, except where indicated.

FRANCE • 2 ♂♂ 1 ♀; Ardèche, Mt Mézenc, SW slopes; 44.90835°N, 4.18781°E; alt. 1652 m; 29.vii.2009; E.J. van Nieukerken leg.; emerged 03.iv–03.v.2010; EventId: EvN no 2009032-K; Genitalia slides: EvN4448 ♂ (whole body slide), EvN4676 ♂, EvN4677 ♀; RMNH.INS.24448, RMNH.INS.24676, RMNH.INS.24677. • 5 ♂♂ 4 ♀♀, cocoons; same data; emerged 03.iv–06.v.2010; no registry numbers; RMNH. • 2 cocoons, 1 with prepupa; Ardèche, Sainte-Eulalie, Bois des Seigneurs; 44.86449°N, 4.1827°E; alt. 1455 m; 23.vii.2017; E.J. van Nieukerken leg.; EventId: EvN no 2017053-K; RMNH.INS.16908. • 4 ♂♂, 10 cocoons (plus exuviae); Ardèche, Sainte-Eulalie, Suc de la Lauzière, S.; 44.84695°N, 4.17325°E; alt. 1483 m; 23.vii.2017; E.J. van Nieukerken leg.; emerged 02–22.iv.2018; EventId: EvN no 2017051-K; RMNH.INS.16584–RMNH.INS.16587, RMNH.INS.16907. • 2 ♀♀; Puy-de-Dôme, Monts Dore, Chastreix-Sancy, Roc de Courlande, S.; 45.52231°N, 2.7688°E; alt. 1339 m; 13.vii.2017; E.J. van Nieukerken leg.; emerged 02.iv.2018; EventId: EvN no 2017034-K; RMNH.INS.16567–RMNH.INS.16568. • 2 ♂♂ 4 ♀♀ 1 ad, 10 cocoons (plus exuviae); Puy-de-Dôme, Monts Dore, Chastreix-Sancy, Res. Nat, Fontaine Salée; 45.51214°N, 2.79792°E; alt. 1338 m; 13.vii.2017; E.J. van Nieukerken leg.; emerged 29.iii–09.iv.2018; EventId: EvN no 2017035-K; RMNH.INS.16569–RMNH.INS.16575, RMNH.INS.16902. • 3 ♂♂; Puy-de-Dôme, Monts Dore, Col de la Croix de St Robert, SE, along road; 45.55873°N, 2.84282°E; alt. 1416 m; 16.vii.2017; E.J. van Nieukerken leg.; emerged 03–12.iv.2018; EventId: EvN no 2017039-K; RMNH.INS.16578–RMNH.INS.16580. • 1 ♂; Puy-de-Dôme, Monts Dore, Vallée de Chaudefour, Res. Nat., upper valley E; 45.52916°N, 2.83496°E; alt. 1346 m; 16.vii.2017; E.J. van Nieukerken leg.; emerged 04.iv.2018; EventId: EvN no 2017037-K; RMNH.INS.16577. • 4 cocoons; Puy-de-Dôme, Monts Dore, Chastreix-Sancy, Roc de Courlande, S.; 45.52231°N, 2.7688°E; alt. 1339 m; 13.vii.2017; E.J. van Nieukerken leg.; EventId: EvN no 2017034-K; RMNH.INS.16901. • 9 cocoons; Puy-de-



Figures 38, 39. Habitats of *Antispilina ludwigi*. **38** (top). Belgium, Rocherath, Naturschutzgebiet der Holzwarche, 24.vi.2017. **39** (bottom). Ardèche, Sainte-Eulalie, Suc de la Lauzière, 23.vii.2017. Photographs: A. Rauw (38), E.J. van Nieuwerkerken (39).

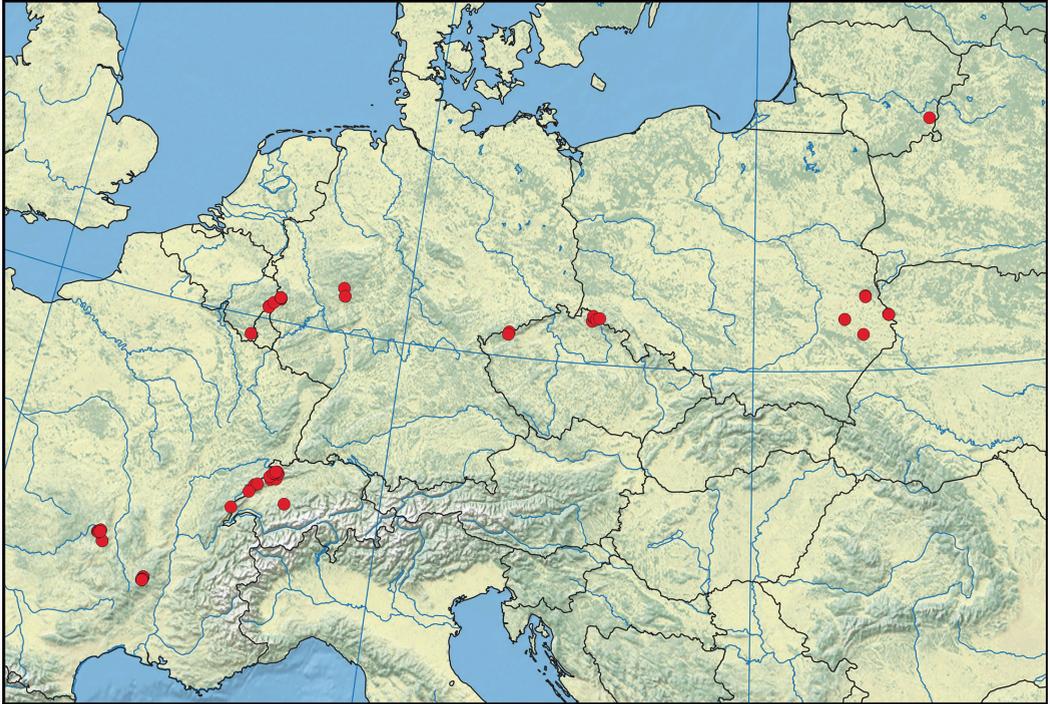


Figure 40. Distribution of records of *Antispilina ludwigi*, including all literature records.

Dôme, Monts Dore, Col de la Croix de St Robert, SE, along road; 45.55873°N, 2.84282°E; alt. 1416 m; 16.vii.2017; E.J. van Nieukerken leg.; EventId: EvN no 2017039-K; RMNH.INS.16905. • 1 cocoon; Puy-de-Dôme, Monts Dore, Vallée de Chaudefour, Res. Nat., upper valley E; 45.52916°N, 2.83496°E; alt. 1346 m; 16.vii.2017; E.J. van Nieukerken leg.; EventId: EvN no 2017037-K; RMNH.INS.16904. • 1 ♀, 5 cocoons (plus exuviae); Puy-de-Dôme, St. Alyre-ès-Montagne, Lac de St. Alyre, S. shore; 45.37424°N, 2.94417°E; alt. 1224 m; 14.vii.2017; E.J. van Nieukerken leg.; emerged 09.iv.2018; EventId: EvN no 2017036-K; RMNH.INS.16576, RMNH.INS.16903.

GERMANY • 2 ♂ 1 ♀ [labelled as paratypes]; Hessen, Dillkreis, Waldaubach, im Feuerhack; 50.666474°N, 8.132751°E; alt. 570 m; 29.vii.1940; A. Ludwig leg.; emerged 10.iii.1941; Genitalia in vial; MfN.

SWITZERLAND • 1 ♂ 1 ♀; Bern, Rüeggisberg; 46.7307°N, 7.45849°E; alt. 1400 m; 07.viii.2017; R. Bryner leg.; emerged 04–06.v.2018; Genitalia slide ♂ 2018–031; RBC. • 2 ♀♀; Bern, St-Imier; 47.12879°N, 6.98725°E; alt. 1095 m; 02.viii.2017; R. Bryner leg.; emerged 04–08.v.2018; RBC. • 1 ♀; same locality; 27.v.2020; R. Bryner & D. Bolt leg.; day catch; collection Daniel Bolt, Domat/Ems. • 1 ♂ 2 ♀♀; Jura, Saignelégier; 47.23961°N, 7.04089°E; alt. 1000 m; 04.viii.2017; R. Bryner leg.; emerged 04–12.v.2018; Genitalia slide ♀ 2018–032; RBC.

Material examined: larvae and leafmines (in collection). All collected from *Bistorta officinalis*.

BELGIUM • 100 larvae, 146 mines; Liège, Aldringen, Thommen; 50.22563°N, 6.02781°E; alt. 475 m; 24.vi.2017; WB leg.; SWC. • 2 larvae, 2 mines; Liège, Aldringen, Ulf; 50.2147°N, 6.03125°E; alt. 462 m; 24.vi.2017; WB leg.; SWC. • 16 larvae, 16 mines; Liège, Büllingen, Kleinfüllenbach; 50.39425°N, 6.32834°E; alt. 644 m; 24.vi.2017; WB leg.; SWC. • 3 mines; Liège, Emmels, Deidenberg; 50.31102°N, 6.14507°E; alt. 481 m; 24.vi.2017; WB leg.; SWC. • 3 larvae (used for DNA analysis, 2 destructively), leafmines; Liège, Rocherath, Naturschutzgebiet der Holzwarche; 50.4238°N, 6.314457°E; alt. 585 m; 23.vi.2017; Steve Wullaert leg.; larval slide; RMNH.INS.30919, RMNH.INS.30927, RMNH.INS.30928, RMNH.INS.43338. • 105 mines; same locality data; WB leg.; SWC. • 4 mines; same locality; 19.viii.2017; WB leg.; SWC.

FRANCE • several mines; Ardèche, Mt Mézenc, Croix de Boutières; 44.90018°N, 4.18277°E; alt. 1512 m; 29.vii.2009; E.J. van Nieuwerkerken leg.; EventId: EvN no 2009033-K; RMNH.INS.42771. • 3 larvae, many mines; Ardèche, Mt Mézenc, SW slopes; 44.90835°N, 4.18781°E; alt. 1652 m; 29.vii.2009; E.J. van Nieuwerkerken leg.; EventId: EvN no 2009032-M/H/K; RMNH.INS.17942–RMNH.INS.17944 (larvae); RMNH.INS.42667–RMNH.INS.42668 (leafmine samples). • 1 larva, 3 mines; Ardèche, Sainte-Eulalie, Bois des Seigneurs; 44.86449°N, 4.1827°E; alt. 1455 m; 23.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017053-M/H/K; RMNH.INS.31178, RMNH.INS.43887. • many mines; Ardèche, Sainte-Eulalie, Pré du Bois, W of Suc de la Lauzière; 44.84959°N, 4.16323°E; alt. 1469 m; 23.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017052-H/K; RMNH.INS.43472–RMNH.INS.43473. • 2 larvae, mines; Ardèche, Sainte-Eulalie, Suc de la Lauzière, S.; 44.84695°N, 4.17325°E; alt. 1483 m; 23.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017051-M/H/K; RMNH.INS.30932–RMNH.INS.30933, RMNH.INS.43470–RMNH.INS.43471. • 2 larvae, mines; Puy-de-Dôme, St. Alyre-ès-Montagne, Lac de St. Alyre, S. shore; 45.37424°N, 2.94417°E; alt. 1224 m; 14.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017036-M/H/K; RMNH.INS.30929–RMNH.INS.30930, RMNH.INS.43463, RMNH.INS.43465, RMNH.INS.43872. • 8 mines; Puy-de-Dôme, Monts Dore, Chastreix-Sancy, Roc de Courlande, S.; 45.52231°N, 2.7688°E; alt. 1339 m; 13.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017034-H/K; RMNH.INS.43868, RMNH.INS.43869. • 2 larvae, many mines; Puy-de-Dôme, Monts Dore, Chastreix-Sancy, Res. Nat, Fontaine Salée; 45.51214°N, 2.79792°E; alt. 1338 m; 13.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017035-M/K/H; RMNH.INS.30931, RMNH.INS.30939; RMNH.INS.43462, RMNH.INS.43870, RMNH.INS.43871. • 1 larva, several mines; Puy-de-Dôme, Monts Dore, Col de la Croix de St Robert, SE, along road; 45.55873°N, 2.84282°E; alt. 1416 m; 16.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017039-K; RMNH.INS.31004, RMNH.INS.43466, RMNH.INS.43875. • 2 mines; Puy-de-Dôme, Monts Dore, Vallée de Chaudefour, Res. Nat., upper valley E; 45.52916°N, 2.83496°E; alt. 1346 m; 16.vii.2017; E.J. van Nieuwerkerken leg.; EventId: EvN no 2017037-K; RMNH.INS.43873.

POLAND • 29 larvae [ethanol, some destructively extracted, larval slide], Dubienka; 51.00998°N, 23.92238°E; alt. 175 m; 02.vii.2004; K. Pałka leg.; EventId: EvN no 2004905-M; RMNH.INS.11854, RMNH.INS.11855, RMNH.INS.12423. • 15 larvae [ethanol, some destructively extracted], Poleski Nat. Park: Bagno Bubnów; 50.94514°N, 22.637°E; alt. 287 m; 01.vii.2004; K. Pałka leg.; EventId: EvN no 2004904-M; RMNH.INS.11852, RMNH.INS.11853.

SWITZERLAND • 5 larvae, Bern, Cortébert; 47.15431°N, 7.12766°E; alt. 1260 m; 04.viii.2017; R. Bryner leg.; RBC. • leafmines; Bern, Saicourt; 47.2555°N, 7.16569°E; alt. 920 m; 02.viii.2017; R. Bryner leg.; RBC. • leafmines; Bern, St-Imier; 47.17653°N, 6.94997°E; alt. 1000 m; 02.viii.2017; R. Bryner leg.; RBC. • leafmines; Bern, Tramelan; 47.24232°N, 7.06144°E; alt. 1010 m; 04.viii.2017; R. Bryner leg.; RBC. • leafmines; Jura, Lajoux; 47.28891°N, 7.1292°E; alt. 930 m; 04.viii.2017; R. Bryner leg.; RBC. • leafmines; Jura, Le Bémont; 47.25269°N, 7.02997°E; alt. 970 m; 04.viii.2017; R. Bryner leg.; RBC. • leafmines; Jura, Montfaucon; 47.2819°N, 7.08989°E; alt. 850 m; 04.viii.2017; R. Bryner leg.; RBC. • leafmines; Neuchâtel, La Brévine; 46.97567°N, 6.58592°E; alt. 1030 m; 05.viii.2017; R. Bryner leg.; RBC. • leafmines; Neuchâtel, Le Cerneux-Péquinot; 47.00417°N, 6.66141°E; alt. 1060 m; 05.viii.2017; R. Bryner leg.; RBC. • leafmines; Vaud, Ste-Croix; 46.84122°N, 6.47154°E; alt. 1090 m; 05.viii.2017; R. Bryner leg.; RBC.

Additional online observations. All observed on *Bistorta officinalis*.

BELGIUM • 8 larvae, 30 mines; Liège, Butchenbach, Schwalm; 19.vii.2018; leg. Evert Van de Schoot & Ward Tamsyn; 50.4980, 6.2562; <https://waarnemingen.be/observation/160366513/>. • 1 larva, 10 mines; Liège, Butchenbach; Schwalm; 19.vii.2018; leg. Evert Van de Schoot; 50.4898, 6.2714; <https://waarnemingen.be/observation/160463202/>. • 3 mines; Liège, Malmedy, Fagne de la Polleur; 22.vii.2017; leg. Wim Declercq; 50.5105, 6.0744; <https://waarnemingen.be/observation/141930607/>. • 13 larvae, 16 mines; Liège, Rocherath, Vallée de la Holzwarche; 24.vi.2017; leg. WB; 50.3961°N, 6.3318°E; <https://waarnemingen.be/observation/140955240/>. • 2 larvae, 2 mines; same locality and date; leg. Chris Steeman & Ben Steeman; 50.4151°N, 6.3283°E; <https://waarnemingen.be/observation/140964609/>. • 1 mine; same locality; 22.vii.2017; leg. Wim Declercq; 50.4172°N, 6.3268°E; <https://waarnemingen.be/observation/141930615/>. • 2 larvae, 2 mines; same locality; 22.vii.2017; leg. Wim Declercq; 50.4240°N, 6.3145°E; <https://waarnemingen.be/observation/141930615/>.

vation/141930621/. • 1 mines; same locality; 14.vii.2018; leg. Jurgen Dewolf & Ruben Recour; 50.4237°N, 6.3147°E; <https://waarnemingen.be/observation/159940474/>. • 20 larvae, 40 mines; same locality; 23.vii.2018; leg. Wouter Mertens; 50.4209°N, 6.3199°E; <https://waarnemingen.be/observation/160514341/>. • 14 larvae, 34 mines; same locality; 23.vii.2018; leg. Chris Steeman ; 50.4237°N, 6.3145°E; <https://waarnemingen.be/observation/160831314/>. • 4 larvae, 25 mines; same locality; 29.vii.2018; leg. Regis Nossent ; 50.4236°N, 6.3146°E; <https://waarnemingen.be/observation/160702446/>. • 1 larva, 1 mines; same locality; 06.ix.2018; leg. WB; 50.4233°N, 6.3141°E; <https://waarnemingen.be/observation/162347416/>. • 2 larvae, 7 mines; same locality; 08.viii.2019; leg. WB; 50.4233°N, 6.3152°E; <https://waarnemingen.be/observation/178051781/>. • 16 larvae, 26 mines; same locality; 10.viii.2019; leg. WB; 50.4209°N, 6.3182°E; <https://waarnemingen.be/observation/179079003/>. • 1 larva, 8 mines; same locality; 08.viii.2020; leg. WB; 50.4246°N, 6.3145°E; <https://waarnemingen.be/observation/203156253/>. • 19 larvae, 76 mines; Liège, Waimes, Rue du Poncé; 24.vii.2018; leg. Chris Steeman & Steve Wullaert; 50.4387°N, 6.1095°E; <https://waarnemingen.be/observation/160817401/>. • 3 larvae, 4 mines; same locality; 09.viii.2020; leg. Eric Wille; 50.4384°N, 6.1093°E; <https://waarnemingen.be/observation/198140856/>. • 14 larvae, 15 mines; Luxembourg, Vance, Marais de Vance; 02.vii.2017; leg. Wim Declercq; 49.6719°N, 5.6807°E; <https://waarnemingen.be/observation/141082788/>. • 7 larvae, 8 mines; Luxembourg, Volaville, Vallée de la Sûre; 20.vi.2020; leg. WB; 49.8658°N, 5.6846°E; <https://waarnemingen.be/observation/194673026/>.

FRANCE • 1 vacated mine; Jura, Les Rousses; 08.viii.2020; leg. Wim Declercq; 46.4963°N, 6.0759°E; <https://observation.org/observation/199070630/>.

Discussion

Hostplant

We follow the databases of POWO (2017–2021) and IPNI (2021) in treating *Bistorta* as a separate genus, even though several floras still include it in *Persicaria*. The monophyly of *Bistorta* is well supported by several molecular studies (Kim and Donoghue 2008; Fan et al. 2013; Schuster et al. 2015). Several of the other Lepidoptera that feed on *B. officinalis* (see below) also feed on the boreo-alpine *Bistorta vivipara* (L.) Delarbre. It is possible that *A. ludwigi* could feed on this species as well, although often the leaves are probably too narrow for the mines. In Japan *B. vivipara* is host for another, unnamed species of *Antispilina* (Lee and Hirowatari 2013).

Phylogeny

In both phylogenetic studies the sister-group relationship between *Antispilina* Hering, 1941 and *Holocacista* Walsingham & Durrant, 1909 is well supported (Milla et al. 2017, 2019). Together these genera are sister to the New World clade *Coptodisca* Walsingham, 1895 plus *Aspilanta* van Nieukerken & Eiseman, 2020, and all these share the reduced venation that is here also observed in *A. ludwigi*. In many morphological details *Antispilina* and *Holocacista* are rather similar, but the absence of an epiphysis and the reduction of the labial palpi to two articles are characteristic for *Antispilina*. The last character together with the hostplant specialisation are considered to be synapomorphies for this genus (van Nieukerken and Eiseman 2020).

Conservation

The habitat where this species occurs, nutrient-poor wet meadows, is much threatened in Europe. Two butterflies feeding on *Bistorta officinalis*, viz. *Boloria eunomia* (Esper, 1799) and *Lycaena helle* (Denis & Schiffermüller, 1775) are amongst the locally most threatened butterflies, although they still have a large distribution area covering most of northern Asia (Swaay and Warren 1999; Gorbunov

2001; Kudrna 2002). *Lycaena helle* occurs on each of the eastern Polish localities of *A. ludwigi*, whereas *B. eunomia* is more local and occurs only in Bagno Bubnów and Dubienka (Anna Mazurkiewicz, personal communication). Since *A. ludwigi* has not been found in Germany in recent years, we have no information on its sympatric occurrence with these butterflies, both of which are very rare and threatened in Germany, *L. helle* is critically endangered, it has disappeared from many former localities due to afforestation and drying of its habitats (Pretschner 1998; Settele et al. 2000).

In Belgium (Wallonia) most finds of *A. ludwigi* are in the Holzwarche valley in the Haute Fagnes area in Rocherath. The Holzwarche valley is very extensive and stretches from the plateau of Losheimergraben to Lake Bütchenbach. Here *Lycaena helle* occurs on almost every location where *A. ludwigi* was found. *Boloria eunomia* has about the same distribution in Belgium as *L. helle*, but is slightly commoner. Both species have a stronghold in the Holzwarche area where the foodplant is abundant (Waarnemingen.be 2020). *Lycaena helle* is considered vulnerable in Wallonia, where it is legally protected since 2001; a Life+ project launched in 2009 in Southern Belgium aimed at restoring its habitats. The objective of the project was to restore and manage at least 250 ha in function of *L. helle* (Goffart et al. 2014). Since the start of this project the online platform “waarnemingen.be” shows increasing numbers of observations for both *L. helle* and *B. eunomia* since 2009. This progress ensures that the host plant is preserved in most areas that are also good for *A. ludwigi* and that this species has the opportunity to expand.

In the Massif Centrale in France, where we found *A. ludwigi* in many places where we checked the hostplant, *L. helle* still has many populations (Muséum national d’Histoire naturelle 2003–2021; Habel et al. 2011; Merlet and Houard 2012), but *B. eunomia* does not occur there (Muséum national d’Histoire naturelle 2003–2021). In the Swiss Jura *A. ludwigi* was found in all visited sites of *L. helle*, and likewise in a locality in the northern Alps.

Other Lepidoptera species feeding almost exclusively on *Bistorta officinalis* are the rare alpine *Boloria titania* (Esper, 1781), and the micromoths *Coleophora pratella* Zeller, 1871 and *Phiaris astrana* (Guenée, 1845). The last species, so far only known from the French and Swiss Jura (Muséum national d’Histoire naturelle 2003–2021; Lepiforum e.V. 2008–2021; SwissLepTeam 2010), also occurs in several of the Swiss localities of *A. ludwigi*, including that in Fig. 37.

In general, we urge lepidopterists who monitor the afore-mentioned butterflies to check the hostplants for the conspicuous leafmines and post photographs of these online in observation platforms. Monitoring these mines is relatively easy, can be done even under poor weather conditions, and contributes to the knowledge of the biodiversity of these valuable habitats.

As *Lycaena helle* is the most common companion species, it is likely that management for that species also will benefit *A. ludwigi*. Most important is a low-intensity management, very light grazing in a rotational way, avoiding the sensitive periods of the butterfly (and moth) April–July, and preventing natural reforestation (Swaay et al. 2012). For populations of *A. ludwigi* at higher elevations, the period to avoid management should perhaps be extended to the first half of August, when there are still larvae in the mines.

Distribution

After we learned about the habitat of this species, it was easy to find it in many places where it had not been previously recorded. This was a clear indication that *Antispilina ludwigi* was overlooked, despite its conspicuous leafmines. Many lepidopterists still collect or observe mostly focusing on adults with artificial lights or by netting, whereas collecting and photographing of larvae and

leafmines is rarely done in many parts of Europe, despite an increasing interest in leafmine studies, especially in the British Isles, the Netherlands and Belgium (Edmunds 2020; Ellis 2020; Wullaert 2021). As the hostplant *Bistorta officinalis* has a wide distribution in Europe and throughout Siberia, we expect that *Antispilina ludwigi* can be found in many more sites in Europe and even northern Asia. In East and South Asia several other species of *Antispilina* have been found, feeding on other species of Polygonaceae, which will be described elsewhere (Lee and Hirowatari 2013; Milla *et al.* 2017). Focussed searching in localities where *Lycaena helle* is known will probably be the easiest way to discover new populations. The new records suggest a wider distribution in the European mountains, and the species should particularly be searched in German mountains, other parts of France, Austria, northern Italy, Slovenia, Romania, Belarus, Ukraine and the European part of Russia.

Our results also stress that focused searching on host plants of poorly known Lepidoptera and other insects may be more successful than anticipated. We observed a similar result in the rare leafminer *Digitivalva arnicella* (Heyden, 1863) (Glyphipterigidae) on *Arnica montana* in the Netherlands and Belgium (van Nieukerken and Koster 1999; Wullaert 2019).

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Castniidae of the Museum of Natural History of the University of Wrocław: new findings from Friedrich Wilhelm Niepelt's collection with comments on Karl Adolf Georg Lauterbach and August Weberbauer

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Abstract. Further results of our research into the Giant Butterfly-Moths (Castniidae) of the Museum of Natural History (University of Wrocław) are presented. Castniids of the Niepelt collection had previously been reviewed. However, while curating other sections of the Lepidoptera collection, we discovered 18 misplaced specimens belonging to nine taxa of Castniidae, several of them bearing typical labels by Niepelt. Among them, two are of particular interest, insofar as they are associated with the world-class botanists August Weberbauer (1871–1948) and Karl Adolf Georg Lauterbach (1864–1937).

Introduction

Examination of rich collections of Castniidae and other insect groups in several Polish museums (González et al. 2013a, b; Domagała et al. 2015, 2017a, b; Domagała and Dobosz 2019) led the authors to continue the exploration of such ever-surprising depositories. The role of museums as important repositories of biodiversity has been stressed on many occasions (e.g., Burrell et al. 2015; Domagała and Dobosz 2019). The information retained in natural history vouchers can shed light on aspects of genetic and climate changes, adaptations to evolving environments, inter- and intraspecific relationships, and even historical events (Suarez and Tsusui 2004; Winker 2004; Hartley et al. 2006; Bi et al. 2013; Domagała and Dobosz 2019).

Polish museums are sources of historically interesting entomological material (González et al. 2013a, b; Domagała et al. 2015, 2017a, b; Domagała and Dobosz 2019; Taszakowski et al. 2019). Silesia held the role of a major center for entomological research, with many highly recognized entomologists and skilled traders who worked in this region (Mencfel 2010; González et al. 2013b; Domagała and Dobosz 2019). Some dealt with exotic fauna and their material is still enhancing private and institutional collections, both locally and worldwide.

Friedrich Wilhelm Niepelt (1862–1936) was one such entomologist and dealer. Niepelt was born in Striegau (Strzegom), a town in the Lower Silesia province in the South West of today's Poland (Calliess 1932; Strand 1932, 1938; González et al. 2013b). He established a prosperous business manufacturing and selling entomological supplies and animals, mainly insects collected in expeditions or traded with collectors from other regions, principally South America (Calliess

1932; Strand 1932). He also became knowledgeable in Lepidoptera and published many works describing new taxa (Röber 1932). He typically sold specimens with pre-printed labels (often in black ink) bearing “Collection Niepelt.” at the bottom and a black border framing the label to allow him to write the name of the taxon and its place of origin (Fig. 2a). Many insects (and other animals) sold by Niepelt are scattered around museums worldwide (González et al. 2013a, b). However, between 1932 and 1936, Niepelt donated about 13,000 specimens of Lepidoptera, originally obtained from South America, Asia and Africa, to the University of Wrocław, which were then deposited in the university museum while he was still alive (Strand 1932; Berner 1996; González et al. 2013b). For this reason, the University of Wrocław honoured him with some sort of distinction (González et al. 2013b). However, it seems that many other specimens were sold (or donated) either by him or via other collectors to the museum on different occasions, before and after his principal donation.

The Castniidae from the Niepelt collection of Lepidoptera at the Museum of Natural History of the University of Wrocław have been reviewed by González et al. (2013b). However, while curating other sections of the Lepidoptera collection, we became aware of several additional specimens bearing the typical Niepelt labels (Fig. 2a). The purpose of this note is to complement the previous work (González et al. 2013b) and provide comments and data on the newly found specimens.

Materials and methods

The Castniidae specimens listed here were found in the Museum of Natural History at the University of Wrocław (Poland) (MNHW) while curating the Lepidoptera collection from 2013 to 2020. With some exceptions, they seem to have come from Niepelt, having either been bought individually or as part of other collections obtained by the MNHW.

The systematic list provided herein follows Lamas (1995), Miller (1995), and Moraes and Duarte (2014), with minor changes.

Every taxon is briefly commented upon, from a historical perspective or from associated collecting data drawn from the label.

Results

Among the many Lepidoptera curated in the insect collection of the MNHW, 18 specimens belonging to nine taxa of Castniidae were found.

Synpalamides fabricii (Swainson, 1823)

Comments. Moraes and Duarte (2014) synonymized the genus *Hista* Oiticica, 1955 with *Synpalamides* Hübner, [1823], an arrangement that we follow for now. This species is almost exclusively found in south-southeast Brazil, where it is usually on the wing from December to February in areas of Atlantic Forest (Moraes et al. 2010; Penco 2011). Very little is known about its biology, but its larvae are known to feed on *Tillandsia aeronthos* (Loisel.) L.B. Sm. (Bromeliaceae) (Enslin 1920; Biezanko 1961).

Material examined. 1♂, *C. boisduvali*, S.[ão] Paulo, [Brazil], coll. ?; 1♀, *C. beskei*, Brasil, Collection Niepelt, (Fig. 1f).

***Yagra fonscolombe* (Godart, [1824])**

Comments. A common species in Southern Brazil and northern Argentina, whose distribution might reach Paraguay (Moraes et al. 2011; Ríos and González 2011). Many collections worldwide have large series of this species, though almost nothing is known about its ecology and behavior (Moraes et al. 2011).

Material examined. 1 ♀, *Castnia fonscolombe* [sic], Brasil, Collection Niepelt, (Fig. 1i).

***Imara pallasia* (Eschscholtz, 1821)**

Comments. This is a species restricted to southeastern Brazil where it is found together with *Imara satrapes* (Kollar, 1839) “...usually [in] primary forest or cloud forest.” (Miller 1986; González and Stünning 2007; González et al. 2010; González and Domagała 2019). Almost nothing is known about its ecology and behavior (Miller 1986).

Material examined. 1 ♀, *C. pallasia*, Esch[scholtz], St.[Santa] Cathar[ina], [Brazil], Collection Niepelt, (Fig. 1c).

***Synpalamides phalaris* (Fabricius, 1793)**

Comments. A highly variable species distributed from Southeastern Brazil, Argentina, Paraguay and Bolivia to French Guiana, Trinidad and Tobago, and Venezuela (González et al. 2010; Ríos and González 2011; González and Worthy 2017; González and Domagała 2019). This is probably a bivoltine species, and individuals have been observed laying eggs on bromeliads of the genera *Guzmania* Ruiz & Pav., 1802, and *Bromelia* L., 1753 (Bromeliaceae), but it is also associated with pineapple and banana crops (Bromeliaceae and Musaceae respectively) in its southernmost distribution (Jørgensen 1930; Miller 1986; Penco 2011; Ríos and González 2011; González and Worthy 2017).

Material examined. 1 ♂, Brasilien, [Coll.?] Lauterbach, 1547, coll.? *Synpalamides phalaris*, det. A. Wanat, (Figs 1b, 2d–g).

***Castnia invaria trinitatis* Lathy, 1925**

Comments. This is a northern subspecies commonly found in the Orinoco River Basin and north of the Amazon River, from Colombia, throughout Venezuela, east to the Guianas and on the Island of Trinidad (González and Stünning 2007; González et al. 2010; Iorio and Zilli 2016; González and Domagała 2019).

Material examined. 1 ♀, Franz Guyana, 222, coll.?, *Castnia invaria volitans*, det. A. Wanat, (Fig. 1d).

***Telchin evalthe quadrata* (Rothschild, 1919)**

Comments. This subspecies was named from specimens collected in Peru and Ecuador and differs from other subspecies, mainly *T. evalthe evalthoides* (Strand 1913), by subtle differences in

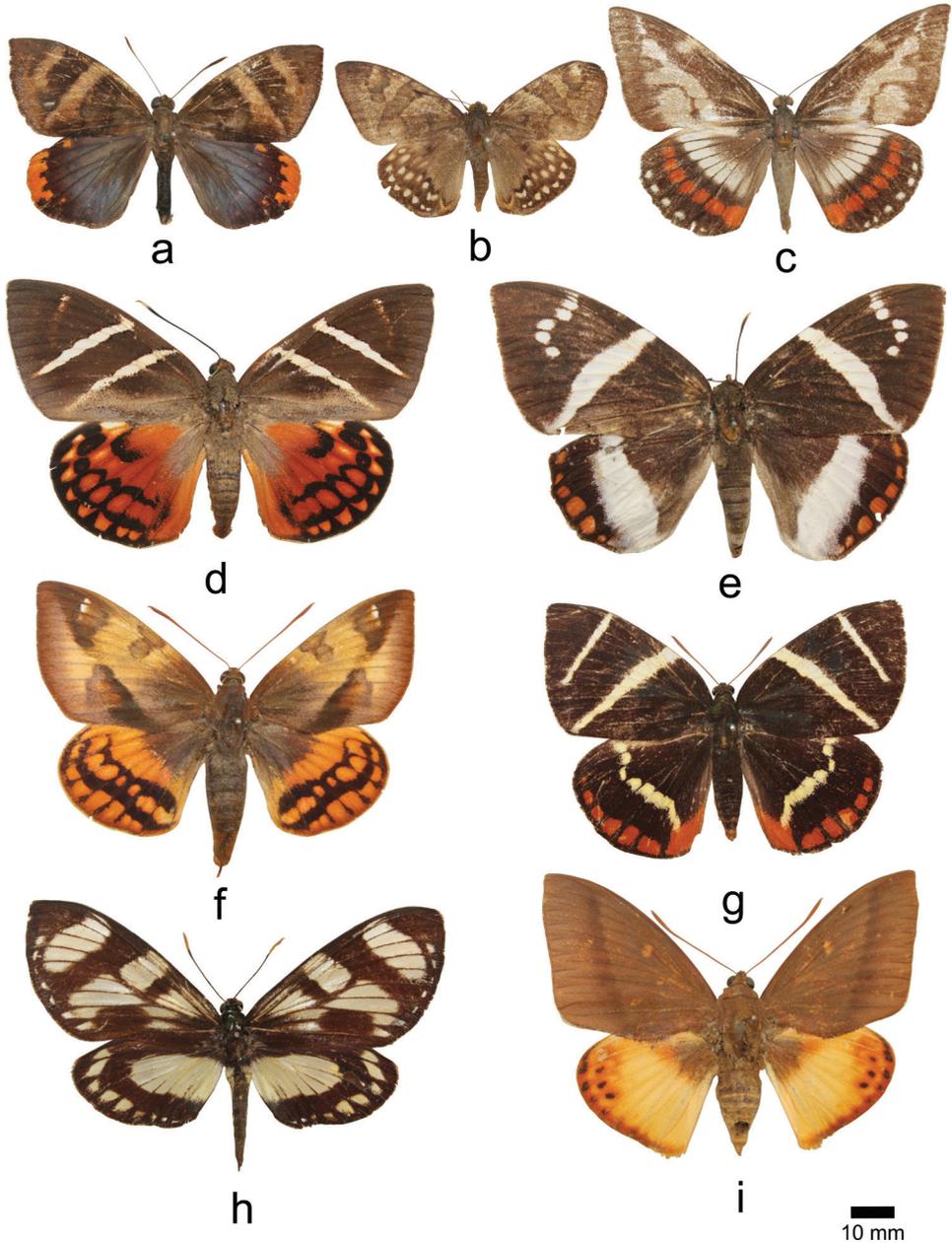


Figure 1. Butterfly-Moths (Lepidoptera: Castniidae) from the Insect collection of the Museum of Natural History, University of Wrocław, Poland. **a.** *Ceretes thais* male, [Brazil] Minas Gerais; **b.** *Synpalamides phalaris* male, Brazil, [Coll.?] Lauterbach, 1547; **c.** *Imara pallasia* female, [Brazil], Santa Catharina, Collection Niepelt; **d.** *Castnia invaria trinitatis* female, [French Guiana], 222; **e.** *Telchin licus* female, Brazil, Collection Niepelt, Peru Weberbauer, S.G.; **f.** *Synpalamides fabricii* Brazil, Collection Niepelt; **g.** *Telchin evalthe quadrata* male, Ecuador, Macas, 1905-08; **h.** *Prometheus heliconioides* female, [Brazil], Tefé, Amazonas, Tjunin; **i.** *Yagra fonscolombe* female, Brazil, Collection Niepelt. Figures are to scale. Scale bar: 10 mm.

the external appearance (Rothschild 1919; Lamas 1995; González et al. 2013b). The species is a member of a group that deserves a full morphological and molecular study to clarify its taxonomic composition.

Material examined. 1♂, Macas, Ecuador, 1905-08, coll.? *Xanthocastnia evalthe* (F.), det. A. Wanat, (Fig. 1g).

Telchin licus (Drury, 1773)

Comments. This is perhaps the most common species in the family, it is highly variable and often associated with sugarcane (*Saccharum officinarum* L., Poaceae), and is also known as a secondary pest of plantains and bananas (*Musa* spp., Musaceae) (González and Fernández Yépez 1993; González and Stüning 2007; González et al. 2013b; González and Domagała 2019). Due to the confusing taxonomy of the few associated subspecies, we prefer to treat this species as monotypic until a more detailed work clears up its infraspecific structure.

Material examined. 3♂♂, no data, *Telchin licus* (Dr.), det. A. Wanat, coll. ?; 1♀, *licoides* ♀, 5.xi. [no locality]; 1♂, Juanjuy [= Juanjui], Peru, 221, *Telchin licus*, det. A. Wanat, coll. ?; 1♂, *C. lindella*[sic], Peru, “illegible”, 19.7.[19]36, coll. ?; 1♂, *Castnia licur*[sic], Colind. Thinp. 17.8.[19]35, coll. ?; 1♂, *Castnia licuides* [sic], N. Brasilien, coll. ?; 1♀, *C. licus* Drury, Brasil, Collection Niepelt, Peru Weberbauer, S.G. [head missing, but antennae attached; one of the antennae broken and glued back], (Figs 1e; 2a–c).

Ceretes thais (Drury, 1782)

Comments. This sexually dimorphic species is commonly found in southern Brazil, but its geographic range includes the northern Argentinian province of Misiones, and it could possibly be found in Paraguay (Ríos and González 2011; González et al. 2013b; González and Domagała 2019). There is a record from Bolivia that might be incorrect (Ríos and González 2011; González et al. 2013b). Unfortunately, almost nothing is known about the biology and ecology of this species (González and Domagała 2019).

Material examined. 1♂, Minas Gerais, [Brazil], 225, coll. ?, *Ceretes thais* det. A. Wanat. (Fig. 1a).

Prometheus heliconioides (Herrich-Schäffer, [1853])

Comments. This species is easily recognized by its color pattern, which mimics *Lycorea* Doubleday, [1847], *Thyridia* Hübner, 1816, and *Methona* Doubleday, [1847] (Nymphalidae), and the moth *Notophyson heliconides* (Swainson, 1833) (Erebidae), which could all form part of a mimetic ring (Lamas 1973; Miller 1986; Ríos and González 2011; González and Domagała 2019). However, a morphological and/or molecular study of its several purported subspecies could clarify their taxonomic status. The specimen has a label identifying it as *Diamuna falcata* [now *Darceta falcata* (Druce, 1883)] an Erebidae to which *P. heliconioides* bears no resemblance. It was probably mislabeled.

Material examined. 1♀, Teffé [= Tefé], Amazonas, [Brazil], *Diamuna falcata* ♀, Teffé [= Tefé], Amaz.[onas], [Brazil], Tijunin. 37, *Gazera heliconioides*, coll. ?, (Fig. 1h).

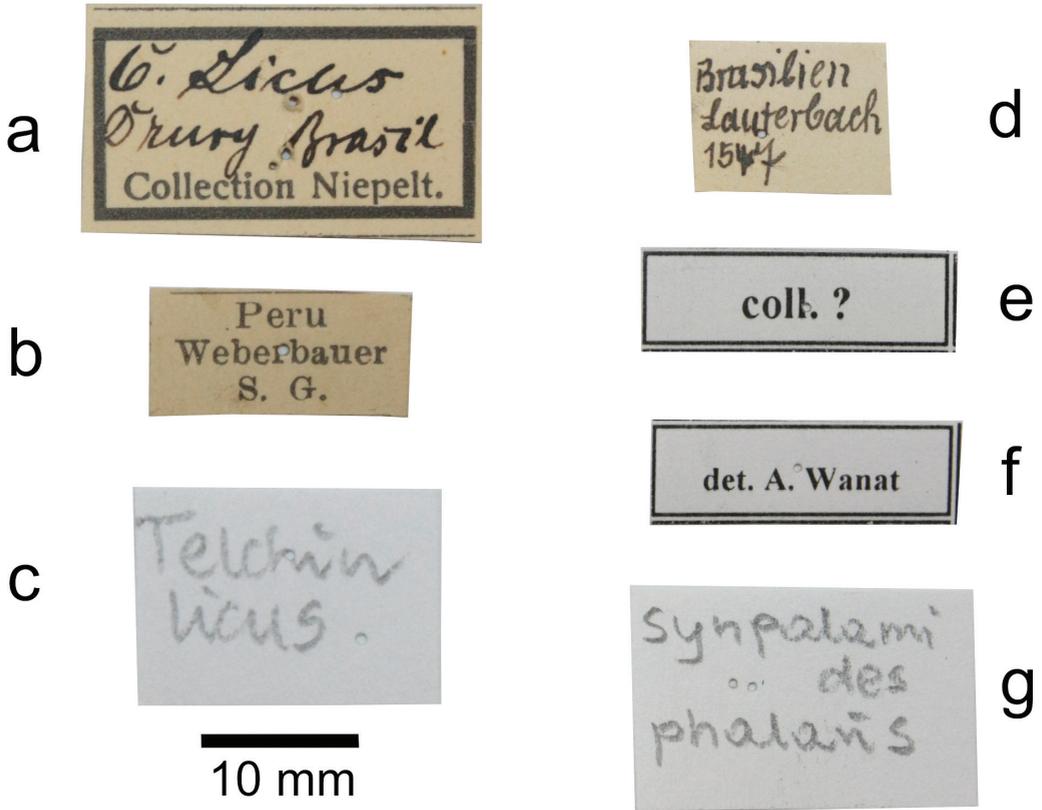


Figure 2. Labels attached to specimens in the collection of Giant Butterfly-moths (Lepidoptera: Castniidae) of the Museum of Natural History, University of Wrocław, Poland. **a–c.** labels attached to a specimen of *Telchin licus*; **d–g.** labels attached to a specimen of *Synpalamides phalaris*. Figures are to scale. Scale bar: 10 mm.

Discussion

Our earlier studies of Castniidae in the MNHW collection included 37 specimens belonging to 22 species and subspecies (González et. al. 2013b). That list is now supplemented with these 18 newly found specimens. Therefore, the collection of Castniidae in MNHW now comprises 55 specimens of 24 species and subspecies.

Two of the newly located specimens, one of *T. licus* and another of *S. phalaris*, deserve special mention.

One of the *T. licus* specimens was found with the typical Niepelt label, but it also has an enigmatic label with the words “Peru Weberbauer S.G.” (see Fig. 2b). This is not the only specimen with this type of label we have found in the MNHW collection (see Domagała and González 2021). Even though the meaning of this label is difficult to assess, we suggest that the specimen might have been part of the botanist August Weberbauer’s (1871–1948) insect collection. Weberbauer was born in Breslau (Wrocław) and was a naturalist, biologist, and widely recognized botanist (Baca de García 1949; Mularczyk 2010; Domagała and González 2021). He made expeditions to Peru and returned to Wrocław, where his father Otto Weberbauer (1846–1881), also a naturalist and botanist, had established various collections, including one with insects. Eventually, August was invited by the Peruvian government to take a permanent job over there. He became a highly

respected researcher and ended his days in Peru (Baca de García 1949). The “Weberbauer” label includes the letters “S.G.” which might mean either “Sammlung Gekauft” (bought collection) or “Sammlung Gespendet” (donated collection). August probably kept his father’s collection and before moving to Peru in 1908 sold it to Niepelt, who then donated it to the University of Wrocław (Domagała and González 2021).

A similar situation is found with a specimen of *S. phalaris*, which we attribute to Karl Adolf Georg Lauterbach. Lauterbach, born on April 21st, 1864, in Breslau (Wrocław), was an explorer and botanist. After his high school education at St. Mary Magdalene Gymnasium in Wrocław, he went to the University of Breslau (Wrocław) in 1885 (Syniawa 2006).

He continued his studies at the University of Heidelberg where, in 1889, he received his Ph.D. in Botany. After graduation, together with his friend, Russian biologist Vladimir Shevyakov (1859–1930), he started a journey around the world. During their travels, they visited the US, Hawaii, New Zealand, Australia, and Java. At this point, Shevyakov returned to Russia, but Lauterbach continued alone and went to the Solomon Islands and New Guinea. He returned to Germany in 1891. Later, in 1896 he undertook a new exploratory expedition to the Bismarck Mountains in New Guinea. During this expedition, he discovered and explored the previously unknown Ramu river. By 1899 he became the director of the Neu-Guinea Compagnie and started his next mission to the Ramu river valley. Expeditions and official duties allowed him to return to his estate in Stabelwitz (part of Breslau since 1928) in 1907, where he kept an impressive collection of exotic plants in his greenhouse; there he carried out scientific work based on material collected during his expeditions. After his 50th birthday, he was awarded the honorary title of professor at the University of Breslau (Wrocław). He died on August 1st, 1937 (Syniawa 2006) when, according to his last will, his collections became the property of the University of Wrocław. The most important part of Lauterbach’s collections was a huge herbarium of over 50,000 sheets (Rostański 1963; Wanat and Pokryszko 2014). However, the donated collection included shells, insects, and birds (Syniawa 2006).

Based on our data and the fact that Lauterbach never traveled to South America, we infer that this specimen was not caught by him. As a devoted naturalist and collector, he was able to buy specimens for his private collection or acquire them through exchanges with other collectors. Unfortunately, information about the type and number of species donated to MNHW has not survived. In our opinion, the number 1547 attached to the specimen is probably an inventory number, by which we can conclude that there were more than 1,500 lepidoptera specimens donated.

Our research sheds new light on the origin of some specimens of butterflies and moths in this museum and shows that interesting collections of Lepidoptera were established by two world-class botanists. Unfortunately, we do not know how large their collections were and which species they contained. Certainly, they are valuable and interesting, and further research at MNHW or other museums could hopefully lead to these pieces of information being unveiled.

Acknowledgments

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Otakar Kudrna 1939–2021

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Otakar Kudrna was born in České Budějovice in 1939, when this Bohemian city, known at the time as Budweis and always renowned for Budweiser Bier and for Koh-i-Noor, had ‘recently’ (1918) joined Czechoslovakia, following the dissolution of the Austro-Hungarian Empire. Nothing has ever been easy in town since then until recent times, starting immediately with the German invasion and occupation (1939–1945) and the many related horrors, its re-assignment to Czechoslovakia and the subsequent deportation of all German-speaking inhabitants.

Otakar’s personal history was no less troubled than that of his city. With the establishment of the ‘new’ communist regime, his father, who seems to us, was a medical doctor, soon ended up in deep disgrace and Otakar narrowly managed to take advantage of the few days of the ‘Prague Spring’ to flee to England. Here he became a British Citizen and took a Masters’ Degree in Cambridge with a thesis developed under guidance by Brisbane Charles Somerville Warren, whose work on the genus *Erebia* is especially well remembered. E. W. Classey published O. Kudrna’s revision of the genus *Hipparchia*, derived from his thesis, in 1977.



Figure 1. Otakar Kudrna photographing the Moorland Clouded Yellow (*Colias palaeno*), from his own webpage (http://www.butterflies.de/Kudrna/kudrna_us.htm).

Otakar's interest in Roger Verity, whose Italian he never came to understand very well, arose from our (GL's) first meeting in Turin, when I hosted him in the early 1970s and showed him the five volumes of "Farfalle diurne d'Italia". I (GL) then told him about my military service (1961), about my two months' sojourn in Florence, at the Military Health School of Costa San Giorgio, near the Museum of "La Specola", and about my visits to Verity's collection, preserved in that Museum. Otakar did not forget to ask me, after a few years, to write for him a letter of introduction to Prof. Lanza, who was then Director. So Otakar began to frequent Florence, a city that he came to love (it reminded him of Prague). He stayed at "La Specola" on several occasions, starting, I seem to remember, from 1976 and until around 1980, also thanks to a series of small grants obtained from some British societies. The purpose of these visits was a revision of Verity's type material, which Otakar selected very carefully and which he re-boxed as a separate collection.

It was precisely at Specola that I (EB) met Otakar for the first time, on the occasion of one of my visits, then numerous, and it was he who prompted me to become an SEL member (1976), and to attend its first Congress, held in Paris in 1978. Otakar was an SEL founding member and Editor of *Nota lepidopterologica* from 1977 to 1980. Then he left due to a series of differences of which it is useless to tell.

A lasting friendship was established between us by a frequent exchange of letters. I (GL) indulged his wishes by accompanying him to visit some habitats that he particularly wished to see. These included the Novara rice paddies, to photograph *Lycaena dispar*, the heaths of the "Piano Rosa", where *Coenonympha oedippus* still abounds, the alluvial soils along the lower course of the Sesia river, (then) densely populated with *Zerynthia polyxena*, the steep slopes of Mount Kastel, in search of *Erebia flavofasciata*, the Laquinthal Alps, to photograph *Erebia christi*, and some of the colonies of this species that I had discovered on the Italian side of the border. He followed me with difficulty but with determination and subsequent satisfaction. He did not say, but I could tell from his gaze that betrayed his natural Teutonic coolness. In 1975, during my visit to the Aeolian Islands, I collected some *Hipparchia* of the *semele* group whose wing morphology and whose behaviour seemed to me different from usual. I sent him some specimens to study their genitalia. The answer was immediate: "it is a new species", which he would later dedicate to me (GL), *Hipparchia leighebi* Kudrna, 1976.

With the death of B.C.S. Warren (1979), who was perhaps his only British friend, Otakar was no longer happy in that country and, after a while, he finally went to settle in Germany, where he had already been engaged with the Alexander König Museum (Bonn) for couple of years. He finally took German citizenship and managed to have his English MD recognized. A position of curator had been opened at that Museum, and he thought of having a go at it. After his Florentine period, Otakar had resumed coming to Italy from time to time. He stayed at GL's either in Novara or in his country house on Lake Orta, or otherwise at EB's in Genoa. It was on one of these occasions that he told me (EB) an anecdote. One morning, climbing the stairs of the König Museum, the Director, who was behind him, told him: "Dr. Kudrna, you have dropped a tissue". And he, taking the packet out of his pocket, counted the tissues and replied: "It's not possible, there are 7 and I always carry 7 with me". He laughed a lot as he told this. Czech humour, maybe. One can surely imagine it was not (only) for that, but the curatorship went to someone else, and he lost the grant he had had with the Museum for several years.

Otakar then came to Genoa with a Visiting Professorship (1983–84 and 1984–85), to teach a course in Conservation Biology at the local University. Subsequently he received a small grant from the University of Catania, to monitor the butterflies of the Aeolian Islands, and he also went to Sardinia a few years later.

In the meantime, he had entered into a contract with “Aula Verlag” for the planned publication of an eight-volume work on “Butterflies of Europe” of which he was Editor. Unfortunately, only three parts were printed, between 1985 and 1990, those of a general nature, while volumes dedicated to taxonomy never saw the light, due to the failure of the Publisher and difficulties with the new management. The second volume, “Introduction to Lepidopterozoology”, written in the form of separate articles, should not be missing from any student’s library, although unfortunately not all the chapters turned out to be at the same level. In the 8th volume, written entirely by the Editor (Aspects of the Conservation of Butterflies in Europe), Otakar introduced a series of indices, including a “Range Affinity Index”, aimed at evaluating how much a given species can truly be considered ‘European’ and therefore of conservation interest in Europe. Chris van Swaay and Martin Warren (1999), among others, adopted it for the compilation of the first “Red Data Book of European Butterflies”.

Since my (EB’s) tenure at the University of Turin (1987), he came to visit us once, I think it was 1991. Later, my wife Cristina Giacomini and I visited him in Germany (he had settled in Munich), during a period in which he had had a contract for the conservation of *Parnassius mnemosyne*. He very kindly also found a way to please Cristina, organising for us a visit an interesting Black grouse ‘lek’, and to a Capercaillie captive breeding site.

With the folding up of the “Aula” project, which greatly saddened him, Otakar moved onto another pet idea of his, that of publishing an atlas of the distribution of European butterflies. Three editions came out (2002, 2011, 2019), always with new updates and clarifications. He was very proud of it.

In retrospect, the times when he came to Italy quite often was probably the happiest period in his life.

Last Christmas (2020) we swapped good wishes. He replied also by sending a gift package to both of us, containing the fruit of his latest effort: “Distribution of Butterflies and Skippers in Europe, 2019”.

Otakar Kudrna was a sometimes a very difficult person. I (EB) told him several times that he was his own worst enemy. I (GL) agree with Emilio but, as a medical doctor, I cannot ignore the weight of the psychological conditioning of a man isolated from his roots for years, without family affections, fleeing from occupied Czechoslovakia, leaving home and all possessions, in constant search for acceptance, first in England and then in Germany, always with poor job and financial prospects. I felt moved when he told me that on leaving his home, he only carried a bag with him containing two books on butterflies. All this partially justifies his tendency to recognise only his own reason, and the numerous disagreements with many colleagues.

We have always considered him a friend, with his strengths and weaknesses; we think we had been a bit of help to him and have learned a lot from him about the world of butterflies. We like to remember Otakar when, tired (perhaps on return from long entomological trip through meadows, woods and mountains), loved to toast dinner with red wine (Chianti, if at all possible), and/or with “il vero verissimo amaro Santa Maria del Monte” (a local bitter), both which he liked a lot, gradually slowing down his words, with his eyes at times turned backwards, until he fell asleep.

Now, like then, he did it again, forever.

Nobody can deny that Otakar has dedicated all his life to the passionate study of butterflies, shifting from taxonomy to conservation, and certainly always providing at least significant contributions.

We attach a list of his publications, which he had circulated to us some time ago, and from which probably only the latest edition of his Atlas is missing.

Otakar Kudrna: List of lepidopterological publications

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Life history of the rare boreal tiger moth *Arctia menetriesii* (Eversmann, 1846) (Lepidoptera, Erebidae, Arctiinae) in the Russian Far East

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Abstract. A thorough description and detailed photographs of all developmental stages of one of the rarest Palaearctic moths, Menetries' tiger moth *Arctia menetriesii* (Eversmann, 1846) (Lepidoptera, Erebidae, Arctiinae), are presented. Eggs were obtained from a female collected in the Bureinsky Nature Reserve, Khabarovsk Krai, Russia. Data relating to specimens from this region significantly supplements previously published data, which was derived exclusively from more westerly parts of the species' range. Larvae were reared mainly on dandelion (*Taraxacum campyloides* G.E.Haglund) in laboratory conditions. Some larvae were fed on *Aconitum consanguineum* Vorosch. leaves and larch (*Larix gmelinii* (Rupr.) Kuzen.) needles during certain periods of their lives. It is hypothesized that toxic compounds found in these plants resulted in high mortality rates among larvae prior to pupation. Metamorphosis anomalies in the form of larva-pupa intermediates and various morphological defects of pupae are documented for *A. menetriesii* for the first time. The assumptions of some researchers about the important role of *Larix* and *Aconitum* in larval development are questioned.

Introduction

Menetries' tiger moth *Arctia menetriesii* (Eversmann, 1846) is one of the rarest and most poorly studied Palaearctic moth species. Although the adults are large with bright colouration and the species is widespread throughout boreal Eurasia (from Finland in the west to Sakhalin Island in the east), it is primarily known from sporadic, disjunctive occurrences. The species is reliably recorded from Finland, Northern European Russia (Republic of Karelia and Arkhangelsk Oblast), the Urals (Sverdlovsk Oblast), Siberia (Yamalo-Nenets Autonomous Okrug, Khanty-Mansi Autonomous Okrug, Kemerovo Oblast, Altai Republic, Republic of Khakassia, Krasnoyarsk Krai, Irkutsk Oblast, Republic of Buryatia, Zabaykalsky Krai, and Republic of Sakha – Yakutia), Russian Far East (Amur Oblast, Khabarovsk Krai, Primorsky Krai, and Sakhalin Island), Kazakhstan, and North China (?Sungari River) (Hori 1926; Krogerus 1944; Dubatolov 1984, 1985, 1990, 2010; Klitin 2009; Bolotov et al. 2013; Berlov and Bolotov 2015).

The holotype of *A. menetriesii* originated from northeastern Kazakhstan ("Songoria") (Dubatolov 1984). However, no representatives of the species have been found in this territory since its discovery.

For a long time, *A. menetriesii* was included in the monotypic genus *Borearctia* Dubatolov, 1984. Recently, *Borearctia* and 18 other arctiine genera have been synonymized with the genus *Arctia* Schrank, 1802 on the basis of molecular genetic data (Rönkä et al. 2016).

A. menetriesii is included in the Red Lists of both countries it currently inhabits. These are Finland, where it is classified as Data Deficient (DD) (Hyvärinen et al. 2019), and the Russian Federation, where it falls under the category of Vulnerable (Vu) (Order of the Ministry of Natural Resources and Environment of the Russian Federation 2020).

In July 2018, one *A. menetriesii* female was collected by the author in the Bureinsky Nature Reserve in the upper reaches of the Pravaya Bureya River (Khabarovsk Krai, Russia) (Fig. 3A). Previously, two specimens were collected by V.D. Nebaykin in the Levaya Bureya River valley in July 1984 (Dubatolov and Lyubechanskii 2005). The new record was approximately 50 km from previously known localities and is the first record of this species in the region in 34 years. It is worth noting that the author conducted a search in *A. menetriesii* habitat in the upper reaches of the Pravaya Bureya River during its flight period (late June to July) for 13 years (2004, 2009–2020). However, this species was discovered only in 2018, which highlights its extreme rarity. Eggs were collected from a female moth, which made it possible to document the species' biology under laboratory conditions and describe the immature stages.

Little is known about the biology of the immature stages of *A. menetriesii*. Krogerus (1944) provided a description of all stages of *A. menetriesii* development as well as very schematic drawings of the first, fourth, and sixth instar larvae, and the pupa. The immature stages were obtained through rearing eggs from a female collected in Central Finland (Saarijärvi, Pyhä Häkki). Larvae were fed mainly on the leaves of *Taraxacum*, as well as *Plantago* and *Polygonum*, in laboratory conditions. A total of two moths (a female and a male) out of 30 eggs reached the adult stage. Krogerus's (1944) paper also contains information on the discovery of a larva on a spruce trunk in Juupajoki (Southern Finland) in 1920. Subsequently, some features of immature stages were briefly described and illustrated by low-resolution photographs, also under laboratory conditions, by Saarenmaa (2011). However, there is still no detailed description of all immature stages. Eggs were collected from a female sampled in the Northern Transbaikalia Region. A total of 19 adults were obtained from 100 larvae, which fed on 15 plant species, among which the preferred species were *Plantago major* L., *Taraxacum campyloides* G.E.Haglund, *Rubus chamaemorus* L., *Vaccinium uliginosum* L., *Salix phylicifolia* L., *Menyanthes trifoliata* L., and *Persicaria maculosa* Gray (Saarenmaa 2011). In addition, larch (*Larix*) has been suggested as an important host plant for larvae in most *A. menetriesii* habitats (Saarenmaa 2011).

The first reliable data of a natural host plant of *A. menetriesii* was obtained in the Baikal Region, where one last instar larva was found feeding on the extremely poisonous plant *Aconitum rubicundum* Fischer (Ranunculaceae) (Berlov and Bolotov 2015). The larva subsequently died, the presumed cause being starvation since *Aconitum* was not available and other plants were refused (Berlov and Bolotov 2015).

Considering the extreme rarity of *A. menetriesii* and the paucity of data on its biology, this study (1) describes and illustrates all developmental stages of the species; (2) presents the first observations on metamorphosis anomalies of this rare moth; and (3) discusses general patterns of its bionomics in a broader ecological context.

Materials and methods

A female of *A. menetriesii* was collected flying low above the ground in sunny weather after a short shower of rain at 2.30 p.m. on July 1, 2018. Locality: Russia, Khabarovsk Krai, Verkhnebureinsky District, Bureinsky Nature Reserve, Dusse-Alin' Mountains, upper reaches of the Pravaya Bureya River, Novyi Medvezhii cordon, 52°07'56"N, 134°17'30"E, 877 m. The habitat consisted of mountain larch forest composed of *Larix gmelinii* (Rupr.) Kuzen. with open-grown young *Picea ajanensis* Fisch. ex Carr. and *Betula platyphylla* Sukaczew trees. The lower layers were dominated by green moss species, *Vaccinium vitis-idaea* L., *Rubus arcticus* L., and *Ledum palustre* L. Individual bushes of *Salix* sp., *Betula divaricata* Ledeb., *Rosa acicularis* Lindl., *Spiraea beauverdiana* C.K. Schneid., and *S. salicifolia* L. were also present.

The captive female laid 105 eggs on July 3, 2018. First to third instar larvae were kept in ventilated plastic cages in groups of 5–10. Fourth to seventh instar larvae were confined to cages individually or in groups of two per cage. The food was changed twice a day. The cages were cleaned of food waste and frass, and treated with an antiseptic (Miramistin 0.01%) every day to prevent the development of infections. The larvae were maintained in laboratory conditions in the city of Khabarovsk indoors at an average temperature of ca. +25 °C under continuous illumination using three LEDs and daylight compact fluorescent lamps with 21–26 W power consumption. It has previously been established that several boreal arctiine species such as *Arctia ornata* Staudinger, 1896 and *Grammia quenseli* (Paykull, 1793), co-occurring with *A. menetriesii* can complete larval development to adults within two months under continuous illumination, thereby avoiding obligatory winter diapause of larvae that occurs under natural conditions (Koshkin 2020).

Most first and second instar larvae of *A. menetriesii* were fed on *Aconitum consanguineum* Vorosch. leaves, while the rest were reared on dandelion (*Taraxacum campyloides* G.E.Haglund) leaves. All larvae were switched to the dandelion diet at the third instar. Approximately twenty larvae of the sixth and seventh instars were switched from dandelion to larch (*Larix gmelinii*) needles in order to test the hypothesis that *Larix* is an important host plant for *A. menetriesii* (Saarenmaa 2011). Pupae and adults were maintained in entomological cages with cloth walls under natural lighting conditions and temperatures of +23 to 25 °C.

Photographs were taken using a Sony SLT-A65 digital camera with a Sony 2.8/50 macro lens. Voucher material is deposited in the author's private collection.

Results

Description of immature stages

Egg. The eggs are dome-shaped with a flat base and of light green colour (Fig. 1A). The surface sculpture of the chorion is finely meshed; the cells are rounded. The egg height and width are 1.5 and 2 mm, respectively. Eggs develop in approximately 9 days at an average temperature of 23–25 °C.

First instar larva. All thoracic segments, as well as the posterior part of the seventh to tenth abdominal segments, are light orange (Fig. 1B, C). The rest of the body is whitish. The spiracles are pale. The head is black and shiny. Each segment has a row of brown warts with hairs. There are 8 warts on the second and third thoracic segments. The first thoracic segment has two warts on each side and a long wart on top. Each of the abdominal segments, with the exception of the last

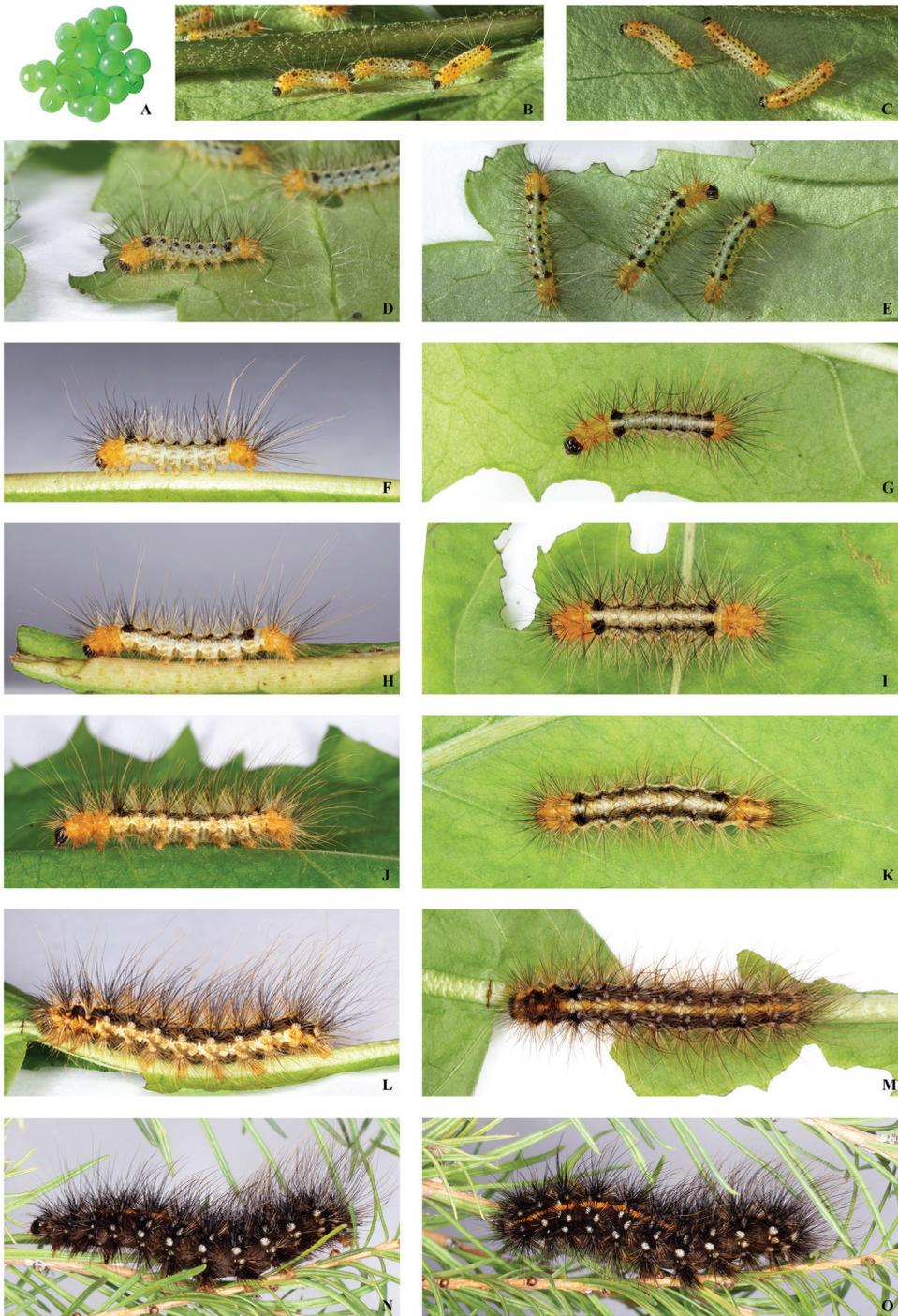


Figure 1. *Arctia menetriesii*. A. Eggs; B–O. Larvae: B, C. First instar larva; D, E. Second instar larva; F, G. Third instar larva; H, I. Fourth instar larva; J, K. Fifth instar larva; L, M. Sixth instar larva; N, O. Seventh instar larva; B, D, F, H, J, L, N. Lateral view; C, E, G, I, K, M, O. Dorsal view.

three, contains 12 warts. Of these, the four largest are located on the dorsal and in the upper parts of the lateral body surfaces. Two small warts are situated at the axial body region and displaced forward relative to the large warts. Round brown spots are found between these warts on the first and seventh abdominal segments. The eighth abdominal segment has only 10 warts; the lowest ones are absent. There are four warts on the ninth abdominal segment; the two largest warts are on top. A large wart is situated on the anal shield on the last segment. Each dorsal and upper lateral wart bears one short black hair. Large warts on the dorsal side of the eighth to tenth abdominal segments have additional white hairs. The rest of the warts bear only white hairs of varying lengths. Thoracic legs and prolegs are brown. Body length is 3–5 mm. Instar duration is 2–3 days when fed on *Taraxacum* and approximately 5 days when fed on *Aconitum*.

Second instar larva. The general colouration of the head and body is similar to that of the first instar (Fig. 1D, E). The warts are larger and vary in colour. The two rows of large warts on the dorsal side of the first to seventh abdominal segments are black, shiny, and sharply distinguished against the general background. Two additional wart rows on the dorsal side of the first and seventh abdominal segments are also coloured black. There are black spots between them, thereby creating the appearance of two large black spots on the top of these segments. The remaining warts on the first to seventh abdominal segments are light brown. Warts on the thoracic and the last three abdominal segments are light orange and identical to the main ground colour. Each wart has an average of five whitish and five black long hairs. The thoracic legs and prolegs are light orange. Instar duration is 3 days when reared on dandelion.

Third instar larva. Similar to the second instar in general (Fig. 1F, G). The exceptions are a brighter orange colouration of the thoracic and the eighth to tenth abdominal segments, and paler lateral and two dorsal rows of small warts on the first to seventh abdominal segments, which hardly stand out against the general whitish background. Large warts on the dorsal side of the second to sixth abdominal segments are bicoloured: black with a bluish tinge on the outside and whitish on the inside. Warts on the dorsal side of the first and seventh abdominal segments form black spots identical to those in the second instar although larger in size. Small dark spots forming two dark dashed lines along the dorsal side are located between the large warts of the abdominal segments. Each wart has up to 11 black and yellowish hairs of different lengths. The black hairs are found exclusively on the dorsal body surface. Instar duration is three days when fed on dandelion.

Fourth instar larva. Very similar to the third instar, differing from it in more pronounced dark lines on the dorsum (Fig. 1H, I). Instar duration is about 5 days when reared on dandelion.

Fifth instar larva. Resembles third and fourth instars larvae, while differing from them in pale warts on the dorsal side of the second to sixth abdominal segments and two well-marked longitudinal dark lines (Fig. 1J, K). Warts on the first and seventh abdominal segments form large dark spots. Small dark spots are situated on the dorsal side of the eighth and ninth abdominal segments. Spiracles are oval, light yellow with a light brown margin. Instar duration is approximately 6 days when fed on dandelion.

Sixth instar larva. The colouration differs significantly from the larvae of the earlier instars (Fig. 1L, M). The head is black. The lateral body sides are either beige or light yellow. The dorsal side is black with a long, wide orange-yellow stripe in the center. Pale colouration on the thoracic segments is brighter, of orange colour. The ventral surface is gray. Warts are large, white, with the exception for those located on the thoracic and last abdominal segments, which are white and orange. There are dense tufts of long hairs on the warts: they are black and light brown on the dor-



Figure 2. *Arctia menetriesii*. A–C. Pupa with insignificant anomalies; D–F. Pupa with severe anomalies; G. Pupa in silken cocoon; H, I. Cremaster; J–L. Female emerged from larva-pupa intermediate (J, K. Head and thorax left covered with the larval cuticle; L. Larval cuticle removed); M, N. Lethal larva-pupa intermediates; A, D, H. Ventral view; B, E, G, K, N. Lateral view; C, F, I, J, L, M. Dorsal view.

sal side and light brown on the lateral sides. The spiracles are white, with the exception of those located on the second to third thoracic segments, which are black. The thoracic legs and prolegs are light orange. Body length up to 35 mm. Instar duration is approximately 12–14 days when fed on dandelion and approximately 20 days when reared on larch.

Seventh instar larva. The larva differs significantly in appearance from the earlier instars and has an overall stockier build (Fig. 1N, O). The head and body are black. A central orange stripe runs along all the segments on the dorsal side. The spiracles are oval, light yellow, and clearly visible against the general background. The head capsule is 3.8–4.0 mm in height and 4.0–4.2 mm in width. All warts are white, large, and have dense tufts of black hairs. Small blotches of paler hairs

are situated between these tufts. Each wart bears up to 40 or more hairs. The thoracic legs are dark brown; prolegs are paler. Total length up to 45 mm shortly before pupation. Instar duration is 21–30 days when fed on dandelion.

Pupa. Total length is 21.5–24.0 mm (average length 22.9 mm); maximum width is 7.5–9.0 mm. Pupa is almost entirely black or brown, slightly shiny (Fig. 2A–F). The cuticle is smooth with a thin coating of bluish-grey wax. Antennae, legs, and proboscis are well developed. Labial palps are visible as small triangular areas at base of proboscis. Antenna is long, extending to 5/6 of the forewing length. Proboscis is long, reaching the level of the antennal apex. Prothoracic legs are slightly shorter than proboscis; mesothoracic legs reach the level of the antennal apex. Metathoracic legs are visible only in distal parts, reaching the level of the wing apex. Abdominal spiracles are narrow, slightly rising above the cuticular surface. Abdominal segments with distinct short setae are arranged around scars of larval warts. The cremaster has a medial groove and two groups of 8–10 brown nail-like setae (Fig. 2H–I). The pupa is in a loosely spun whitish silken cocoon covered with larval hairs (Fig. 2G). The development of the pupae takes 9–10 days.

Adult. The forewing length is 31 mm for a wild female, 25–29 mm for reared males, and 28–31 mm for reared females. The ground colour of the wings is either yellow or yellow-orange. The forewing and hind wing of a wild female are bright orange-yellow and identical in colour (Fig. 3A). The forewings of reared specimens are paler than the hind wings (Fig. 3B–F). The pattern is formed by black stripes running along the veins and black transverse medial and subterminal lines, which can be partially reduced. The black discal spot is clearly visible both on the forewings and hind wings. The costal margin of the hind wing is red. Some reared specimens also have a reddish outer margin to the hind wing. The pattern of the wing underside is identical to that of the upperside, although slightly paler; the costal margin of the forewing is red. The antenna is black, serrate in males and filiform in females. The top of the head is red, and the forehead is black. The labial palp is black dorsally and red ventrally. The patagium is black, with a yellow anterior and a red posterior margin. The tegula is black, yellow on the outer margin. The upper side of the thorax is black with two longitudinal yellow stripes. The abdominal segments are black dorsally and ventrally, and orange along the margins. The front and middle legs are black dorsally and yellow ventrally; the coxae and femora have red hairs. The hind legs are yellow.

Developmental features. Low to moderate mortality was observed among larvae of the first to sixth instars. However, approximately 75% of larvae that reached the last instar died immediately before pupation.

A significant number of metamorphosis anomalies occurred during pupation. Some of them manifested as larva-pupa intermediates due to disrupted moulting (Fig. 2J–L, M, N). Four specimens exhibited this anomaly, only one of which completed metamorphosis to adult (female); the remaining three died. Upon adult emergence, the surviving larva-pupa intermediate broke free of the pupal cuticle at the abdominal segments, while the head and thorax were left covered with the larval cuticle (Fig. 2J, K). This female laid 19 unfertilized eggs. Eventually, the larval cuticle was mechanically removed, leaving the fully formed head and thorax of the imago (Fig. 2L). The antennae, legs, and wings remained in a reduced state. The rest of the anomalies were pupal (Fig. 2A–F). They manifested themselves as abnormal positions of the legs, antennae, and wings, as well as uneven pupal colouration.

Fourteen larvae reached the pupal stage. One of the most malformed pupae died. Although the remaining 13 survived to adult eclosion, only four adults (two females and two males) fully or al-



Figure 3. *Arctia menetriesii*. Adults: **A.** Wild female (Khabarovsk Krai, Bureinsky Nature Reserve, Novyi Medvezhii cordon); **B–F.** Reared specimens: **B, E.** Female; **C, D, F.** Males; **E, F.** Live specimens.

most fully spread their wings (Fig. 3B, D–F); one male had a severely deformed left forewing (Fig. 3C). The rest of the adults were unable to inflate their wings. All pupae had anomalies of varying severity. Pupae with insignificant anomalies transformed into adults with fully or almost completely formed appendages. Pupae with severe anomalies produced adults that were unable to inflate their wings. Similar metamorphosis anomalies were described for *Spodoptera littoralis* (Boisduval, 1833) and *S. exigua* (Hübner, 1808) (Lepidoptera, Noctuidae) reared on food supplemented with azadirachtin and methoxyfenozide (Martinez and van Emden 2001; Enriquez et al. 2010).

The adults hatched on September 12–23, 2018. The development cycle of *A. menetriesii* from oviposition to adult emergence took 72–83 days under laboratory conditions.

Discussion

The description of the immature stages of *A. menetriesii* provided here supports in general and significantly expands on the information available for this species from Europe and Transbaikalia (Krogerus 1944; Saarenmaa 2011). Some differences are found in the appearance of the second to

fifth instar larvae and pupa. According to data from Finland, the paired spots on the first and seventh abdominal segments are reddish brown in the second and third instar larvae (Krogerus 1944). According to our data, they are black. There is also an indication that the longitudinal dark lines on the first to seventh abdominal segments appear only at the fifth instar. According to our data, the lines are clearly visible in the fourth instar larvae, and even more pronounced at the fifth instar. In addition, according to data obtained in Finland, the cremaster contains 10 setae, while we counted 14 to 20 setae in our study.

The unusually low ratio of resulting adults compared to the initial number of eggs is similar to the results obtained by other researchers (Krogerus 1944; Saarenmaa 2011). This is due to a high mortality rate among last instar larvae and numerous metamorphosis anomalies. The latter may be caused by larval ingestion of secondary plant compounds, such as those found in *Aconitum* leaves and possibly also larch needles. The norditerpenoid alkaloids in *Aconitum* are known to have strong insecticidal activity (Gonzalez-Coloma et al. 2004). It is necessary to further establish the role of *Aconitum* in *A. menetriesii* larva diet and the effect of norditerpenoid alkaloids on larval development and mortality. It is possible that *A. menetriesii* larvae partly feed on *Aconitum* to gain alkaloids as a defense against predators in natural conditions, but that too much *Aconitum* can be lethal. This is exactly what other tiger moths do, and has been well-studied in *Grammia incorrupta* (H. Edwards, 1881), for example (Mason et al. 2014; Christian Schmidt, pers. comm.). Perhaps this explains the discovery of *A. menetriesii* larva on *Aconitum* (Berlov and Bolotov 2015). Despite an active search for aconite through the habitat in which the *A. menetriesii* female was collected in the upper reaches of the Pravaya Bureya, it has never been seen there. Small groups of aconite plants (*Aconitum* cf. *macrorhynchum*) are located 5 km away across a mountain pass in the valley of the Niman River. Considering the low activity of the adults and the good condition of the collected moth, it is unlikely that the latter had flown from there. No larvae of any moth species or damage done by them were found during a detailed examination of aconite plants from the Niman River valley in various years. In addition, the effect of a number of substances contained in larch needles on *A. menetriesii* larva development has to be established. Despite the assertions of colleagues on the important role of larch in larval diet (Saarenmaa 2011), all the larvae fed on this plant died before pupation in our case. Meanwhile, several larvae in the middle of the last instar, which were switched back to rearing on dandelion leaves, succeeded in pupating.

It is worth noting that no metamorphosis anomalies of the immature stages were observed when rearing two other arctiine species (*Arctia ornata* and *Grammia quenselii*) coexisting with *A. menetriesii* on a dandelion diet under the same laboratory conditions.

Menetries' tiger moth is extremely rare since the adults are difficult to detect, as they are not attracted to light, are either diurnal or crepuscular, and fly reluctantly. It is possible that larvae are also subject to high mortality in nature due to the metamorphosis anomalies observed in this study. Additionally, high mortality due to parasitoids may also be the case, as has been found in other arctiine species from the same region. For instance, *Arctia ornata* occurs sympatrically with *A. menetriesii* in the study area. All 23 sixth-instar larvae of this species collected there in July 2017 were parasitized by the larvae of a tachinid fly (Diptera, Tachinidae). It has been shown that parasitoid infestation significantly reduces imago abundance in several other arctiine species from Siberia (Shilenkov and Richter 1998) and the Arctic (Bolotov et al. 2015).

Further studies on the ecology of *A. menetriesii* are required in order to determine what biotic and abiotic factors determine the low abundance of the species in nature and to develop a management plan for its conservation.

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Description of *Striogylia simianshana* sp. nov. (Lepidoptera, Limacodidae) from Chongqing in southwest China

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Abstract. The discovery of *Striogylia simianshana* sp. nov. (Lepidoptera: Limacodidae) resulted from a research project investigating the biodiversity of the Simian Mountain Nature Reserve in Chongqing, Southwest China. This new species is characterised by several distinct features, namely the black, broken postmedial line of the forewing and the long filiform antenna found in males. The shape of its valva, transtilla, juxta and phallus also distinguish it from other congeners. Furthermore, images of the adult habitus and male genitalia are compared with similar species *S. obatera* Wu, 2011 and *S. acuta* Wu, 2020, which further illustrate characteristics unique to *S. simianshana*. A distribution map and key for Chinese *Striogylia* species are provided.

Introduction

The genus *Striogylia* was erected by Holloway in 1986, with *S. snelleni* Holloway, 1986 as the type species. At the same time, Holloway transferred *S. foliola* (Snellen, 1900) to this genus, which was originally placed in the genus *Heterogenea* Knoch, 1783. Later, in 1990, Holloway described a third species *S. spinosa* from Sumatra, Indonesia (Piepers and Snellen 1900; Holloway 1986, 1990). In recent years, Wu (2011, 2020) described two additional species distributed in China: *S. obatera* (Guizhou) and *S. acuta* (Shaanxi). Currently, the genus consists of these five species ranging from Indonesia and Malaysia to China.

The genus is generally characterised by the adult male filiform antennae and the oblique postmedial line running almost from the apex to the posterior margin of the forewing. In the male genitalia, the uncus and gnathos are weak or absent. The transtilla is well developed and strongly sclerotised.

This study focuses on the description of a new species, *S. simianshana* sp. nov., found in Mt. Simian of Chongqing Municipality, China. Although so far only two male specimens have been collected, their appearance differs from other congeners, particularly in the male genitalia. Hence, in this study, we formally describe these specimens as a new species.

Material and methods

The specimens were collected at a 220V/450W mercury light and a DC black light in Mt. Simian. Wingspan was measured from forewing apex-apex and the forewing length from the wing base to the apex. Standard methods for dissection and preparation of the genitalia slides were used (described by Kononenko and Han 2007). The specimens were photographed using a Nikon D700 camera while the photographs of the genitalia slides were captured using an Olympus photo microscope aided by Helicon Focus software and then further processed using Adobe Photoshop CS6. The type material of the new species is deposited in the collection of the Northeast Forestry University (NEFU), Harbin, China.

Abbreviation used

NEFU Northeast Forestry University, Harbin, China.

Taxonomic account

Genus *Striogyia* Holloway, 1986

Striogyia Holloway, 1986. *Malay. Nat. Jour.*, 40 (1–2): 136. Type species: *Striogyia snelleni* Holloway, 1986 (Malaysia: Sarawak).

Key to the Chinese species

- | | | |
|---|--|--|
| 1 | Forewing with a distinct bar-shaped discal spot..... | <i>S. acuta</i> Wu |
| – | Forewing without distinct discal spot, but with an oblique postmedial line..... | 2 |
| 2 | Postmedial line obvious, pale grey, running from apex to 3/4 of the posterior margin; the apical process of juxta chimney-shaped | <i>S. obatera</i> Wu |
| – | Postmedial line barely visible, black, broken, running from the apex to the 1/3 of the posterior margin; the apical process of juxta three pronged, with acute apex..... | |
| | | <i>S. simianshana</i> Wu, Wu & Han, sp. nov. |

Striogyia simianshana Wu, Wu & Han, sp. nov.

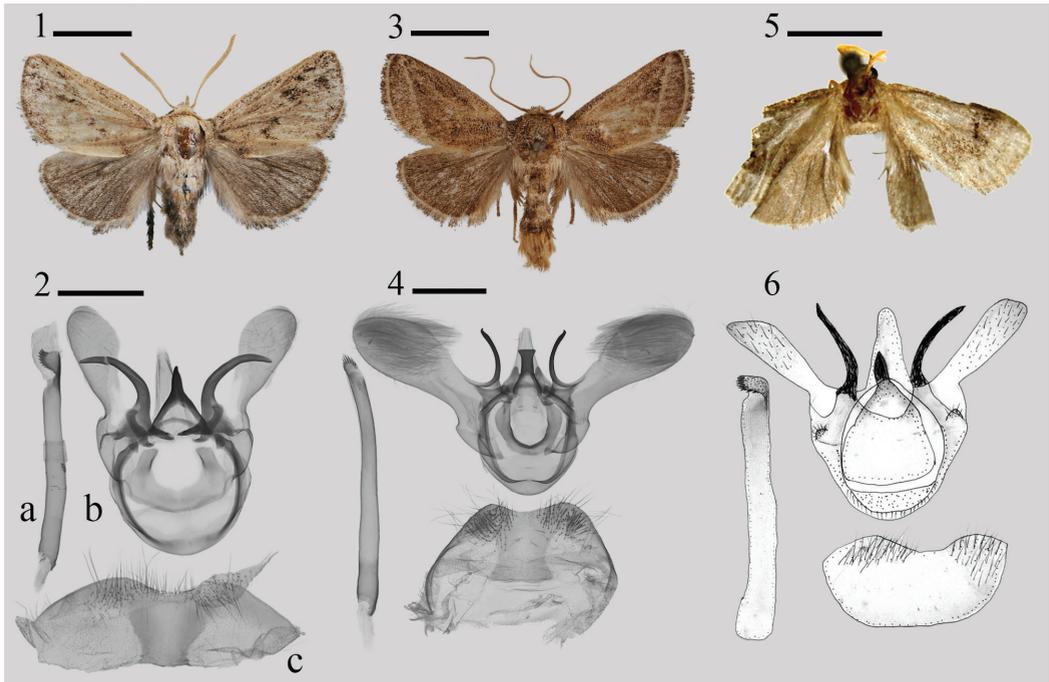
<http://zoobank.org/AEC3247A-16FA-4088-8620-BC0DD5431AFA>

Figures 1, 2

Material examined. *Holotype*: ♂, CHINA; Chongqing Municipality, Mt. Simian; 28°34'55"N, 106°21'03"E; 13 Jul. 2019; C. Zhang, X.Y. Zhang, D. Feng leg.; genitalia No. WuJ-281-1; coll. NEFU.

Paratype: 1♂, CHINA; same data as for holotype; coll. NEFU.

Diagnosis. The new species is similar in appearance to *S. obatera* Wu, 2011 (Fig. 3), but can be distinguished from the latter by comparing the antenna, forewing and abdomen. The male antenna of *S. simianshana* is long, and slightly thicker than that of *S. obatera*; the postmedial line of the forewing is black and broken, running from the apex to the posterior margin at ca. 1/3 distance from the wing base; the abdomen is dark brown posteriorly. The male antenna of *S. obatera* is thin; the forewing postmedial line is pale grey and it runs from the apex to the posterior margin at ca. 3/4



Figures 1–6. *Striogyia* spp., adults and male genitalia, with 8th sternite: **1, 2.** *S. simianshana* sp. nov., male, holotype; **3, 4.** *S. obatera* Wu, 2011, Prov. Jiangxi, China, genitalia No. WuJ-325-1; **5, 6.** *S. acuta* Wu, 2020, holotype (after Wu 2020) **a:** phallus, **b:** male genitalia, **c:** 8th sternite. Scale bars: adults, 5 mm; male genitalia, 1 mm.

from the wing base; the abdomen is yellow posteriorly. The visible difference in appearance between this new species and *S. acuta* (Fig. 5), and other congeners is that the latter have a distinct discal spot or a complete postmedial line on the forewing.

In the male genitalia, the new species is similar to *S. acuta* (Fig. 6), but also displays significant differences. In *S. simianshana*, the apex of the valva is rounded; the paired ox horn-shaped processes are strongly curved outwards, with a broad base; and the plate in the apex of the phallus is nearly triangular (Fig. 2). The valva of *S. acuta* is narrower than that of *S. simianshana*; the pair of processes is only slightly curved outwards, with a narrow base; and the plate in the phallus apex is almost rectangular (Fig. 6). The new species shows visible differences in the male genitalia compared to *S. obatera* (Fig. 4) with the apical process of juxta in *S. obatera* being chimney-shaped, while the structures of the other two species are pointed.

Description. Male. (Fig. 1) Forewing length 10 mm; wingspan 22 mm.

Head. Vertex densely covered with greyish-white scales; labial palpus pale brown; the antenna filiform, yellowish-brown.

Thorax. Mainly grey with a few greyish brown scales; tegula pale grey. Forewing base colour greyish-brown, while the colors of the base, costal margin, and terminal areas are darker and mixed with black spots; the black, oblique, broken postmedial line running from the apex to 1/3 of the posterior margin; terminal line dark brown; fringe greyish-white to dark brown. Hindwing base colour dark brown, while the colour of costal margin area is paler; terminal line distinct, brown and the fringe is brown.



Figure 7. Map and habitat of *S. simianshana* sp. nov.. **A.** Collecting site: Chongqing Municipality, Mt. Simian (red dot); **B.** Collecting site close to a subtropical mixed forest.

Abdomen. Dorsally yellowish-brown to dark brown, with mixed yellow and black; 8th sternite (Fig. 2c) slightly sclerotised, concave in distal margin, bearing dense spines.

Male genitalia (Fig. 2a, b). Uncus and gnathos absent. Tegumen narrow, weakly sclerotised. Valva long, extremely narrow at base, rounded at apex; 1/2 of the costa from the base part of valva weakly sclerotised, almost transparent and membranous; the base of sacculus slightly upheaved, with a small triangular process. Transtilla strongly sclerotised, bearing a pair of long, ox horn-shaped processes curved outwards, distinctly broader at the base. The juxta consisting of two parts, the apical part three pronged; the basal part ring-shaped, with width greater than height. Vinculum ring-shaped. Saccus inconspicuous. Phallus slender, longer than the valva, a nearly triangular plate formed on one side of the apex, densely bearing saw-toothed small spines on the edge.

Female. Unknown.

Distribution. China (Chongqing Municipality: Mt. Simian) (Fig. 7A).

Etymology. The species is named for its type-locality in Mt. Simian, Chongqing, China.

Bionomics. The moths fly in July. The specimens were collected with a light trap close to a subtropical mixed forest (Fig. 7B).

Remarks. The Simian Mountain Nature Reserve is located in the southwest of Chongqing Municipality. The region has a subtropical humid monsoon climate with abundant rainfall, and the vegetation types are mainly tropical and subtropical coniferous and broad-leaved mixed forests.



Figure 8. Distribution map of Chinese *Striogyia* spp., circle: *S. simianshana* sp. nov. (Chongqing Municipality); triangles: *S. obatera* Wu, 2011 (Prov. Guizhou, Jiangxi, Zhejiang and Hubei); square: *S. acuta* Wu, 2020 (Prov. Shaanxi).

The main vegetation found around the site where the specimen was collected include *Fagus longipetiolata* Seemen (Fagaceae), *Castanopsis fargesii* Franch. (Fagaceae), *Engelhardia roxburghiana* Wall. (Juglandaceae), *Fokienia hodginsii* (Dunn) A. Henry & H.H. Thomas (Cupressaceae), different kinds of bamboo, and a large number of shrubs and ferns growing in the ground cover layer of the forest. However, the larval host of this species is yet to be determined as no specimens have been collected in its immature stage.

The distribution of the Chinese *Striogyia* species is provided (Fig. 8).

World checklist of the genus *Striogyia*, with distributions

- S. acuta* Wu, 2020 (China: Shaanxi)
- S. foliola* (Snellen, 1900) (Indonesia: Java)
- S. obatera* Wu, 2011 (China: Guizhou, Zhejiang, Jiangxi, Hubei)
- S. simianshana* Wu, Wu & Han, sp. nov. (China: Chongqing)
- S. snelleni* Holloway, 1986 (Malaysia: Sarawak)
- S. spinosa* Holloway, 1990 (Indonesia: Sumatra; ? Singapore)

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The ant associates of Lycaenidae butterfly caterpillars – revisited

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Abstract. Based on a global compilation of data on ant associates of 523 Lycaenidae species, a synthesis is attempted as to which ants participate in these interactions. Ants from 63 genera have thus far been observed as visitors of facultative myrmecophiles or as hosts of obligate myrmecophiles among the Lycaenidae. Over 98% of records come from nectarivorous and trophobiotic ants in just three subfamilies, viz. Formicinae, Myrmicinae and Dolichoderinae, with the genera *Crematogaster* and *Camponotus* occupying the top ranks. Accumulation analysis suggests that rather few ant genera remain to be added to the list of associates. The representation of ant genera as attendants of lycaenid immatures is related to their global species richness, but with some notable exceptions. Ants that form ecologically dominant, large, long-lived colonies are over-represented as hosts of obligate myrmecophiles. The taxonomic diversity of lycaenid-ant associations is highest in the Oriental and Australian region, and lowest in the Neotropical and Afrotropical region. Among tropical African lycaenids, this is due to two butterfly lineages (genus *Lepidochrysops* and subfamily Aphnaeinae) that have massively radiated in the Neogene, but mostly maintaining their general affiliations with either *Camponotus* or *Crematogaster* ants, respectively. Many tropical and subtropical lycaenids nowadays form associations also with invasive alien tramp ants, giving rise to novel mutualistic interactions.

Introduction

The caterpillars of many species in the butterfly family Lycaenidae associate with ants (reviewed in: Fiedler 1991; Pierce et al. 2002). Multimodal communication between caterpillars and ants forms the mechanistic basis of these unusual associations (Fiedler et al. 1996; Casacci et al. 2019). With regard to their ecological outcome, these interactions cover the whole range from very loose non-aggressive occasional encounters, across facultative or obligate cases of mutualism, into rare cases of obligate social parasitism. In the latter, caterpillars enter ant nests to feed on ant brood or to beg trophallactic feeding. Along this continuum there occurs also a shift in the functional role of the ants. Whereas in facultative associations ants act as visitors of the caterpillars while these are feeding on their host plants, in cases of obligate mutualism or even social parasitism the ants serve as hosts for the butterflies. The identity and fidelity of ant visitors of facultative myrmecophiles obviously depends on the structure of the local ant community in each habitat and is thus quite unpredictable. Here the caterpillars, or also the female butterflies when selecting oviposition sites, have little control over which ant species will attend the larvae over their developmental period. As a consequence, facultative ant associations are usually unspecific, i.e. caterpillars of the same

lycaenid species may be visited by a more or less varied range of different ants. Host associations of obligate mutualists and parasites, in contrast, are far more specific. Either the mother butterfly establishes the association with appropriate hosts when selecting oviposition sites (ant-dependent oviposition: Pierce et al. 2002), or the caterpillars later on need to be actively adopted by proper host ants for completing their life cycle, as is the case with butterflies in the famous *Phengaris* (*Maculinea*) clade (Hayes 2015).

Out of the huge diversity of ants on Earth, only a fraction qualifies to act as potential partners in associations with lycaenid immatures. Three intertwined aspects of ant ecology are particularly relevant in that regard: nectarivorous feeding habits (Blüthgen and Feldhaar 2010), trophobiosis (Ness et al. 2010), and trophallaxis (Meurville and LeBoeuf 2021). Only ants that form mutualistic associations with honeydew-producing insects or with nectar-secreting plants and which share all the anatomical, physiological and behavioural characters essential for harvesting and sharing nutritive liquids are also able to attend lycaenid caterpillars.

Twenty years ago, I reviewed which ants participate in these interactions (Fiedler 2001). It turned out that out of the large array of ants that fulfil the aforementioned characters, ecologically prevalent taxa like *Crematogaster* and *Camponotus* by far dominate among ant visitors or hosts, but with characteristic variation between facultative and obligate interactions, or between biogeographical regions. Since that last attempt of a global synthesis, many new observations have been recorded. In particular, with the rise of the internet many pieces of information have now become accessible that remained elusive two decades ago. I therefore here set out to revisit the identity of ant associates of lycaenid butterflies. In particular, I will address the following research questions:

- How much has our understanding grown over the last 20 years? How complete is the coverage of ants attending lycaenid immatures in the meantime?
- Is the importance of ant taxa as associates of lycaenid immatures related to their global species richness?
- Is the visitor range of facultatively myrmecophilous caterpillars wider than the host ant range of obligate myrmecophiles?
- Are ant associations consistently more diverse in tropical rather than temperate regions?

Material and methods

Data collection

Starting from the data base underlying my earlier paper (Fiedler 2001), I continued to systematically collect journal articles that report on lycaenid-ant interactions. I also went through multiple faunal monographs in search of such records. Using Google Scholar, I searched for additional published records using search strings like *lycaenid ants attend*, *lycaenid ants associate*, or *lycaenid ants visit*. I also systematically (species by species) went through well curated and reliable web sites such as lepiforum.org (2021; Europe), butterflycircle.blogspot.com (Singapore), or Kunte et al. (2021) (India). Finally, I searched the pertinent web project “Ant-Butterfly Interactions” (Kaminski 2021) for additional records. The aim of this procedure was to obtain a data base as comprehensive as possible.

I only considered records of ant associations that were taken in the field. Observations from confrontations under laboratory or rearing conditions were disregarded. While essential to better

understand mechanistically the communication processes between caterpillars and ants, the focus of the present study is on interactions that form in nature. I also restricted my analyses to records where the involved ants had been identified at least to genus level, or where it was possible for me to post-hoc infer ant identity at genus level from accompanying photographs. Unfortunately, even in some rather recent and otherwise very detailed publications on lycaenid life-histories the identity of attendant ants was not assessed by ant taxonomists, and reports remain vague accordingly (e.g. van der Poorten and van der Poorten 2013).

Within the Lycaenidae, I excluded species in the subfamilies Poritiinae and Miletinae sensu Espeland et al. (2018). While in certain African representatives of the Poritiinae caterpillars occur exclusively on trees dominated by large colonies of *Crematogaster* ants (e.g. Sáfián and Larsen 2009; Sáfián and Collins 2014), these hairy larvae never possess nectar glands and therefore no trophobiosis with ants can take place in these cases. These caterpillars, which feed on lichens or algae growing on bark of ant trees, are functionally best described as commensalic to the *Crematogaster* ants which occupy the host trees. Larvae of most Miletinae are predators of honeydew-producing insects such as coccids, aphids or membracids, with a few species having evolved into social parasites of specific ants (Maschwitz et al. 1988; Lohman and Samarita 2009; Kaliszewska et al. 2015). Like in Poritiinae, Miletinae caterpillars have no nectar glands and in most cases ant associations they encounter are regulated by the trophobiotic interactions of their homopteran prey. I therefore decided to omit these (few) species from the analyses below, which also was the case in the 2001 study and thereby facilitates direct comparisons.

From this data base, I extracted record pairs of (butterfly species \times ant genus). I used the ant genus (rather than species) as level of analysis for the following reasons. (1) Nectarivorous ants can rather readily be identified to genus level, even by non-specialists. In contrast, even in well documented faunas species-level identification of ants regularly requires access to special literature and to high-quality microscopy and biometry (for Europe: Seifert 2018). Both these resources are not available to most lepidopterists when encountering caterpillar-ant associations. (2) Unresolved cryptic species diversity is prevalent among ants. Even putatively well-known ant “species” like *Lasius niger* and *Lasius alienus* in Europe turned out to represent species complexes (Seifert 1991; Seifert and Galkowski 2016). Therefore, ant species-level “identifications” that have not been scrutinized by myrmecologists, or that can be retrieved only from older literature, are suspect. In contrast, generic affiliations of most ants have remained quite stable (see discussion below for a few exceptional cases relevant to visitors of lycaenid larvae). (3) Ant generic identities can often be inferred from photographic records, but species-level identifications are impossible in most such cases.

Within each butterfly species, I aggregated all association records with multiple species from the same ant genus into one record pair. For example, if one butterfly species was recorded as being visited by five different *Lasius* species, or if five sources mentioned associations with “*Lasius niger*”, this was condensed into one single entry for ‘*Lasius*’. This procedure aimed at avoiding inflated representation of certain easily recognizable ants, or inflated records for butterfly species whose caterpillars are frequently found by lepidopterists. This approach also circumvents possible multiple counting of the same association, but under different ant species names. For example, in an old reference a caterpillar may have been reported as being attended by “*Lasius niger*”, yet in a later paper exactly the same association might have been corrected to “*Lasius platythorax*”. These ambiguities vanish at the ant genus level.

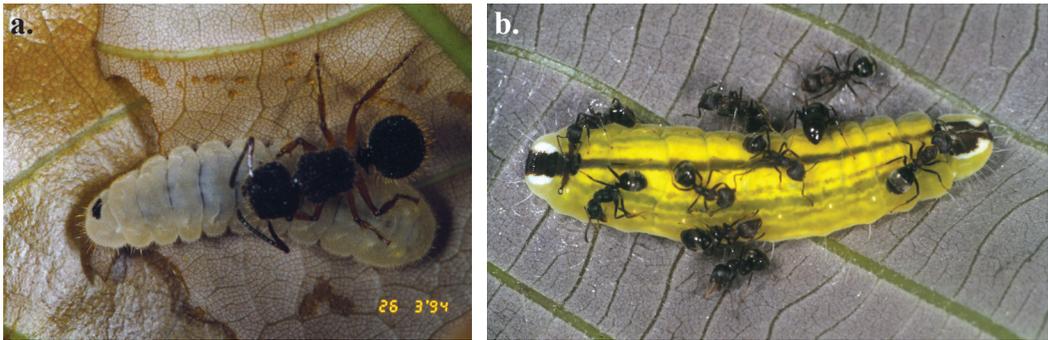


Figure 1. Exemplar species of (a.) a facultative myrmecophile (*Jamides virgulatus* attended by *Echinopla* sp.; left) and (b.) an obligate myrmecophile (*Flos anniella* attended by *Dolichoderus* sp., right) amongst the Lycaenidae. Observations from Poring, Sabah, Malaysia. Photo author K. Fiedler.

Data scoring

For each butterfly species, I scored whether its ant association is facultative or obligate (Fig. 1). Butterflies were scored as obligate myrmecophiles if their early stages are (almost) continually accompanied by ants, often with larger numbers of worker ants around, and especially if the females are known to oviposit only in the presence of their host ants. Ant-parasitic nest-inquiline lycaenid species were also classified as obligate myrmecophiles. All other butterfly species with ant associations were categorized as facultative myrmecophiles. I also noted whether the butterfly species occurs in one of the following biogeographical regions: Nearctic, Neotropical, Afrotropical (Africa south of the Sahara, including Madagascar), Palearctic, Oriental (S and SE Asia, including the Indo-Malayan archipelago), or Australian (Australia, New Guinea and surrounding islands). In the few cases where butterfly species occur in more than one faunal region, the ant association records were allocated to the region where the pertinent observations had been made. This procedure avoids considering ant genera that may attend the caterpillars in one biogeographical region, but which do not occur in the other such region. For each ant genus observed, the global number of described species according to current taxonomy was extracted from the database AntWeb (2021).

Statistical analysis

The coverage of ant genera recorded in association with lycaenid caterpillars was assessed through the iNext Online software tool (Chao et al. 2016). Correlation analyses and calculation of diversity metrics were done using the package PAST 4.07 (Hammer et al. 2001).

Results

Global patterns of ant associates

The current compilation comprises data on ant associates of 523 lycaenid species (see Suppl. material 1: Appendix S1 for records and Suppl. material 2: Appendix S2 for the evaluated data sources). Ants from 63 genera in the seven subfamilies Dolichoderinae, Ectatomminae, Formicinae, Myrmicinae, Myrmeciinae, Ponerinae, and Pseudomyrmecinae have been observed to participate in these interactions (Fig. 2). This is an increase by 10 genera relative to the earlier

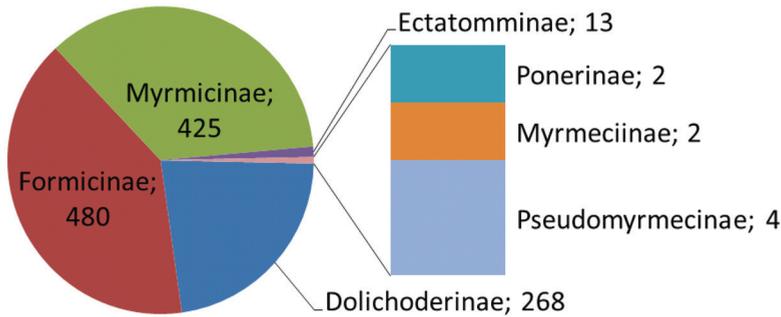


Figure 2. Representation of trophobiotic ant subfamilies in myrmecophilous associations of lycaenid butterflies. Figures indicate numbers of (butterfly species × ant genus) record pairs.

analysis. Altogether, 1194 record pairs are now available, compared to 817 data points in 2001, i.e. a substantial increase (by 46.1%) in the amount of observations. Collectively, observations with ants in the subfamilies Dolichoderinae, Formicinae and Myrmicinae account for 98.2% of all record pairs. The 10 globally most important ant genera as associates of lycaenid butterflies are (in descending order): *Crematogaster* (221), *Camponotus* (145), *Lasius* (66), *Tapinoma* (64), *Formica* (62), *Pheidole* (60), *Technomyrmex* (40), *Iridomyrmex* (36), *Plagiolepis* (33), and *Polyrhachis* (33). Most ant genera newly recorded since 2001 are known to attend larvae of just 1–3 lycaenid species and thus play only a very minor role. Two exceptions are related to shifts in the taxonomic circumscription of ant genera. Ant species now allocated to *Nyländeria* (recorded with 8 lycaenid species) were formerly included in *Paratrechina* (LaPolla et al. 2010). And the monobasic taxon *Iberoformica* (associated with 9 species) was only recently accepted as a distinct genus (Gómez et al. 2018). In contrast, ‘*Rhoptromyrmex*’ was formerly viewed as a distinct genus, but has been downgraded into synonymy with *Tetramorium* (Ward et al. 2015).

Twelve ant genera have experienced a particularly strong increase (more than 10 additional record pairs) in their representation in the list of visitor or host ants. These are, in decreasing order: *Camponotus* (+55 spp.), *Crematogaster* (+43), *Tapinoma* (+23), *Technomyrmex* (+22), *Formica* (+22), *Plagiolepis* (+21), *Lasius* (+20), *Pheidole* (+19), *Monomorium* (+15), *Tetramorium* (+14), *Polyrhachis* (+13), and *Anoplolepis* (+11). All these had already earlier been well represented in the list of ant associates. Overall, the representation of ant genera in the list of associates was highly correlated across the data sets of the two points in time ($r = 0.986$, $p < 0.0001$; Fig. 3). *Camponotus* received disproportionately more new records than *Crematogaster*.

Overall, the documented diversity of ant associates, with 63 genera in 2021, appears slightly higher than the 53 genera reported 20 years ago (Fig. 4). A combined rarefaction-extrapolation analysis revealed a very high coverage of 0.9890 for 2001, and even 0.9899 for 2021. Even if extrapolating to over 1600 record pairs, the number of expected ant genera would only increase to about 66 (95% confidence interval: 60–73 ant genera).

The global species richness of the observed ant genera was positively related to their representation in the list of ant visitors and hosts ($r = 0.589$; $p < 0.001$), but with remarkable scatter (Fig. 5). Ants of the genus *Pheidole*, the by far most speciose ant genus on Earth, remain relatively under-represented as associates of lycaenid butterflies. The same is true for *Polyrhachis* (a highly

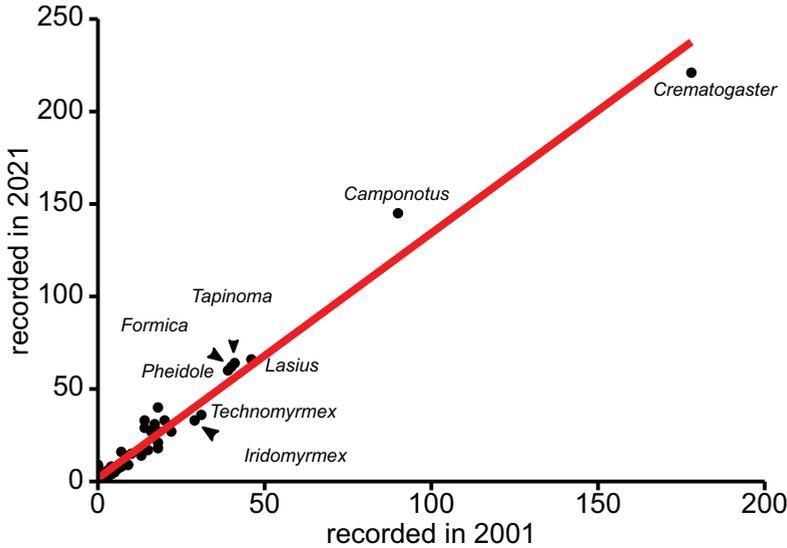


Figure 3. Representation of ant genera in the list of visitors or hosts of lycaenid caterpillars, comparing the 2021 with the 2001 data set. Each dot represents one ant genus. An ordinary least squares (OLS) regression line is fitted into the data cloud for visual clarity.

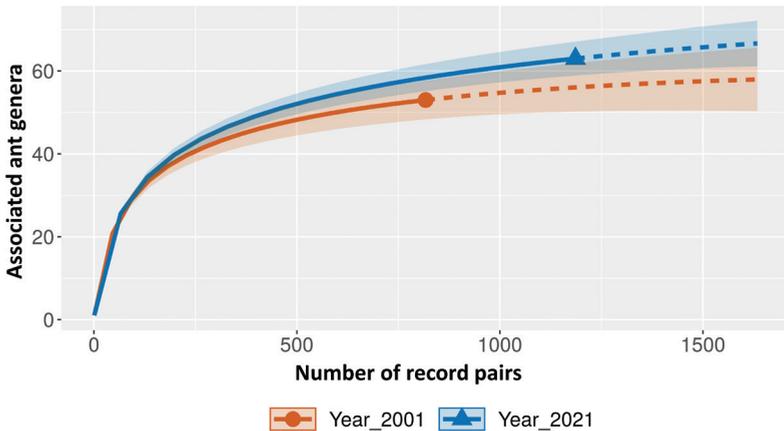


Figure 4. Rarefaction-extrapolation curves for the ant genera recorded as visitors or hosts of lycaenid caterpillars, comparing the data collections from 2001 and 2021, in relation to sampling success. Solid lines: rarefaction; dashed lines: extrapolation. Symbols denote observed level of records in either year.

trophobiotic ant genus of the Old World tropics), *Tetramorium*, and *Temnothorax*, even though all these ant genera experienced a substantial increase in record numbers (see above). In contrast, ants of the genus *Crematogaster* are distinctly over-represented relative to their global species richness. To a lesser extent, this also applies to *Formica*, *Lasius* and *Tapinoma*. Two extreme cases of deviance are the weaver ants *Oecophylla* (only 3 species recognized, but recorded from 27 lycaenid species) and *Anoplolepis* (9 species, yet also recorded with 27 lycaenid species).

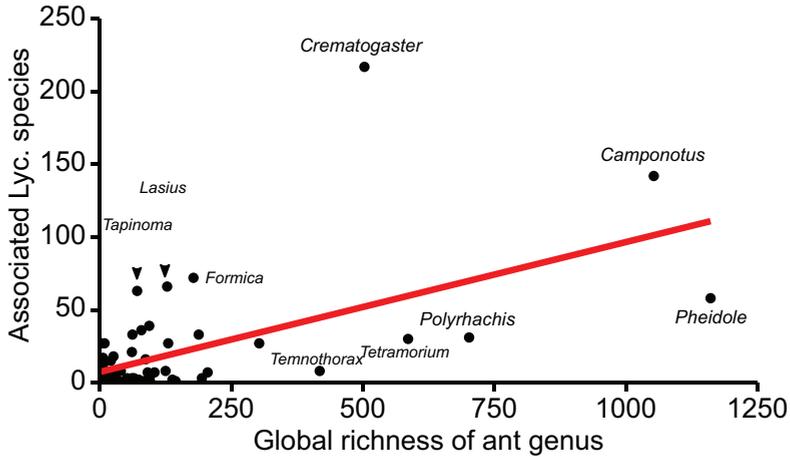


Figure 5. Representation of ant genera as hosts and visitors of lycaenid caterpillars, in relation to their global species richness. Each dot represents one ant genus. An OLS regression line is fitted into the data cloud for visual clarity. Ant genera below the regression line are under-represented, while those above the regression line are over-represented in relation to their global species diversity.

Obligate versus facultative myrmecophiles

Obligate myrmecophiles made up a considerable fraction in the data base (210 of 523 lycaenid species; 40.1%). As expected, the breadth of ant visitor ranges (Fig. 6) per butterfly species was far larger in facultative myrmecophiles than the breadth of host ant ranges among obligate myrmecophiles (Welch test, $t = 12.19$; $p < 0.0001$). Apart from a few exceptional ‘aberrant’ visitors that have been reported under unusual circumstances, obligate myrmecophiles are essentially affiliated with ant species within just one single genus each. In contrast, facultatively myrmecophilous caterpillars are visited by a much broader diversity of ants, reflecting the variation and unpredictability in local ant community composition and the number of records available per species from different studies. Thus far, larvae of 10 facultatively myrmecophilous lycaenid species have been observed being visited by ants from 10 or more genera: *Lampides boeticus* (15), *Ogyris oroetes* (13), *Plebejus melissa* (12), *Icaricia icarioides* (11), *Theclinessthes albocincta* (11), *Ogyris amaryllis* (10), *Jamides celeno* (10), *Echinargus isola* (10), *Nacaduba berenice* (10), and *Glaucopsyche lygdamus* (10).

Ant genera with stronger representation as visitors of facultative myrmecophiles also tended to serve as hosts for a larger number of obligate myrmecophiles ($r = 0.661$; $p < 0.0001$; Fig. 7). Four ant genera stand out as over-represented in this comparison: *Crematogaster*, *Oecophylla*, *Anonychomyrma*, and *Iridomyrmex*. In contrast, obligate associations with *Camponotus* ants appear to be slightly less numerous than one might expect from their strong representation in the visitors list at facultative myrmecophiles.

Diversity of lycaenid-ant associations

Contrary to expectation, the diversity of ant associations was not consistently highest in tropical realms. Rather, recorded associations in the Neotropical and Afrotropical regions showed lowest diversity, whereas ant partner diversity was highest among lycaenid butterflies from the Oriental and especially the Australian region (Fig. 8a). Ant interactions amongst Afrotropical lycaenids

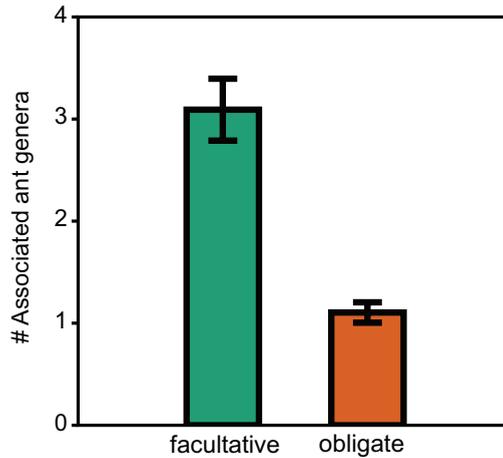


Figure 6. Mean number of genera of attendant ants that have been observed as visitors of facultative or as hosts of obligate myrmecophiles per Lycaenidae species. Error bars are 95% confidence intervals based on 9999 bootstrap randomizations.

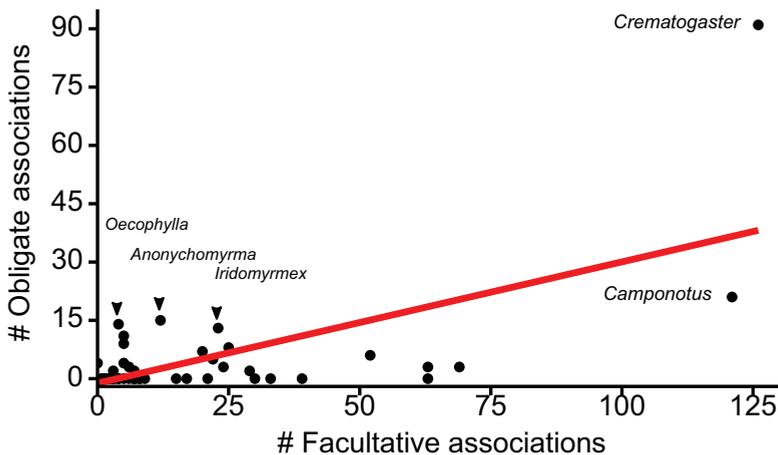


Figure 7. Representation of ant genera as hosts of obligately myrmecophilous lycaenid caterpillars, in relation to their frequency as visitors of facultative myrmecophiles. Each dot represents one ant genus. An OLS regression line is fitted into the data cloud for visual clarity. Ant genera below the regression line are under-represented, while those above the regression line are over-represented.

revealed the strongest dominance of one single ant genus, viz. *Crematogaster* in that case, accounting for almost half of all record pairs. In all other regions, the most prevalent ant genus accounted for only 15–25% of all available record pairs (Fig. 8b). *Crematogaster* ants were also the dominant visitors or hosts in the Oriental region (50 cases). This role was taken by *Iridomyrmex* in the Australian region (35), and by *Formica* in the Nearctic (26). In the Neotropical and Palearctic region, *Camponotus* ants were most frequently recorded at caterpillars (with 16 and 56 lycaenid species, respectively).

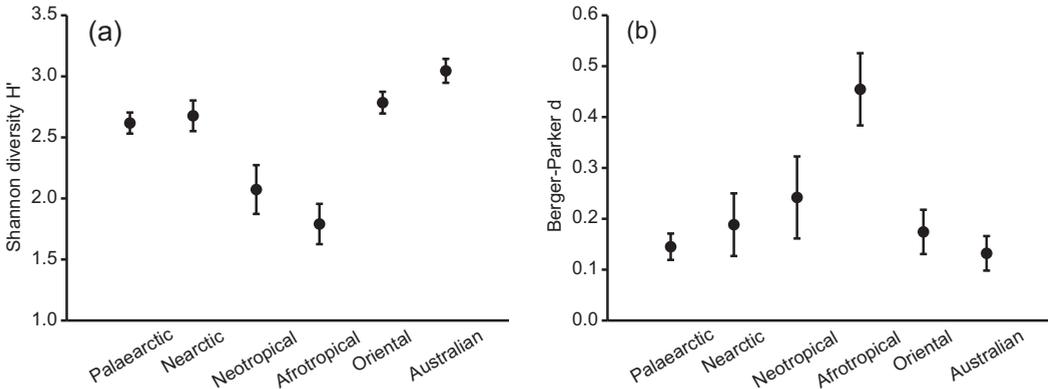


Figure 8. Diversity (a. measured as Shannon's H' metric) and dominance (b. expressed as Berger-Parker's d index) of recorded ant associations of Lycaenidae caterpillars across six biogeographical regions. Error bars denote 95% confidence intervals based on 9999 bootstrap replicates.

Discussion

Even though documentations of butterfly-ant interactions have substantially increased over the past 20 years, the global systematic, ecological, and biogeographical patterns to be recognized have turned out remarkably robust. Extrapolation analysis based on sample coverage suggests that further ant genera await discovery as visitors or hosts of lycaenid butterfly caterpillars, especially from still under-explored regions such as South America or tropical Africa. Yet, even a massive increase in records will likely just moderately augment the list of attendant ant genera. As expected, all recorded ant visitors and hosts belong to nectarivore or omnivore ant clades that frequently engage in trophobiosis with honeydew producing insects or in mutualism with plants bearing extrafloral nectaries. Based on signatures of stable C and N isotopes, many of these ants show a tendency towards “herbivorous” lifestyles, i.e. they are predacious on other insects only to a limited extent (Blüthgen et al. 2003; Feldhaar et al. 2010; Quinby et al. 2020).

Ants from just three subfamilies (Formicinae, Myrmicinae and Dolichoderinae) make up the vast majority (>98%) of recorded butterfly-ant associations. Within these subfamilies, only few genera are disproportionately represented. Globally, *Crematogaster* and *Camponotus* ants retain the top ranks. One important driver of that pattern are species-rich radiations of a few butterfly clades that maintain obligate, and in part parasitic, relationships with exactly these ants. Notable examples include the ant-parasitic genus *Lepidochrysops* in Africa (Espeland et al. in press) and the subfamily Aphnaeinae. The latter clade, with about 250 species distributed in Africa and southern to eastern Asia, shows strong co-evolution with its host ants, including multiple shifts to social parasitism and aphytophagy (Heath 1997; Boyle et al. 2015; Talavera et al. 2020), but in many cases bound to *Crematogaster* ants.

These features are also responsible for the strikingly low diversity of, and high dominance among, ant associations in the Afrotropical realm, where the preponderance of *Crematogaster* becomes most pronounced. If one were to include also the African Poritiinae into a similar analysis, the prevalence of *Crematogaster* would even increase further, since most species in the lichen-feeding tribes Liptenini and Epitolini appear to be associated with arboreal *Crematogaster* ant colonies (Larsen 2005).

Diversity of reported ant associations remained strikingly low for the Neotropical Lycaenidae species. Collectively, four arguments can be brought forward to explain that pattern. First, the life histories of South American lycaenids remain very incompletely documented, despite much research efforts in recent years, especially in Brazil (e.g. Bächtold et al. 2017 and references therein). Hence, a recording bias for sure still persists. Second, in the Neotropical region myrmecophilous caterpillars of many Riodinidae species occupy part of the ecological opportunities that elsewhere are exclusively held by lycaenids. Indeed, phylogenetic evidence suggests that not only myrmecophily in the Riodinidae evolved independently from the analogous associations in the Lycaenidae, but also that within the Riodinidae ant-associations evolved at least twice (Espeland et al. 2018). Recently, even parallel evolution of social parasitism with ants has been discovered among Neotropical Riodinidae (Kaminski et al. 2021). Therefore, various evolutionary options for myrmecophilous lycaenids might be pre-occupied by potentially competing riodinids. Third, most South American lycaenids belong to one single, though highly species-rich clade, namely the tribe Eumaeini (Robbins and Lamas 2004). In this tribe, caterpillars usually possess only a reduced set of ant organs (viz. they lack a pair of eversible tentacle organs, and in many species also the dorsal nectar gland is reduced). Fourth, ant assemblages in many Neotropical habitats are strongly dominated by two ant groups that never maintain trophobiotic associations with any other insects, viz. leafcutter ants and army ants (Hölldobler and Wilson 2010; Kronauer 2020). The frequent ecological dominance of these ants might further constrain the establishment of caterpillar-ant associations. Against this background, I hypothesise that even with much improved coverage of life-histories of Neotropical lycaenids the diversity of their ant associations will remain lower than in the Oriental or Australian faunal region. Nevertheless, South America is the most likely continent for the discovery of novel ant genera participating in caterpillar-ant interactions. For example, I predict that highly nectar-dependent *Cephalotes* ants (Hu et al. 2018; currently not recorded with any lycaenid species) will finally show up in the list of ant visitors at lycaenid larvae, as well as representatives of other omnivore or nectarivore genera like *Azteca* (thus far recorded only twice as visitors of lycaenids; see Brandão et al. (2012) for the functional diversity of Neotropical ants).

Some patterns in these associations may still be influenced by recording biases. For example, the over-representation of Holarctic ant genera like *Lasius* and *Formica* mirrors the ecological prevalence of these ants in northern temperate woodland and grassland biomes. Thus, for lepidopterists in Europe, Japan and North America these ants are the most likely visitors to be encountered when searching for lycaenid caterpillars in the field. However, many records published during the past two decades from the Mediterranean area (e.g. Lafranchis et al. 2007; Obregón-Romero and Gil-T. 2011; Obregón et al. 2015; Galanos 2020) have contributed to levelling out that bias and brought forward a much broader coverage of ant visitors at European lycaenid caterpillars.

On the other hand, especially in the Old World tropics a few ant genera remain under-represented. *Polyrhachis* ants, for example, are often highly trophobiotic, as also revealed by their isotopic signatures (Blüthgen et al. 2003). While additional associations between caterpillars and *Polyrhachis* ants have been recorded over the past two decades, they still lag behind what one might expect from their global species richness. Because *Polyrhachis* ants are usually arboreal, and often thrive in the canopy of tropical forests, the rather low representation of these ants might indicate a lack of coverage of lycaenid life-histories in that particular ecosystem. Insects of tropical tree crowns generally remain under-studied, and this also pertains to biota associated with social insects (Pérez-Lachaud and Lachaud 2014).

Facultative caterpillar-ant associations are essentially opportunistic and unpredictable. Those nectar-ivorous ants that dominate in a given ecosystem are also the most likely to be observed attending caterpillars, with further partitioning between ant species due to microhabitat preferences, times of day, and actual population densities. In contrast, more predictable patterns emerged among obligate myrmecophiles – with substantial parallels to host ant use among the rather few socially parasitic lycaenid clades (Fiedler 2012). Ecologically dominant ant species that form large and long-lived colonies are particularly rewarding hosts. These ants also harbour the largest arrays of myrmecophiles when it comes to nest inquilines (Parmentier et al. 2014; Parker 2016). This explains well the over-representation of rather species-poor, but highly dominant ants like *Oecophylla*, *Anonychomyrma*, or *Iridomyrmex*.

In recent years, invasive alien species have attracted ever more interest by ecologists, conservationists and evolutionary biologists alike (Kenis et al. 2009). Some of the most influential ‘neobiota’ are ants. For example, among the 100 ‘worst invasive species’ identified by the IUCN (Lowe et al. 2000) five ant species are listed, three of which (*Linepithema humile*, *Anoplolepis gracilipes* and *Pheidole megacephala*) are well represented as visitors of lycaenid caterpillars. Indeed, the strong increase in records of *Anoplolepis* as attendants of lycaenid caterpillars is entirely due to many new associations observed in tropical countries like India, Singapore, Indonesia or Australia. Other invasive ‘tramp’ ants (McGlynn 1999) frequently observed as attending lycaenid caterpillars include *Technomyrmex ‘albipes’*, *Tapinoma melanocephalum*, *Nylanderia bourbonica*, *Ochetellus glaber*, and *Paratrechina longicornis*. It has been commonly observed that invasive ants establish as efficient partners in generalized mutualistic interactions with other arthropods, while disruptions of mutualisms have often been reported in specific and highly co-evolved systems (Ness and Bronstein 2004; Toby Kiers et al. 2010). Very recently, also the reverse phenomenon has been recorded for the first time in butterfly-ant interactions: native *Lasius neoniger* ants in North America now attend caterpillars of an invasive lycaenid species, the European *Polyommatus icarus* that has become established in parts of the United States and Canada (Dexheimer et al. 2021).

In conclusion, the striking associations between lycaenid butterflies and ants continue to provide a fascinating topic from ecological as well as evolutionary perspectives. While we have arrived at a robust understanding of which ants, where, and why participate in these interactions, many facets await discovery, especially when it comes to elucidating hitherto completely unknown life histories. Still, for the majority of lycaenid species the intensity of their ant association remains insufficiently known and the identity of their interaction partners undisclosed. The present analysis, which would have been impossible without the recording efforts of many lepidopterists and citizen scientists around the world, therefore, is not only an attempt of a synthesis twenty years after a first such endeavour. It also aims at stimulating and inspiring colleagues to continue with “descriptive natural history” in the Anthropocene era of biodiversity loss and biotic homogenization.

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Supplementary material 1

Appendix S1

Authors: Konrad Fiedler

Data type: excel table.

Explanation note: Compilation of ant visitors or hosts recorded at 523 Lycaenidae species, where the taxonomic identity of ants has been documented at genus or species level. For each butterfly species its occurrence in gross biogeographical regions is also noted as a binary variable. In another column it is given whether the ant association is considered obligate (1) or not (0). The 10th column summarizes the number of ant genera involved in recorded interactions with each lycaenid species. The prefinal column contains the ant visitors or hosts, as they have been identified in the sources considered. It was impossible to validate whether all species level identifications are correct in view of current ant taxonomy. The final column gives the sources from which data on the identity of ant visitors or hosts were extracted. For a full bibliography see Suppl. material 2: Appendix S2.

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Link: <https://doi.org/10.3897/nl.44.68993.suppl1>

Supplementary material 2

Appendix S2

Authors: Konrad Fiedler

Data type: pdf-file.

Explanation note: List of published references (journal articles, book chapters and books) used to compile the list of ant visitors or hosts at 523 species of Lycaenidae butterflies.

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Link: <https://doi.org/10.3897/nl.44.68993.suppl2>

Systematics of *Problepsis wiltshirei* (Prout, 1938), comb. nov. (Lepidoptera, Geometridae, Sterrhinae) – an endemic species to the Zagros Mountains in the Middle East

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Abstract. Within Iran, the Zagros Mountains show high biodiversity, with a wealth of endemic species. One of these is the geometrid moth *Somatina wiltshirei* Prout, 1938, originally described from Iran and Iraq. In the present study, one mitochondrial and up to nine protein-coding nuclear gene regions were used along with a comparative morphological examination to investigate the systematic position of this species. The results support the reclassification of this species as *Problepsis wiltshirei* **comb. nov.** Since the original species description is superficial, we provide a re-description supported by rich illustrations of morphological characters and distribution. In addition, *Problepsis wiltshirei* **comb. nov.** is reported as a new species for the fauna of Turkey. The importance of the habitat for the conservation of this species is discussed.

Introduction

In the traditional classification of Scopulini (Geometridae: Sterrhinae), species were classified into genera based on the number of forewing areoles. Genera with one areole included *Problepsis* Lederer, 1853 and *Scopula* Schrank, 1802, and species with two areoles were classified in *Somatina* Guenée, [1858] (Prout 1934–1939). Sihvonen (2005) found evidence for the view that the number of areoles in the forewing is homoplastic and therefore not valuable as the only diagnostic character, as the state of two areoles also occurs in some *Problepsis* and *Scopula* species. Thus, even today, quite a few species are erroneously placed in the genus *Somatina*. Some of those have recently been reclassified (e.g., Sihvonen 2005; Xue et al. 2018; Sihvonen et al. 2020). However, the classification of other species within *Somatina* (sensu Sihvonen 2005) need to be re-examined.

The type species of *Somatina* is *S. anthophilata* Guenée, [1858] described from India. Scoble (1999) listed 50 species within the genus, mainly distributed in Africa, Asia and Australia. Recent phylogenetic studies showed that many *Somatina* species belong to other genera: In a morphological phylogenetic study, Sihvonen (2005) transferred four *Somatina* species to *Scopula*, namely *S. indicataria* (Walker, 1861), *S. mendicaria* (Leech, 1897), *S. microphylla* (Meyrick, 1889), *S. nucleata* (Warren, 1905) and two species to *Problepsis* (*P. centrophora* (Prout, 1915), *P.*

triozellata Bastelberger, 1908). *Scopula microphylla* and *P. triozellata* were classified in *Somatina* by Hausmann and Scoble (2007), who listed 46 species within this genus. Xue *et al.* (2018) transferred *Somatina transvehens* (Prout, 1918) to *Problepsis*.

In a multi-gene phylogenetic analysis, two more species were transferred from *Somatina* to *Problepsis* namely, *P. figurata* (Warren, 1897) and *P. vestalis* (Butler, 1875), consequently decreasing the number of *Somatina* species at present to 41 (Sihvonen *et al.* 2020).

Somatina species share the following morphological characters (after Sihvonen 2005, none of those are unique synapomorphies): weak discal spots on fore- and hindwing, forewing with two areoles. The male hind tibia is characterized by the presence of a hair pencil. The male genitalia are characterized by socii being not fused, and sacculi and valvuli being asymmetrical. The juxta bears wing-like processes on the anterior margin, with the apex fused to the sacculus of the valva. Sternite 8 in males is variable, x-shaped and with weakly developed or absent mappa, normally without cerata.

The genus *Problepsis* was described based on the type species *Caloptera ocellata* Frivaldszky, 1845 and belongs to Scopulini, the largest tribe within the subfamily Sterrhinae (Sihvonen 2005; Müller *et al.* 2019; Sihvonen *et al.* 2020). This genus currently comprises 53 species distributed in the Old World and Australia (Hausmann 2004; Sihvonen and Siljander 2005; Stadie and Stadie 2016; Feizpour *et al.* 2018; Xue *et al.* 2018).

Problepsis species share the following morphological characters (none of those are unique synapomorphies): ocellate discal spots on fore- and hindwing, forewing mainly with one areole, occasionally with two areoles (Hausmann 2004; Sihvonen 2005). The male hind tibia is laterally flattened, spoon-shaped and characterized by the presence of a hair pencil (Sihvonen 2005; Feizpour *et al.* 2018). The male genitalia are characterized by fused socii and a dentate or smooth ventral margin of the tegumen (Sihvonen 2005; Xue *et al.* 2018). Sternite 8 in males is elongated, the cerata are absent, rudimentary or fully developed; if present, then often fused to the mappa (Sihvonen 2005).

Recently, *Problepsis cinerea* (Butler 1886) was reported from the south Iranian province Hormozgan as the only species belonging to the genus *Problepsis* in Iran (Feizpour *et al.* 2018). Additionally, *Somatina wiltshirei* Prout, 1938 is the only species of the genus *Somatina* described from the Zagros Mountains in Iran and Iraq. Wiltshire (1957) considered *S. wiltshirei* to be restricted to the Zagros woodland belt.

The Zagros Mountains cover an area of 533,543 km², extending with a length of 2000 km from Eastern Turkey and Northern parts of Iraq to the whole Western and Southwestern parts of Iran (Mouthereau *et al.* 2011; Kazemi and Hosseinzadeh 2020). In Iran, these mountains show a high rate of endemism, including reptiles, amphibians and plants (Gholamifard 2011; Safaei-Mahroo *et al.* 2015; Noroozi *et al.* 2018; Kazemi and Hosseinzadeh 2020). Additionally, due to its location in low and middle latitudes (between 25–40°N) and milder climate conditions during the Last Glacial Maximum (LGM), this area played an important role as refugia for many biota (van Zeist and Bottema 1977; Rajaei *et al.* 2013; Ashrafzadeh *et al.* 2016; Mohammadi *et al.* 2021).

As a part of the revision of Iranian geometrid moths, the present study aims to clarify the systematic position of *S. wiltshirei*, using an integrative approach; to illustrate species-specific characters, and to give an overview of its distribution in the Zagros Mountains. To achieve this, we used a multi-gene molecular analysis along with the examination of external and internal morphological characters and distribution data. We also discuss the importance of the habitat for the conservation of this species.

Material and methods

Type specimens, as well as additional specimens used in this study, were borrowed and studied from the following collections (acronyms after Evenhuis 2007):

IMCA	Insect and Mite Collection Ahvaz University, Iran;
NHMUK	Natural History Museum London, United Kingdom;
PCPS	Private Collection of Pasi Sihvonen, Veikkola, Finland;
PCWW	Private Collection of Werner Wolf, Bindlach, Germany;
SMNK	Staatliches Museum für Naturkunde Karlsruhe, Germany;
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany;
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany;
ZSM	Zoologische Staatssammlung München, Germany.

Criteria for the selection of taxa

To test the combination of *Somatina wiltshirei* with the genus *Problepsis*, we studied type material of *S. wiltshirei*, type species of *Problepsis* (*P. ocellata*), and type species of *Somatina* (*S. anthophilata*) using morphological and molecular data, and additional specimens of both genera were used in the molecular analysis. Moreover, we included *P. cinerea* in our investigations, as it is the only species of the genus *Problepsis* in Iran (Feizpour et al. 2018). For the molecular analysis, already available other Scopulini data were used (Murillo-Ramos et al. 2019, Sihvonen et al. 2020). Lissoblemmini was proposed as sister to Scopulini in a previous phylogenetic study and therefore it was chosen as the outgroup in our study (Sihvonen et al. 2020).

Morphological examinations

Type material and original descriptions were used for the identification of specimens. Documentation and photography of external characters were carried out using a Visionary Digital photography system (LK Imaging System, Dun. Inc., equipped with a Canon EOS 5DSR) and an Olympus E3 digital camera. Preparation of the genitalia was carried out following standard methods (e.g., Robinson 1976). The vesica was everted following the method described by Sihvonen (2001). Photography of the genitalia characters before embedding took place following the methods proposed by Wanke and Rajaei (2018), Wanke et al. (2019) and Wanke et al. (2021) using a Keyence VHX-5000 digital microscope. Genitalia structures were finally embedded in Euparal and photographed using a Keyence VHX-5000 digital microscope.

The morphology of male and female antennae, as well as the male hind leg, were studied using a Zeiss Scanning Electron Microscope (SEM, EVO-LS15). Antennae and hind leg were mounted on holders and sputter-coated with 6 nm gold-palladium using a Leica coating system (EM ACE 200), before imaging with SEM.

For the drawing of the wing venation, wings were placed on a microscope slide and covered with a drop of ethanol (70–96%). In this setup, all venation is visible and can be photographed. For the photography, we used a Visionary Digital photography system (LK Imaging System, Dun. Inc., equipped with a Canon EOS 5DSR). In Graphic (vers. 3.1 for Mac) these photographs served as templates for the vector drawing of the wing venation by tracing the veins from it.

Molecular techniques

For the extraction of DNA, the whole abdomen and a leg from a single dry collection specimen were used following the manufacturer's protocol of the DNeasy Blood and Tissue kits (Qiagen, Hilden, Germany). Amplification of DNA was conducted following Wahlberg and Wheat (2008) and Wahlberg *et al.* (2016). We attempted to amplify one mitochondrial (cytochrome oxidase subunit I, COI) and up to nine protein-coding nuclear gene regions: Ribosomal Protein S5 (RpS5), wingless (*wgl*), cytosolic malate dehydrogenase (MDH), glyceraldehydes-3-phosphate dehydrogenase (GAPDH), Elongation factor 1 alpha (EF-1alpha), Arginine Kinase (ArgK), Isocitrate dehydrogenase (IDH), sorting nexin-9-like (Nex9), sarco/endoplasmic reticulum calcium ATPase (Ca-ATPase). Sequences were sent to Macrogen for sequencing. The Genbank accession numbers are provided in Appendix 1.

Phylogenetic analysis

In addition to the data generated in this study, we retrieved sequences of Scopulini taxa from the dataset of Sihvonen *et al.* (2020). The final dataset comprises 29 taxa. The concatenated length of the alignment was 6800 bp including gaps.

We ran maximum likelihood analyses with a data set partitioned by codon using RAxML-HPC2 V8.2.12 (Stamatakis 2014) on the web-server CIPRES Science Gateway (Miller *et al.* 2010). We implemented the GTR+CAT option, and support for nodes was evaluated with 1000 rapid bootstrap (RBS) (Stamatakis *et al.* 2008). The final tree was rooted with species of Lissoblemmini (Sihvonen *et al.* 2020). Trees were visualized and edited in FigTree v1.4.3 software (Rambaut 2012).

Distribution patterns

Tracing of geographical coordinates was conducted using 'Google Earth Pro' (vers. 7.3.3.7786 for Mac). Distribution patterns were plotted and prepared in QGIS (vers. 3.16.0 for Mac). The elevation profile in QGIS was prepared using Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) downloaded from <https://earthexplorer.usgs.gov>.

Results

In total, five genes of a single specimen of *S. wiltshirei*, six genes of a single specimen of *P. cinerea* and eight genes of a single specimen of *S. anthophilata* were successfully amplified and sequenced (see Appendix 1). As a result, *S. wiltshirei* clustered within the genus *Problepsis*, supporting its affiliation to this genus (Fig. 1). Additionally, according to the results of our morphological examination, *S. wiltshirei* shows the generic characters of the genus *Problepsis* (e.g., ocellate discal spots on the fore- and hindwing, the spoon-shaped hind tibia and the presence of a hair pencil in the male hind legs). The following morphological characters of the male genitalia also support the affiliation with *Problepsis*: fused socii and a smooth internal margin of the tegumen (compared against morphological data in Sihvonen 2005; Feizpour *et al.* 2018; Xue *et al.* 2018; Sihvonen *et al.* 2020) (see Figs 15–17). A re-description of this species is given in the taxonomy part of the discussion.

Discussion

Systematics

In sense of the traditional classifications of the genera *Problepsis* and *Somatina*, the latter genus was regarded as polyphyletic (see Sihvonen 2005). Recent studies based on morphology (Sihvonen

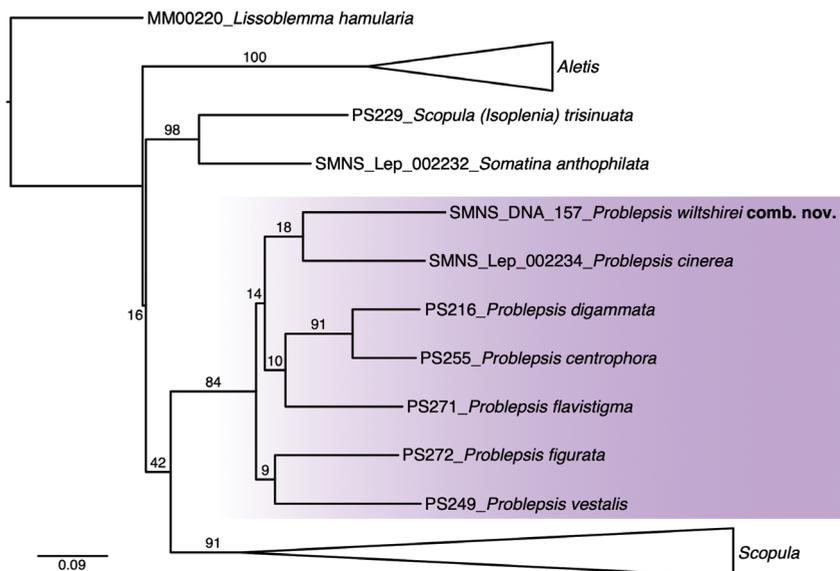


Figure 1. Phylogenetic position of *Problepsis wiltshirei* comb. nov. within the tribe Scopulini, supporting its combination in genus *Problepsis*. The numbers above the branches are Rapid Bootstrap support (RBS) on the best scoring ML tree (Stamatakis 2008). Values ≥ 85 (%) indicate supported clades.

2005; Xue et al. 2018), as well as multi-gene phylogenetic studies, resulted in the assignment of several *Somatina* species to *Problepsis* (Sihvonen et al. 2020). These results support the possibility of the monophyly of the genus *Somatina*, when non-*Somatina* species are reclassified (Sihvonen 2005; Xue et al. 2018; Sihvonen et al. 2020). In addition, Sihvonen (2005) identified three non-unique synapomorphies for *Somatina*, which support its monophyly (asymmetrical sacculi of valvae; asymmetrical valvuli of valvae; juxta with wing-like processes on anterior margin, with apex fused to sacculus of valva) (compare also Figs 15–17).

Our present results show *S. wiltshirei* nested within *Problepsis* (RBS = 84). Therefore, we transfer *S. wiltshirei* from *Somatina* to *Problepsis* comb. nov. Among the species included in our phylogenetic hypothesis, *P. cinerea* was recovered with low support as the sister species to *P. wiltshirei* (RBS = 18).

Additional *Problepsis* species and possibly more genetic data are needed to find the most closely related species of *P. wiltshirei*. Based on COI sequences, as available on BOLD database, the genetically closest neighbour of *P. wiltshirei* are *P. ocellata* and *P. cinerea*. Both with a genetic distance of 4.2%, calculated using K2P model: Kimura (1980) with MEGA X (Kumar et al. 2018; Stecher et al. 2020).

Taxonomy

Problepsis wiltshirei (Prout, 1938), comb. nov.

Figs 2–9, 14B, 15, 18, 21–25

Somatina wiltshirei Prout, 1938. In: Seitz, A. (Ed.), Die Großschmetterlinge der Erde. Supplement zu Band 4, 220. 2 ♂ Syntypes (Iraq: Kurdistan, Rowanduz [Rowanduz Gorge], Berserini [Berserini Gorge]) examined based on photo; 1 Syntype specimen [sex is not given in the original publication], [Iran]: Fars, Ardekan Talochosroe [Tall Khosrow, today in prov. Kohgiluyeh and Boyer-Ahmad] (in NHMUK).

Material examined. 2 ♀, Iran, Esfahan, Gandoman S, Gerdeish-e, 200 m, 12./13.vi.2002, leg. J.-U. Meineke, A. Hofmann, Kallies et al., g.preps 0759, 0760/2020 D. Wanke; 1 ♀, Iran, Khuzestan [now Kohgiluyeh va Boyerahmad], Yassoudj [Yasuj], Sisakht, 2250 m, 13.vi.1972, leg. Ebert, Pazouki; 1 ♂, 2 ♀, same data, 13.–14.vi.1972, leg. Ebert & Falkner, g.prep. (♂) 0762/2020 D. Wanke; 2 ♂, same data, Sisakht 50 km NW, 15.–18.vi.1975, leg. Ebert, Falkner, g.prep. 0761/2020 D. Wanke; 1 ♂, same data, 15 km SE Yassudj [Yasuj], 2050 m, 15.vi.1972, leg. Ebert & Falkner, g.prep. 0907/2020 D. Wanke; 1 ♂, S-Iran, Prov. Fars, Tange Surkh, 50 km NW Ardekan, 2250 m NN, 12.–15.vi.1975, leg. Ebert, Falkner; 2 ♂, S-Iran, Fars, Daschte Ardjan, Kotal-Pirehsan, 2000 m, 18.vi.1972, leg. Ebert & Falkner; 1 ♀, S-Iran, Miyān-Kotal, östl. Kazerun, 51°40'E, 29°30'N, 1900 m, 4.–7.vi.1969, leg. G. Ebert; 1 ♀, S-Iran, Fars, Kaserun, Mian-Kotal, 1900 m, 11.vi.1972, leg. Ebert & Falkner; all in SMNK.

1 ♀, Iran, Kohkiluyeh va Boyerahmad, Yasuj, Sisakht, Dena, 2799 m, 30°57'23.6"N, 51°23'28.9"E, 30.vii.2016, leg. Sh. Feizpour, g.prep. 0712/2020 D. Wanke; in SMNS.

1 ♂/♀, Iran, Khuzestan, Emamzadeh, Abdollah-low altitude; Saite 4b, 31°22'24"N, 50°7'51"E, 1408 m, 23.ix.2018, Trap1, leg. Mohammad Ahmadi; 1 ♂/♀, Iran, Khuzestan, Emamzadeh, Abdollah-high altitude; Saite 4a, 31°23'10"N, 50°9'29"E, 2120 m, 13.vii.2018, Trap 2, leg. Mohammad Ahmadi; 1 ♂/♀, Iran, Prov. Khuzestan, Mal aqa, 1100 m, 31°35'57"N, 50°00'50"E, 30.vii.2011, leg. Mehdi Esfandiari; 1 ♂/♀, Iran, Prov. Fars, Bolhayat & Kotal-e-Pirzan, 2000 m, 29°36'48"N, 51°56'28"E, 2. & 9.vi.2011, leg. Mehdi Esfandiari; 1 ♂/♀, Iran, Prov. Fars, Kohmare Sorkhi, 1900 m, 29°28'11"N, 52°08'44"E, 28.iv.2011, leg. Mehdi Esfandiari; all in IMCA.

1 ♀, Türkei [Turkey], prov. Hakkari, Çığıl Suyu-Tal [Zap-Tal], 22 km SW Hakkari, 28.vi.1984, LF, leg. Werner Wolf; in PCWW.

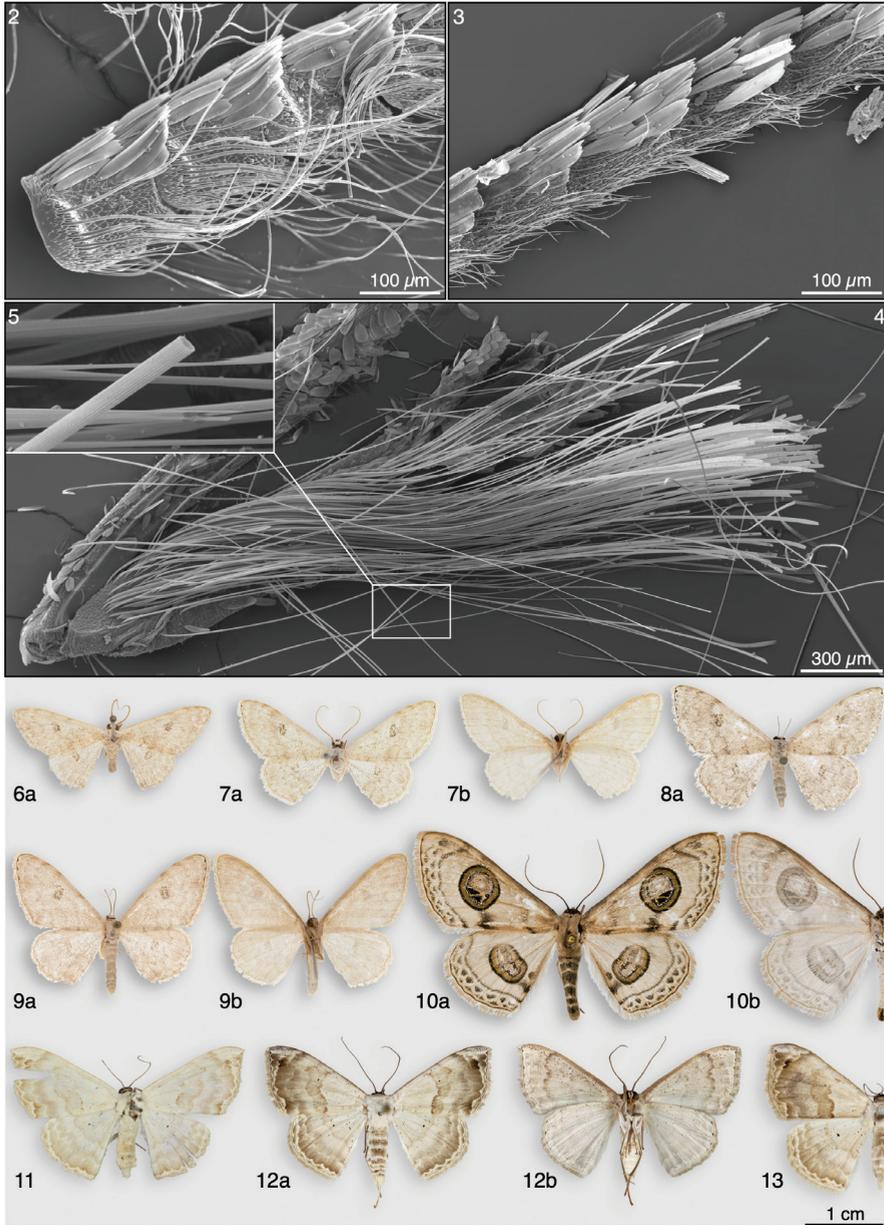
1 ♂, 1 ♀, Iran, Fars, Straße Ardekan-Talochosroe [Tall Khosrow, today in prov. Kohgiluyeh und Boyer Ahmad], Comé [Komehr], 7.viii.1937, 2600 m, coll. Brandt; in ZFMK.

1 ♂, Iran, Fars, Straße Ardekan-Talochosroe [Tall Khosrow, today in prov. Kohgiluyeh und Boyer Ahmad], Comée [Komehr], 2600 m, viii.1937, coll. Brandt, ZSM g.prep. No. 1602; in ZSM.

Re-description. Wings and body (Figs 2–9). Wingspan ♂ 24–28 mm, ♀ 29–32 mm; females slightly larger than males. The proboscis well developed. The length of the labial palpi about equal to the diameter of the eye. Frons, thorax and abdomen concolorous with the wings. Chaetosemata arranged as two patches. Antennae ciliate-fasciculate in males and filiform in females (Figs 2, 3). Male hind tibia with reduced tarsal segments; flattened laterally; longitudinally spoon-shaped; with hair pencil. Hair pencil consisting of two types of differently modified scales as illustrated for *P. cinerea* by Feizpour et al. (2018). One type of scales apically flattened, while the other scales are tubular and hollow (Figs 4, 5). Ground colour of wings beige, intermixed with some slightly darker ochreous or brown scales; basal areas slightly lighter beige. Fore- and hindwing with a small, light yellowish ocellus, bordered with a thin dark outer line. Discal spots sometimes not visible; more pronounced in the forewings (Figs 6–9).

Venation (Fig. 14B). Two areoles present in forewing. Veins R1, the common stalk of R2–4 and R5 arising from the second areole. In hindwing Sc+R1 slightly curved in basal area, approximating to the cell in the postbasal area; A1+2 originating separately; A3 absent.

Male genitalia (Fig. 15). Uncus absent. Socii strongly developed fused at apex. Internal margin of tegumen smooth. Valva with two curved arms (dorsal and ventral arm of valva), both sclerotized, narrow and long, apically pointed (Fig. 15a, d). Aedeagus strongly sclerotized, slender, tapering towards the apex; its basal part dorso-ventrally flattened; vesica without cornuti (Fig. 15b). Sternum A8: anterior margin with two indentations; lateroanteriorly on both sides pointed. Lateral sides towards posterior part concave; posterior margin curved. Cerata located in posterior half of sternum A8, directed towards centre (Fig. 15c).



Figures 2–13. Morphological characters of Iranian *Problepsis* species and *Somatina anthophilata*. 2–5. SEM photos of *Problepsis wiltshirei* comb. nov.; 2. Part of ciliate-fasciculate antennae of male (Iran, Yasuj, Sisakht, g.prep. 0762/2020 D. Wanke); 3. Detail of filiform antennae of female (Iran, Fars, Mian-Kotal); 4. Male hind tibia with hair pencil (Iran, Yasuj, Sisakht, g.prep. 0761/2020 D. Wanke); 5. Close up on tubular and hollow modified scale of hair pencil (Iran, Yasuj, Sisakht, g.prep. 0761/2020 D. Wanke); 6–9. Wing pattern of *Problepsis wiltshirei* comb. nov.; 6. Male paratype (Iraq, Kurdistan, Berserini); 7. Male (Iran, Fars, Straße Ardekan-Talochosroe, g. prep. 1602 ZSM); 8. Female (Iran, Yasuj, Sisakht, g.prep. 0712/2020 D. Wanke); 9. Male (Iran, Yasuj, Sisakht, g.prep. 0761/2020 D. Wanke); 10. Female of *Problepsis cinerea* (Iran, Hormozgan, Geno protected area); 11–13. Wing pattern of *S. anthophilata*; 11. Paralectotype (India); 12. Male (Thailand, Lampang, Muban Phichai); 13. Female (Thailand, Lampang, Muban Phichai). a = upperside; b = underside.

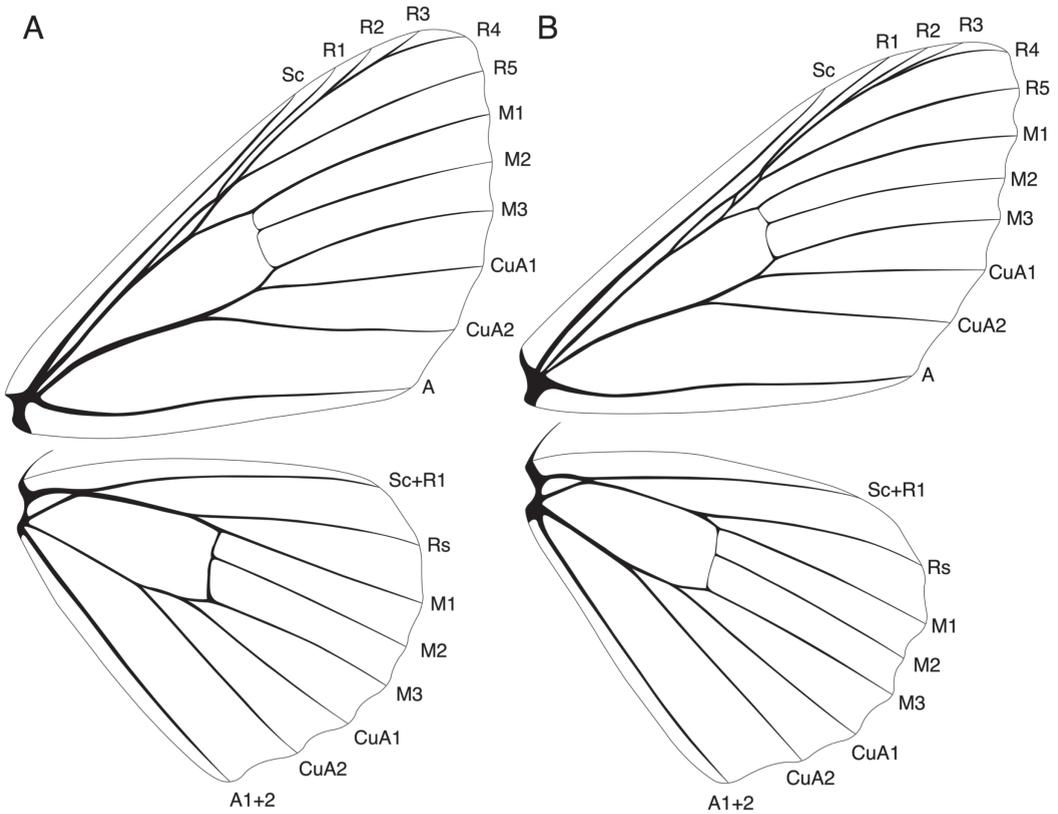


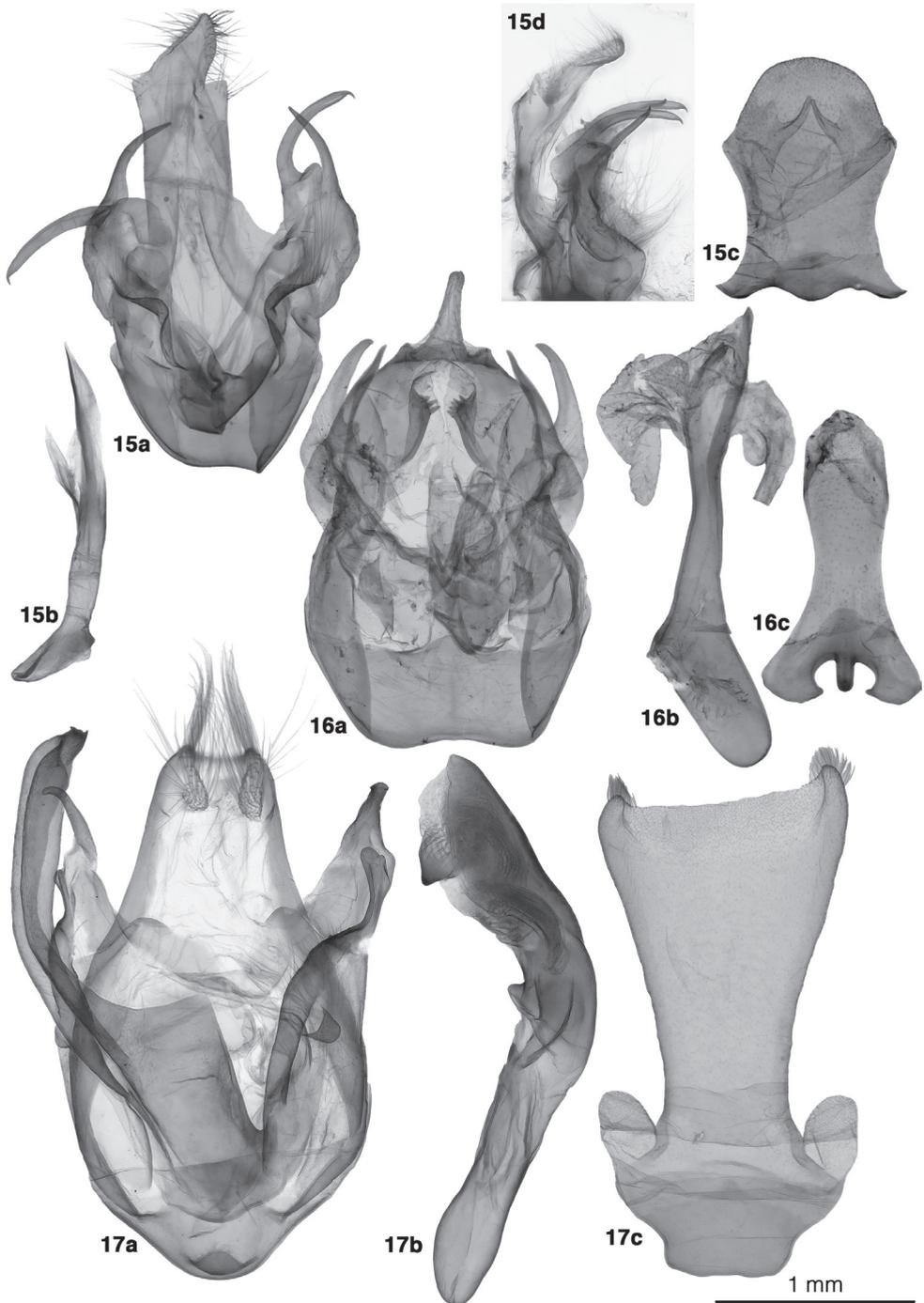
Figure 14. Wing venation of male specimens of *Problepsis* species; **A.** *Problepsis ocellata* (type species for the genus) and **B.** *Problepsis wiltshirei* comb. nov. Note: *Problepsis ocellata* (**A.**) with one areole in the forewing and *Problepsis wiltshirei* comb. nov. (**B.**) with two areoles in the forewing.

Female genitalia (Fig. 18). Papillae anales short and broad. Apophyses anteriores $2/3$ length of apophyses posteriores. Antrum strongly sclerotized. Lamella antevaginalis strongly sclerotized; basal part broad, laterally extended; posteriorly curved, folded, tapered to lateral side. Ductus bursae short, strongly sclerotized. Corpus bursae membranous; signum present as a sclerotized, narrow and dentate ridge.

Diagnosis. *P. wiltshirei* cannot be confused with any other *Problepsis* or *Somatina* species within this region. In Iran only *Problepsis cinerea* is known from South Iran and it does not occur within the range of *P. wiltshirei* comb. nov. Additionally, it cannot be confused with this species, as it differs strongly by wing pattern (see Figs 6–10) and by genitalia (Figs 16, 19). *Somatina pythiaria nigrimacula* Hausmann, 2009; a species distributed in Oman has been shown differing by a greyer suffusion on wing pattern, the different structure of the sternum A8 and molecular data (Hausmann 2009).

Phenology. Flying from July to October, possibly in two generations (Wiltshire 1943). This coincides with the investigated specimens, but can be expanded from April to October.

Biology. Larva described by Wiltshire (1943) as grayish, intermixed with a complex pattern of grey dots and marks. Pale grey dorsal and ventral lines, the latter rather whitish on somites 4–8. Pupal period lasting 8 to 15 days. The cocoon is woven between leaves and litter (Wiltshire 1943).



Figures 15–17. Male genitalia of Iranian *Problepsis* species and *Somatina anthophilata*; **15.** *Problepsis wiltshirei* comb. nov. (**a.** Iran, Yasuj, Sisakht, g.prep. 0762/2020 D. Wanke; **b, c.** Iran, Yasuj, Sisakht, g.prep. 0761/2020 D. Wanke; **d.** Iran, Yasuj, g.prep. 0907/2020 D. Wanke); **16.** *Problepsis cinerea* (**a–c.** Pakistan, Kaghan-Tal, 375/2017, S. Feizpour); **17.** *Somatina anthophilata* (**a–c.** Thailand, Lampang, Chae Hom, g.prep. 1177/2021 D. Wanke). a = genitalia capsule; b = aedeagus; c = sternum A8; d = genitalia capsule lateral view.

Wiltshire (1943) noted *Fraxinus* sp. (Oleaceae) and *Acer* sp. (Sapindaceae) as food plants for *P. wiltshirei*. As *Problepsis* species have been observed feeding on Oleaceae species (Robinson *et al.* 2002; Stadie and Stadie 2016) *Acer* sp. is an exceptional food plant, which needs confirmation.

Habitat. This species occurs in the Middle Heights of the mountains, especially the woodland zone (Wiltshire 1957) and mountain steppe, at elevations from 1100 m up to 2800 m (Figs 21–25). The habitat is covered with different herbaceous plants and shrubs, dominated by *Prunus* sp. (Rosaceae), *Artemisia* sp. (Asteraceae), *Astragalus* sp. (Fabaceae) and *Acantholimon* sp. (Plumbaginaceae).

Distribution. So far recorded in the Zagros Mountains, from northern Iraq (Kurdistan) into south-western Iran (Kohgiluyeh-va-Boyer-Ahmad and across the border to the provinces, Khuzestan, Esfahan and Fars) (Fig. 25). Additionally, here we record this species for the first time for the fauna of Turkey (see examined material). The large gap between the populations in northern Iraq, Turkey and central Zagros in Iran is possibly caused by insufficient sampling in these areas.

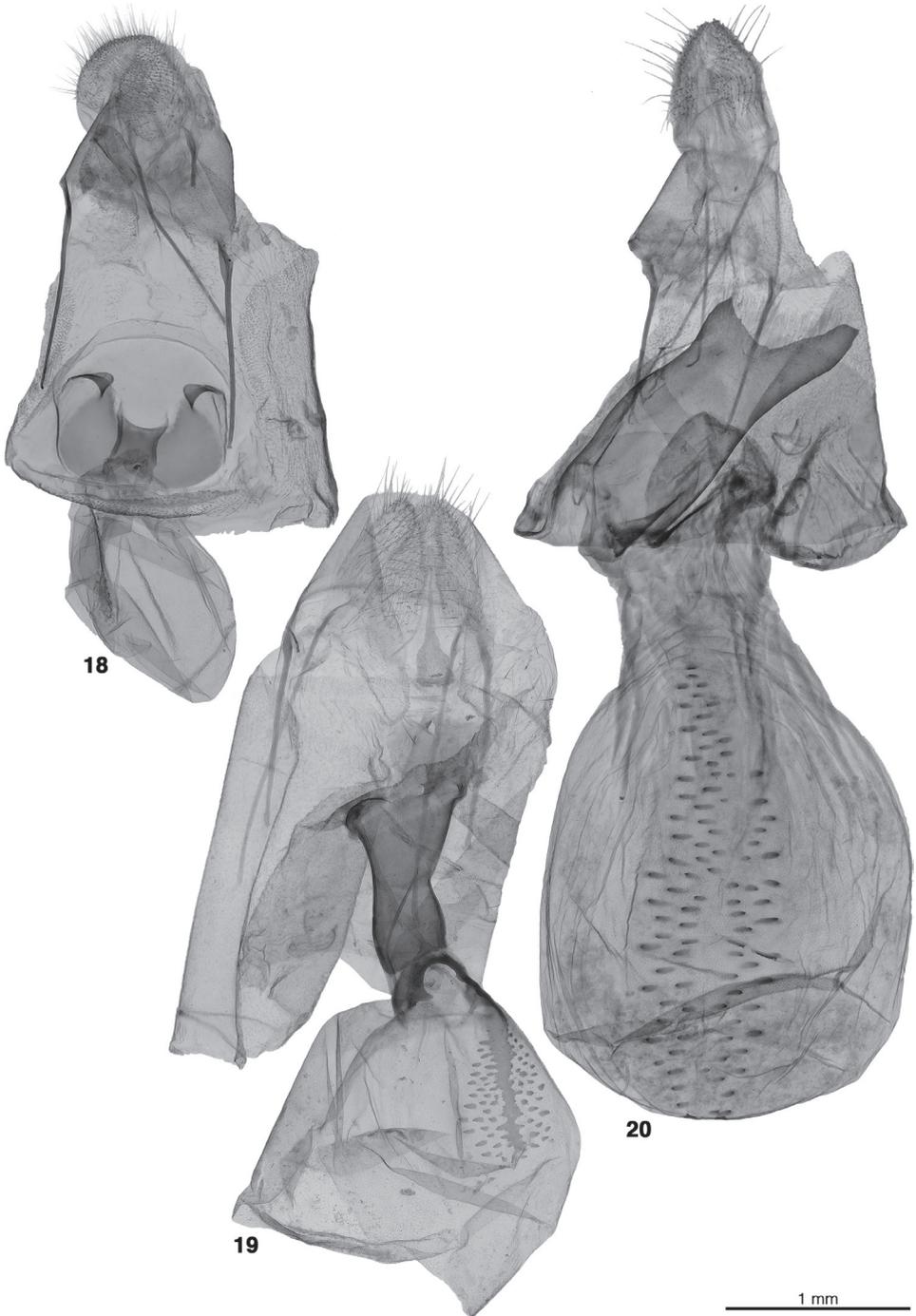
Zagros Mountains as a refuge for *Problepsis wiltshirei*

Major issues in conservation biology for protection efforts are the identification of areas with high biodiversity, high rates of endemism and past events, like glacial refugia or environmental changes (Médail and Diadema 2009; Cañadas *et al.* 2014; Noroozi *et al.* 2018; Kazemi and Hosseinzadeh 2020).

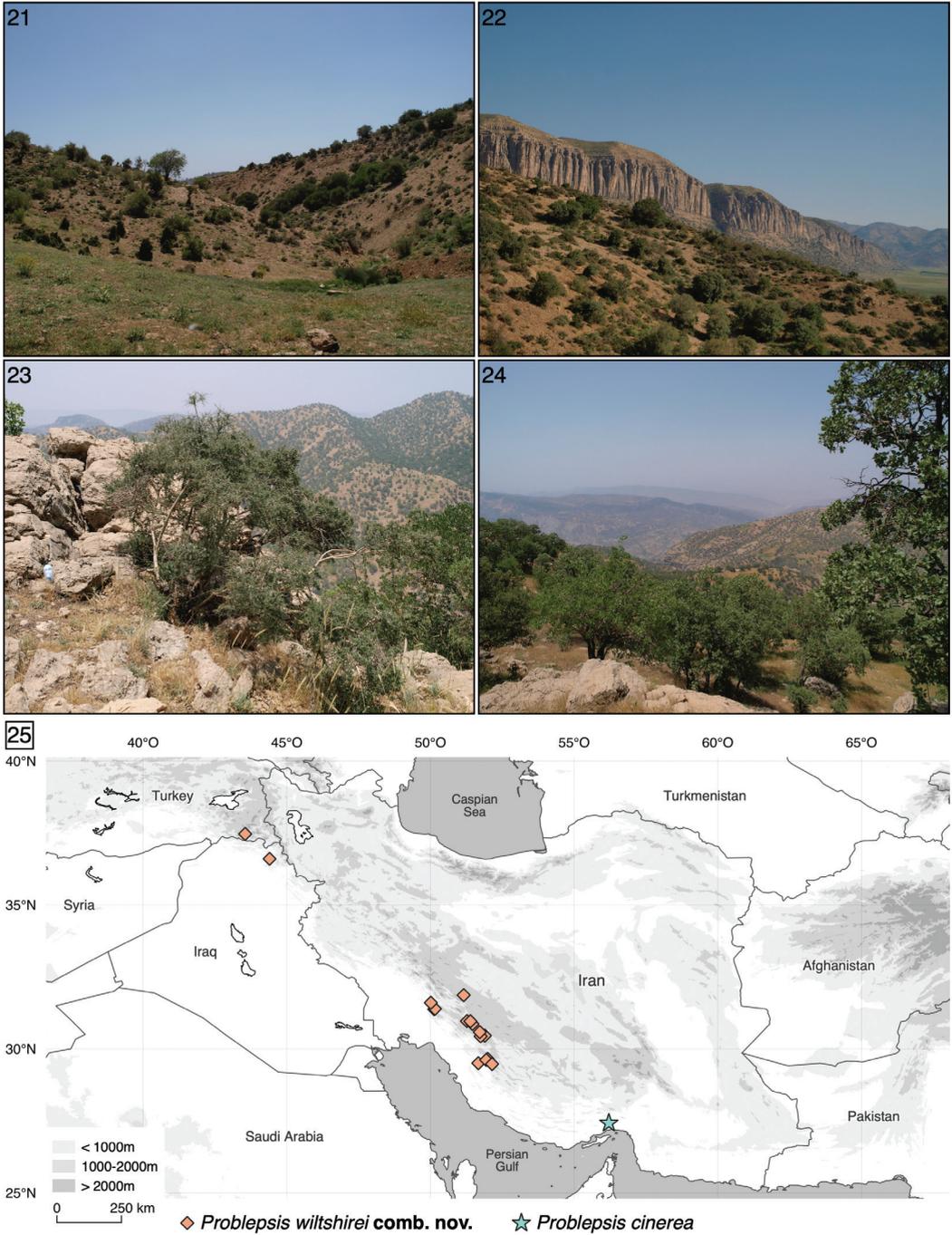
The Zagros Mountains have been identified as an area with a high species diversity of flora and fauna (Rechinger 1963–2015; Firouz 2005; Noroozi *et al.* 2008; Sayadi and Mehrabian 2016). Akbarirad *et al.* (2016) showed that brush-tailed mice of the genus *Calomyscus* (Calomyscidae: Rodentia) are highly diverse, due to the topography of these mountains which cause their geographic isolation. Similar findings were made for the Iranian herpetofauna, where the mountains and their diverse environmental conditions play an important role in the separation and isolation of species (Gholamifard 2011; Kazemi and Hosseinzadeh 2020). The important role of the Zagros Mountains can also be seen through various groups of arthropods (e.g., Paknia *et al.* 2008; Marusik and Zamani 2015; Zamani *et al.* 2018). For Lepidoptera, high species diversity of different families has been observed in the Zagros Mountains (e.g., Nazari 2003; Trusch and Hausmann 2008; Rajaei *et al.* 2012; Tshikolovets *et al.* 2014; Keil 2015; Yakovlev 2015; Wanke *et al.* 2020).

Regarding the endemism rate, the Zagros Mountains show the highest richness compared to other Iranian mountain ranges (Akhani 2004; Noroozi *et al.* 2016; Kazemi and Hosseinzadeh 2020; Khajoei Nasab and Khosavi 2020). It has been shown that 45% of Zagros vascular plants are restricted to this region (Noroozi *et al.* 2019). Additionally, this applies to endemic alpine plant species, where the highest rates of endemism were found in the Zagros (Noroozi *et al.* 2016). Comparably high endemism has been found in Lepidoptera (e.g., Rajaei 2012; Tshikolovets *et al.* 2014; Keil 2015).

Moreover, the Zagros Mountains have played a crucial role as a refuge for diverse fauna and flora during glaciation events. Malekoutian *et al.* (2020) found in a phylogeographic analysis, the occurrence of the Yellow-spotted Mountain Newt (*Neurergus derjugini*) derives from three different refugia in the Zagros mountains. Similar findings for the survival of Iranian Brown Bears (*Ursus arctos*) in Zagros refugia during the Last Glacial Maximum (LGM) were proved by Ashrafzadeh *et al.* (2016). Based on genetic and paleo-bioclimatic data, Rajaei *et al.* (2013) found this region to be a refuge for two *Gnopharmia* species and their host plants (*Prunus scoparia*) during the LGM (23,000–18,000 years ago). Furthermore, it has been shown that the highest haplotype diversity of these two *Gnopharmia* species is present in southwestern parts of the Zagros Mountains and served as a population source for the postglacial expansion of these species (Rajaei *et al.* 2013).



Figures 18–20. Female genitalia of Iranian *Problepsis* species and *Somatina anthophilata*; **18.** *Problepsis wiltshirei* comb. nov. (Iran, Esfahan, Gandoman, g.prep. 0759/2020 D. Wanke); **19.** *Problepsis cinerea* (g.prep. 374/2017, S. Feizpour); **20.** *Somatina anthophilata* (Thailand, Lampang, Muban Phichai, g.prep. 1176/2021 D. Wanke).



Figures 21–25. Habitat in the Zagros Mountains and distribution map of Iranian *Problepsis* species; 21, 22. Iran, Fars, Dasht-e Arjan at 2158 m altitude; 23, 24. Iran, Kohkiluyeh va Boyer-Ahmad, Tange-Tamoradi at 2254 m altitude; 25. Distribution pattern of Iranian *Problepsis* species.

The results of our study confirm that *P. wiltshirei* is an endemic species in the Zagros mountains and has so far been restricted to two areas of this mountain range. The first area in northern Iraq and south-eastern of Turkey falls into the Irano-Anatolian biodiversity hotspot, a region of remarkable species endemism, covering high elevations of central and eastern Turkey, Armenia, NE Iraq and Iran (Mittermeier et al. 1999; Noroozi et al. 2018). In its second area of distribution, *P. wiltshirei* inhabits the southwestern parts of the Zagros Mountains, a habitat outstanding for its rich biodiversity (e.g., Hosseinzadeh et al. 2014; Farashi and Shariati 2017; Noroozi et al. 2018).

Although several areas are protected in the Zagros Mountains (e.g., Arjan, Bakhtegan, Karkheh, Bamu etc.), this unique nature reserve is currently threatened, mainly by human activity. Every year 15,000 ha of Iranian forests burn (in 2020 wildfires burned down over 50,000 ha of oak forests in the Zagros Mountains) and centuries-old trees are destroyed in the process (Kheshti 2020). In ecosystems such as the Zagros Mountains, these high fire intensities threaten its species diversity and richness (Heydari et al. 2016). Further threats to biodiversity are overgrazing by sheep and goats in the marginal arid areas, as well as the land erosion caused by agriculture (Jowkar et al. 2016). Also, poaching and sporadic poisoning of animals occurs from time to time, even within protected areas, causing significant damage to its fauna (Jowkar et al. 2016). *P. wiltshirei* is distributed in this threatened area of high biodiversity and we still know only very little about its distribution and biology. Our study emphasizes the importance of further investigations of the Lepidoptera fauna of the Zagros, to better understand biodiversity hotspots and areas of endemism in the context of species conservation.

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Appendix 1

Table A1. Sterrhinae taxa used in this study, with identification, process code, and GenBank accession numbers for each gene. Data from Sihvonen *et al.* (2020)⁽¹⁾ & Wanke *et al.* (current paper)⁽²⁾.

Taxon identification	Code	ArgK	Ca-ATPase	COL-begin	COL-end	EF1a-begin	EF1a-end	GAPDH	IDH	MDH	Nex9	RpS5	WntGeo
<i>Lissolemma hamularia</i> ⁽¹⁾	MM00220	–	–	JF784708	–	–	JF785331	–	–	–	–	–	–
<i>Aletis helcia</i> ⁽¹⁾	PS268	MK738556	MK738887	MK739619	–	MK740001	MK740001	MK740647	–	–	MK741674	MK742030	MK742585
<i>Aletis monteiromis</i> ⁽¹⁾	PS270	MK738557	MK738888	MK739620	–	–	–	–	–	–	–	–	MK742586
<i>Aletis variabilis</i> ⁽¹⁾	0x17	–	–	MG767890	MG767890	–	MG768276	MG767671	–	–	–	MG767479	MG767344
<i>Aletis forbesi</i> ⁽¹⁾	0x28	–	–	MG767889	MG767889	–	MG768275	–	–	–	–	MG767478	MG767343
<i>Scopula (Isopenia) trisnuata</i> ⁽¹⁾	PS229	–	MK738851	MK739391	MK739391	MK739967	MK739967	MK740614	MK740872	MK741191	MK741640	MK742000	MK742550
<i>Somatina amphiphilata</i> ⁽²⁾	SMNS_L.ep_002232	MZ798167	MZ798169	MZ753906	MZ753906	MZ798171	MZ798171	–	MZ798173	MZ798174	–	MZ798175	MZ798177
<i>Problepsis wiltshirei</i> ⁽²⁾	SMNS-DNA-157	MZ798179	–	MW803363	–	MW803364	MW803364	–	–	–	–	MW803365	MW842913
<i>Problepsis cinerea</i> ⁽²⁾	SMNS_L.ep_002234	MZ798168	MZ798170	MZ753905	–	MZ798172	MZ798172	–	–	–	–	MZ798176	MZ798178
<i>Problepsis vestalis</i> ⁽¹⁾	PS249	MK738538	MK738869	MK739406	MK739406	MK739983	MK739983	MK740630	MK740881	–	MK741657	MK742014	MK742568
<i>Problepsis figurata</i> ⁽¹⁾	PS272	MK738559	MK738890	MK739424	MK739424	MK740003	MK740003	MK740649	–	–	MK741676	MK742032	MK742588
<i>Problepsis flavistigma</i> ⁽¹⁾	PS271	MK738558	MK738889	MK739423	MK739423	MK740002	MK740002	MK740648	MK740896	–	MK741675	MK742031	MK742587
<i>Problepsis digamma</i> ⁽¹⁾	PS216	MK738512	MK738839	MK739614	–	MK739958	MK739958	MK740605	MK740860	MK741179	MK741628	MK741990	MK742538
<i>Problepsis centrophora</i> ⁽¹⁾	PS255	MK738544	MK738875	MK739411	MK739411	MK739989	MK739989	MK740636	MK740886	–	MK741663	MK742019	MK742573
<i>Scopula nemorivagata</i> ⁽¹⁾	PS232	MK738524	MK738853	MK739616	–	MK739968	MK739968	MK740616	–	MK741193	MK741642	MK742001	MK742552
<i>Scopula johnsoni</i> ⁽¹⁾	R1872	–	–	MG767915	MG767915	–	MG768299	–	MG768488	MG768103	–	MG767500	MG767348
<i>Scopula tenera</i> ⁽¹⁾	SH1155	–	–	MG767781	MG767781	MG768176	MG768176	–	MG768396	MG768017	–	MG767408	–
<i>Scopula immorata</i> ⁽¹⁾	MM00586	–	–	GU828645	GU828645	GU829261	GU829261	–	GU830032	GU830351	–	GU830646	GU829536
<i>Scopula nr karischii</i> ⁽¹⁾	SH0432	–	–	MG767773	MG767773	MG767773	MG767773	MG767575	MG768391	MG768013	–	MG767404	–
<i>Scopula punctilineata</i> ⁽¹⁾	PS251	MK738540	MK738871	MK739407	MK739407	MK739985	MK739985	MK740632	MK740883	–	MK741659	MK742016	MK742570
<i>Scopula nr laevipennis</i> ⁽¹⁾	R1050	–	–	MG767897	MG767897	MG768281	MG768281	MG767677	–	–	–	–	–
<i>Scopula nr vitellina</i> ⁽¹⁾	SH0448	–	–	MG767771	MG767771	MG768168	MG768168	MG767573	MG768389	MG768011	–	MG767402	–
<i>Scopula sp.</i> ⁽¹⁾	PS241	MK738532	MK738861	MK739617	–	MK739976	MK739976	MK740623	–	MK741201	MK741650	MK742008	MK742560
<i>Scopula nr calcarata</i> ⁽¹⁾	SH0421	–	–	MG767770	MG767770	MG768167	MG768167	–	MG768388	MG768010	–	MG767401	MG767318
<i>Scopula nr serena</i> ⁽¹⁾	PS 243	MK738533	MK738863	MK739618	–	MK739978	MK739978	MK740625	–	MK741203	MK741652	MK742010	MK742562
<i>Scopula amata</i> ⁽¹⁾	LUSNN664273	–	–	KY370874	–	–	–	–	–	–	–	LT674233	LT674262
<i>Scopula nr nigrintotata</i> ⁽¹⁾	PS262	MK738550	MK738881	MK739417	MK739417	MK739995	MK739995	MK740642	MK740892	–	MK741668	MK742024	MK742579
<i>Scopula ternaia</i> ⁽¹⁾	MM08463	–	–	MK739598	–	–	–	MK740574	–	MK741142	–	MK741945	–
<i>Scopula frigidaria</i> ⁽¹⁾	MM10459	–	–	–	–	–	–	–	–	MK741144	–	MK741947	MK742493

Tabwecala robinsoni gen. nov., sp. nov., from Vanuatu and its systematic position in the ‘Ophiusini-Poaphilini’ clade (Lepidoptera, Erebidae)

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Abstract. A new erebid, *Tabwecala robinsoni* gen. nov., sp. nov., from the Vanuatu Islands (Espiritu Santo) (West Pacific Ocean) is described. The new species, superficially resembling species of the genera *Artena*, *Achaea* or *Leistera*, shows a peculiar combination of characters which suggested its placement in a new genus. This is provisionally placed in tribe Poaphilini but following a review of the features purporting to show the separation of Ophiusini and Poaphilini, it is shown that morphological rationale supporting the current arrangement of these tribes is still lacking. Noteworthy modifications affect the hindleg of male *Tabwecala robinsoni*, with greatly shortened and swollen metatibia bearing a dorsal hair-pencil.

Introduction

Following an analysis of the macrolepidoptera of the archipelago of Vanuatu (formerly known as New Hebrides), Robinson (1976) recorded 29% of the species as endemic (105/364). However, based on the relatively young age of the islands and because, compared to e.g. New Caledonia and Fiji, no groups showed radiation into species complexes, he concluded that the moth fauna of Vanuatu was “recent and derived solely by transoceanic dispersal”. It is also worth noting that only one endemic (and undescribed) genus from Vanuatu was known to Robinson (1976), which may be taken as a proxy of low overall morphological diversification in the islands and hence as additional evidence for their comparatively recent faunal settlement. Substantially similar figures can be drawn from Bradley’s (1962) review of the microlepidoptera from Aneityum, Vanuatu’s southernmost island, with 26% endemic species (18/69) and no endemic genus. Some endemic genera from the archipelago had indeed been described by Meyrick (1906, 1924), notably *Loxotrochis* Meyrick, 1906 (Immidae) and *Hedroxena* Meyrick, 1924 (Cosmopterigidae), but the former had very soon been shown to be based on a misreading of the locality of Espiritu Santo (Brazil) as Espiritu Santo (Vanuatu) (Meyrick 1907), although this emendation has sometimes been overlooked (e.g., Viette 1949). Numerous new endemic species have since been discovered in Vanuatu, especially by Holloway (1979) but also by other scholars, who even spotted large-sized colourful butterflies and moths such as *Polyura sacco* Smart, 1977 (Nymphalidae), *Gnathothlibus saccoi* Lachlan & Moulds, 2001, *G. vanuatuensis* Lachlan & Moulds, 2003 (Sphingidae) and *Eudocima oliveri* Zilli & Brou, 2017 (Erebidae) (Smart 1977; Lachlan and Moulds 2001, 2003; Zilli et al. 2017). It is thus easy to assume that these islands still host several lepidopterological treasures, whose discovery will benefit from studying expedition collections from

the archipelago. As usual, most research on the Lepidoptera from Vanuatu has been dedicated to butterflies (e.g., Butler 1875; Gross 1975; Tennent 2004, 2006, 2009), while only two main surveys have targeted moths. The first was Robinson's, during a Royal Society/Percy Sladen Trust expedition in 1971. The other took place in 2006 as part of an IBISCA ("Investigating the Biodiversity of Soil and CANopy") project focused onto the island of Espiritu Santo. The full results of the two surveys have not been published, although syntheses appeared in Robinson (1976), Holloway (1979), during a zoogeographical comparison of Robinson's data with the fauna of New Caledonia, and Kitching (2011), reporting on the results of the IBISCA-Santo expedition. Robinson (1975), however, provided a list of preliminarily identified species from Vanuatu in his monograph on Fijian moths, but some material was left unstudied. This material is available at the Natural History Museum of London and its study already yielded the new species of *Eudocima* Billberg, 1820 mentioned above. This contribution reports on the discovery of another endemic erebid moth during Robinson's expedition, which is described here, and probably represents the new genus briefly mentioned by him in 1976. In fact, due to its unusual features, the erection of a new genus to accommodate the new species becomes necessary.

Material and methods

Study material originated from the expedition by G.S. Robinson to the New Hebrides in 1971 preserved in the Natural History Museum of London (NHMUK). Photographs and dissections were performed according to the procedure already outlined in Zilli (2020), with minor updates of software for operating the camera (Helicon Remote version 3.9.12), image stacking (Helicon Focus vers. 7.5.8) and processing (Adobe Photoshop 2021 vers. 22.3.1). As in numerous erebid groups, the female abdominal sternum A7 is strongly modified in the new species and gives rise to a so-called lodix plate (Goater et al. 2003). This is tightly joined with the ostium bursae but, with some care, a tiny membrane between the two can be cut with microsurgical scissors, which was done to reveal the real configuration of the ostium bursae and, as in this case, the sterigma. Legs and proboscides were prepared following the same dissection and mounting methods as the genitalia. Pictures of forewing veins were taken after partial descaling of the wing disc undersides following wetting of the wing membrane with absolute ethanol. Terminology of veins is mainly based on Wootton (1979) and Kristensen (2003). However, assessment of the homologies between two strikingly different intraspecific configurations of the forewing radials that have been observed was found to be affected by what sections are considered to constitute the chorda, especially as regards the distal closure of the areole. Accordingly, the branching pattern from the areole is reported in two ways, a purely descriptive one, in which the areole is considered as a term of reference, and an interpretative one to better express the relationships between the observed patterns. The latter takes the cell as term of reference and incorporates modifications of convenience to make clearer if the branch of a vein precedes (') or follows (") a cojoined section with other veins.

Results

Taxonomy

Tabwecala gen. nov.

<http://zoobank.org/F744DF74-AE2D-4236-8089-076C74D3EB81>

Type species. *Tabwecala robinsoni* sp. nov. (described below), by present designation.

Etymology. The generic epithet derives from the combination of “Tabwe-” (from Mt Tabwemasana in Espiritu Santo Island) and “-cala” (from the Greek “κἄλη”, meaning “nice”); it is feminine in gender.

Diagnosis. The absence of sexual dimorphism in the labial palpi, the presence of two anterior spines on the male profemur, the absence of spines on male tibiae, the presence of an androteca on male mesotibia, the strongly modified male metatibia bearing a dorsal hair pencil, the tuba analis without scaphium and with a deep, hood-like scaphial pocket, and the sterigma projected posteriorly into a free end, represent altogether a combination of characters not seen, at the author’s best knowledge, in other genera of the Erebiidae.

Description. Male (Fig. 1). **Head.** Large, feebly sunk into thorax, frons slightly bulged, unscaled at middle (scales evidently brushed off by labial palps after emergence as in numerous other Erebiinae), vertex roughly scaled, eye large, globular, antenna filiform, scape stout, barrel-like, covered by scales projected into small dorsal hood, pedicel small globular, flagellum consisting of short cylindrical, ventrally very shortly ciliate antennomeres, pilifer conspicuous, with long bristles, haustellum well developed, with tiny flat apical sensilla, labial palpus slender, upcurved, first joint roughly scaled, second joint compactly scaled, third joint long and thin, rod-like, two thirds as long as second, with no apical club.

Thorax. Stout, both patagium and tegula broad and long, roughly scaled, meso-metanotum with hair-like scales, without crests; pectus conspicuously hairy. Wings broad; forewing vein R1 from middle of cell, areole present, splitting between Rs_2 and Rs_3 close to termen in apical area of wing, but topology of Rs branches from cell very variable (see dedicated paragraph below), M visible in outer half of cell, other veins as in other Erebiinae, with CuA_2 from before middle of cell; hindwing veins as in other Erebiinae. Legs slender (Fig. 3); foreleg: profemur elongated, slightly wider at base and gradually tapered distally, with paired preapical spines, protibia not spined, barely shorter than femur, and feebly incrassate at middle, with epiphysis half length of tibia, protarsus conspicuously spined ventrally on tarsomeres I–IV, spines arranged into 3 rows, terminal spines of each tarsomere longest, spines replaced by bristles on tarsomere V, pretarsus with semi-circular arolium, onychia sharply bent, with midventral tooth, and pulvilli short; midleg: longest of the three legs, mesofemur long and slender, of almost uniform width, mesotibia greatly developed, longer and wider than mesofemur, its edges wrapping internally so as to originate a groove (androteca, cf. Berio 1955, 1959, 1965) enclosing a long hair-pencil kept in place by flat scales, mesotibial spurs one terminal pair, mesotarsus slender, spines and bristles on I–V as in protarsus, pretarsus as in protarsus; hindleg: metafemur slender and of almost uniform width, $7/10$ as long as mesofemur, metatibia not spined and greatly modified, very short, about $2/3$ length of metafemur, and swollen distally and dorsally so as to show a teardrop outline with dorso-apical bulge (respecting tibio-tarsal axis) for insertion of conspicuous pencil of long, hair-like androconial scales, this leaning middorsally along basal tarsomere, metatibial spurs two pairs, long and flimsy, first pair from middle of metatibia, second pair from well before apex, mesotarsus with basal tarsomere greatly developed, thick and longer than tarsomeres II–V altogether, widest at base and gradually tapered apically, clothed externally with thin long setae and showing midventrally in its distal two thirds comb of long bristles, tarsomeres II–V and pretarsus as in fore- and midleg.

Abdomen. Sternum A2 broad, subrectangular, with short, broad-based anterior apodemes, other segments of pregenital abdomen with subrectangular urotergites and urosternites, much wider than high, tergum A8 trapezoid, sternum A8 shallowly cleft on its posterior margin.

Male genitalia (Fig. 5). Tegumen and vinculum robust, the latter shorter than tegumen and without inwardly produced saccus, valva oblong, with strongly sclerotised proximo-ventral portion, deriving from fusion between costal process and clasper, narrowly joined to sacculus, this produced into short saccular process, and dorso-distal membranous portion, which is broadly but shallowly corematous dorsally at base, where a conspicuous scent tuft is inserted. Uncus with dorsal process far from base. Tuba analis of complex configuration, dorsally membranous, showing distinct hood-like scaphial pocket (best seen in side view) above anus to accommodate tip of uncus. Juxta long, symmetrical, of the 'X'-type, articulated at very base of valvae. Phallus arched and compressed, with recurved foot-shaped coecum, showing small sclerotised platelet at base of vesica in distal excision of ventral edge of its shaft, vesica multi-lobed.

Female (Fig. 2). **Head.** As in male, no sexual dimorphism detectable, including labial palpus, except for base of flagellum, slightly thinner, and periscapular scales, shorter and not forming hood.

Thorax. Pro-metathorax and wings as in male, legs without the sexual secondary modifications seen in male (namely, profemoral spines, mesotibial androteca, shortened and swollen metatibia bearing dorsal scent pencil and weak spurs, strongly developed basal segment of metatarsus with setae and comb), mesotibia irregularly spined externally, metatibia not spined, basal segment of metatarsus as long as tarsomeres II+III, with three rows of spines ventrally (Fig. 4); other features as in male.

Abdomen. As in male but tergum A7 broad and high, approximately square-shaped, and sternum A7 greatly reduced to narrow and long subrectangular lodix plate (Fig. 6) overlapping ostium bursae.

Female genitalia (Fig. 6). Complete sterigma present and of complex configuration, corresponding to broadly dilated midventral section of intersegmental membrane A7–A8 produced mid-ventrally into stout, strongly sclerotised longitudinal outgrowth that terminates posteriorly into free end overlapping midventral sclerotisation which extends between from post-sterigmatal area to sternum A8; ostium bursae opening at approximately one third from anterior margin of sterigma. Bursa copulatrix with broad cervix and appendix anteriorly oriented originating from left of this. Ovipositor short, papillae anales soft, elongated, densely setose. Gonapophyses rod-like.

Venational variation. Two different configurations regarding topology of forewing Rs veins, not linked to the sexes of specimens examined, have been found. As noted in the 'materials and methods', these are reported here after a descriptive approach (*italics between brackets*) and an interpretative one (normal text and Figs 7, 8).

(1) [*Areole long; Rs_1 from just beyond middle of areole; Rs_2 and Rs_3 long stalked, from upper distal corner of areole; Rs_4 from lower distal corner of cell*] Rs_1 and stalk (Rs_2+Rs_3) long stalked, from before end of cell, areole very long, bound superiorly by stalk ($Rs_1+(Rs_2+Rs_3)$) and stalk (Rs_2+Rs_3), inferiorly by Rs (viz. cell) and Rs_4 , and closed by short anastomosis that from Rs_4 reaches stalk (Rs_2+Rs_3) (Fig. 7).

(2) [*Areole short; Rs_1 from 4/5 length of areole; stalk of Rs_2 and Rs_3 shortly stalked with Rs_4 , from end of areole*] Rs_1 and Rs_2 ' stalked, from before end of cell, Rs_2 ' free from bifurcation with Rs_1 for short tract, then anastomosed and cojoined into short stalk ($(Rs_2''+Rs_3)+Rs_4''$) which then separates into long stalk ($Rs_2''+Rs_3$) and Rs_4'' , areole thus short, bound superiorly by stalk (Rs_1+Rs_2') and Rs_2' , and inferiorly by Rs (viz. cell) and Rs_4' (Fig. 8).



Figures 1, 2. Habitus of *Tabwecala robinsoni* gen. nov., sp. nov., from Vanuatu, Espiritu Santo, Mt Tabwemasana. 1. Holotype ♂; 2. Paratype ♀. Scale bar: 1 cm (1, 2.).

Distribution. The genus is currently known only from a restricted area of the Pacific (Vanuatu: Espiritu Santo).

Systematic position. Features of the new genus indicate its position in tribe Poaphilini of the Erebinae (Erebidae), a group which is however morphologically ill-defined, as it will be reviewed in the discussion below.

***Tabwecala robinsoni* sp. nov.**

<http://zoobank.org/A6832F40-B17C-498D-B714-6B9217405BB6>

Type material. **Holotype:** VANUATU • ♂; “New Hebrides”, [Espiritu] Santo, Mt Tabwemasana Ridge; alt. 1372 m; 2 Sept. 1971; G.S. Robinson [leg.]; Roy[al] Soc[iety] Expedition; NHMUK010354772; NHMUK. **Paratypes** (3♂♂, 5♀♀): VANUATU • ♂; same data as for holotype; NHMUK010918854; NHMUK • ♂; same data as for holotype; NHMUK010918855; NHMUK • ♀; same data as for holotype; NHMUK010354773; NHMUK • ♀; same data as for holotype; NHMUK010918853; NHMUK • ♂; Mt Tabwemasana, Nokowula; alt. 1128 m; 1 Sept. 1971; G.S. Robinson [leg.]; Roy[al] Soc[iety] Expedition; NHMUK010354774; NHMUK • ♀; same data as for preceding; NHMUK010918633; NHMUK • ♀; same data as for preceding; NHMUK010918636; NHMUK • ♀; same locality as for preceding; alt. “CK-“ 1067 m; 3–4 Sept. 1971; G.S. Robinson [leg.]; Roy[al] Soc[iety] Expedition; NHMUK010918856; NHMUK.

Etymology. The species is dedicated to the memory of the collector of the type series Gaden S. Robinson (1949–2009), former researcher and curator of Lepidoptera at the then British Museum (Natural History). The specific epithet is a noun in the genitive case.

Diagnosis. The new species looks superficially similar to species of the ophiusine genus *Artena* Walker, 1858, especially members of *Artena rubida*-group, namely *A. reggiantii* Zilli & Lourens, 2018, *A. velutina* (L.B. Prout, 1919) and *A. rubida* (Walker, [1863]), but is easily recognisable by the non-sexually dimorphic, slender rod-like third joints of labial palpi, rough instead of plain scaling of head and thorax, uniformly dark-coloured forewing without pale antemarginal field, larger, more centrally- and transversely positioned pale band of the hindwing and conspicuous scent tufts on the upperside of male metatibiae. Also somewhat resembling in habitus members of the poaphiline genus *Achaea* Hübner, 1823 and the yet incertae sedis genus *Leistera* Swinhoe, 1909, the latter showing another unusual combination of characters (type species, *Catephia pulchristrigata* Bethune-Baker, 1906, examined), e.g. no androteca as in Catephiini (Berio 1992) but unlike these with spines on male meso- (weakly) and metatibiae, uncus with dorsal peak and valva structured as in several members of the Ophiusini + Poaphilini clade, including also single tubular



Figures 3, 4. Legs of *Tabwecala robinsoni* gen. nov., sp. nov. 3. Male; 4. Female (this also with procoxa). Scale bar: 2 mm. (3, 4.)

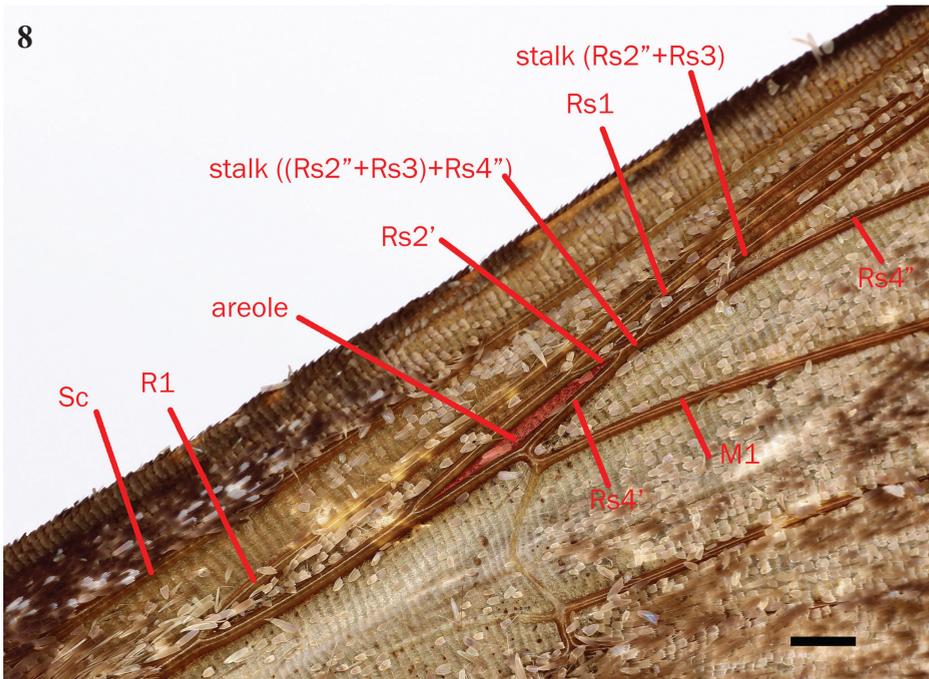
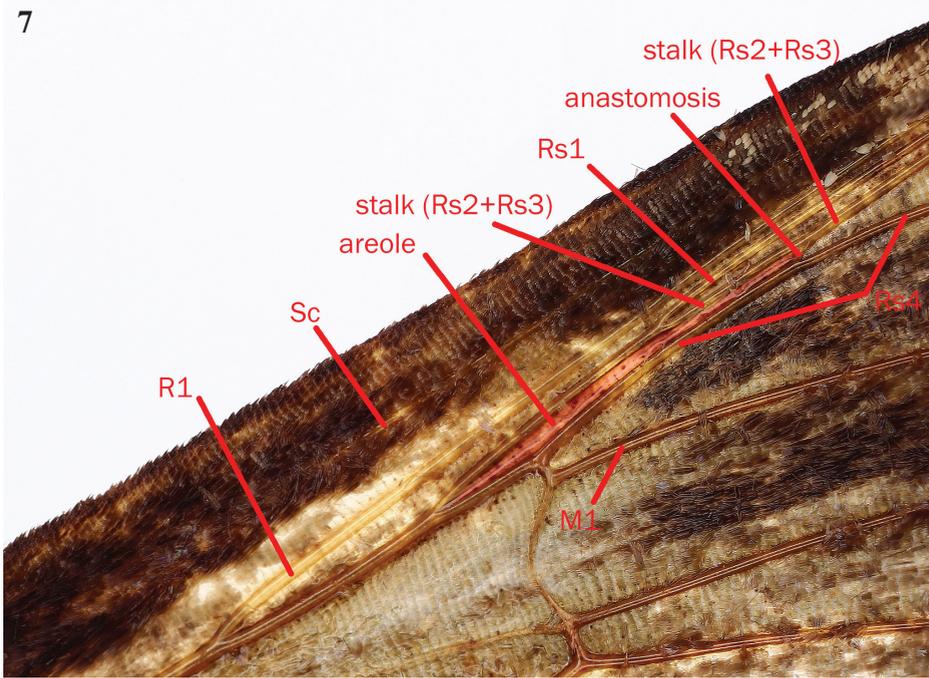
5



6



Figures 5, 6. Genitalia of *Tabwecala robinsoni* gen. nov., sp. nov. **5.** Male, paratype; **6.** Female, paratype (sternum A7 on left). Scale bar: 1 mm (**5, 6.**).



Figures 7, 8. *Tabwecala robinsoni* gen. nov., sp. nov., different branching patterns of veins from forewing areole (shaded light red) with interpretation of homologies (see criteria in Material and methods). 7. Long-areoled configuration; 8. Short-areoled configuration; M – medial; R – radial; Rs – radial sector; Sc – subcostal. Scale bar: 1 mm (7, 8.).

dorsal corema from its base. Nonetheless, no *Achaea* species with forewing completely deprived of pattern are known to date, and the arabesqued ornamentation of forewing of species of *Leistera* will prevent any confusion.

Description. Male (Fig. 1). **Habitus.** Wingspan 74.5–78 mm (mean = 76 mm, n = 4). Ground colour of head, body trunk and forewing uniformly dark blackish brown, with some scattered sprinkles of silvery scales. Forewing broad subtriangular with no evident pattern, apex smoothly rounded, termen overall slightly convex, feebly undulated at veins, anal margin straight, fringe concolorous with wing disc; hindwing broad and rounded, termen as in forewing but slightly produced at vein 1A+2A and with feeble white terminal line, colour dark chocolate brown, except for broad transverse white discal band, this widest at middle and with margins blurred, and with very feeble light-blue hue (visible if swinging the wing), ending before anal margin. Metatibial scent pencil blunt-ended and reaching in length almost the whole basal tarsomere, its basal third chocolate brown-coloured, mesially and distally brightly honey-coloured. Underside almost unicolorous dark blackish brown.

Male genitalia (Fig. 5). Tegumen high, very tapered superiorly, with small thorn-like projections before apex; vinculum semicircular; valva oblong-obovate, with hairy distal membranous section, sacculus small, lozenge-shaped, with small apical outwardly-produced horn-like process, ventral sclerotised part centrally positioned, in shape of wide-based sub-rectangular transverse plate ending distally into two processes, inferior one (interpreted here as a clasper proper) thumb-like, perpendicular to longitudinal axis of valva, and superior one (interpreted as of costal derivation) similarly shaped but longer and much stouter, subparallel to costal margin, with reclinate tip, inflatable saccate corema on dorsal side with thick tuft of long hair-like scales; uncus long and reclinate, bulbous at base, its dorsal process subbasal and horn-like with forward projected tip, distally sinuous with middorsal hump and downcurved pointed tip; tuba analis wholly membranous. Juxta narrow, sub-rectangular, slightly sinuous at sides, with slightly divergent projections at corners, the inferior pair articulated with valvae. Phallus bent at basal third, vesica small, with paired opposite long thin diverticula and central, slightly bilobed bulge protruding from central corpus.

Female (Fig. 2). **Habitus.** Wingspan 71.5–77.5 mm (x = 75.6 mm, N = 5). As in male, except for legs (described under generic diagnosis), and with white band of hindwing wider at middle of wing disc. Sternum A7 (Iodix) posteriorly bilobate (Fig. 6).

Female genitalia (Fig. 6). Tergum A8 wide and short, its ventro-lateral belts facing the sternum about half as high as the dorsal part, long and with rounded ends, separated only by narrow sternal section, apophyses anteriores thin; basal sterigmatal plate broad and rugulose, trapezoid, its ventral longitudinal outgrowth narrow, sub-rectangular, posteriorly bifid with conspicuous, pointed asymmetrical processes, and with anterior excision extending posteriorly as a narrow furrow for about one third of its whole length, ostium bursae opening at bottom of short infundibular depression in correspondence of posterior end of midventral furrow, sternum A8 with narrow elongated sclerotisation proceeding from post-sterigmatal area. Ductus bursae very short, strongly sclerotised, joining with corpus bursae at junction between broad, dome-shaped cervix, which thus extends posteriorly to it, and large ovoid fundus bursae (note that the several irregular dark blotches visible in fig. 6 appear in completely other positions in another preparation, thus they seem tissue remains not pertaining to the bursa, though they appear tightly linked to it and not separable in the well cleaned preparations); appendix bursae conical. Intersegmental membrane A8–A9 short. Papillae anales elongated sub-rectangular, apophyses posteriores approximately 1.5 times as long as anteriores.

Distribution. Currently known only from the island of Espiritu Santo in the Vanuatu archipelago.

Bionomics. The original series was collected in a period of four days on the Mt Tabwemasana range, the highest peak of the island of Espiritu Santo and whole Vanuatu archipelago, at elevations between 1067 and 1372 m, which correspond to sites of *Agathis-Calophyllum* and montane cloud forests (Munzinger et al. 2011).

Discussion

Tabwecala robinsoni shows features which agree with what is nowadays mostly referred to as the Ophiusini + Poaphilini clade (e.g., Homziak et al. 2019). The concept of Ophiusini, historically revised many times (Kitching 1981; Kühne and Speidel 2004; Homziak et al. 2016), has recently been split between the tribes Ophiusini and Poaphilini (Lafontaine and Schmidt 2010, 2013; Zahiri et al. 2012), the latter being revived from Euclidiini, mainly based on molecular evidence. In the analyses by Zahiri et al. (2012), confirmed also by Homziak et al. (2019), each group has been recovered as monophyletic with good support but also as sister to the other in a well-supported clade, which raises the issue whether splitting them taxonomically was strictly necessary. Further to this, there are no known autapomorphies supporting the separation of the two tribes.

Zahiri et al. (2012) mention for the Ophiusini that “*Ophiusa*, *Thyas* and *Artena* all have a strongly modified apex to the proboscis, with strong and enlarged spines and erectile, reversed hooks that are used in fruit-piercing or lachrymal-feeding behaviour”. Such statement, attributed to Holloway (2005), was evidently a lapsus for the Calpinae (or Calpini), the erectile reversed hooks being a well-known character exclusively occurring in Calpinae/i (Speidel et al. 1996; Kitching and Rawlins 1998; Zaspel et al. 2011). In fact, Holloway (2005: 11) noted that the three genera have only enlarged spines and that these were not erectile like those of the Pericymini, and stated that strongly sclerotised, erectile, reversed hooks occur instead in Calpini and Scoliopterygini. During the present study, it was decided to compare the structure of the proboscis of *Artena* (*A. dotata* Fabricius, 1794, examined) and *Achaea* (*A. serva* Fabricius, 1775, examined), genera attributed respectively to Ophiusini and Poaphilini (Zahiri et al. 2012). No tearing hooks were observed. In contrast, the same basic structure was detected, both taxa showing only thin, nail-like spines and other sensilla in the apical section of proboscis. The fruit-piercing behaviour does not allow the separation of the two groups either, as also noted by Zahiri et al. (2012), since it has been recorded by Bänziger (1982) both in genera of the restricted Ophiusini (e.g., *Artena*, *Ophiusa*, *Thyas*) and others now placed in Poaphilini (e.g., *Achaea*, *Ophisma*, *Bastilla*, *Grammodes*) (Zahiri et al. 2012; Lafontaine and Schmidt 2013). In relation to lacriphagy, Bänziger (1973) summarised all data known to date and neither recorded Ophiusini nor Poaphilini. These results are in full agreement with Bänziger’s (2021: 139–140) independent review of the issue just published.

Homziak et al. (2016), in their historical review of the classification of the Erebinae, noted the treatment of Ophiusini and Poaphilini by most recent authors but also that early authors did not separate them, and often recorded features shared or scattered across taxa that are currently separated into the two groups. They noted that the restricted concept of Ophiusini matches the section comprising *Artena*, *Ophiusa* Ochseneimer, 1816 and *Thyas* Hübner, 1824 that was circumscribed by Holloway (2005) on basis of absence or strong reduction of dorsal valval coremata and absence of a powdery or waxy bloom on the pupa. Holloway had also mentioned a dorsal elliptical mark on larval A5 uniting *Artena* and *Thyas*, but its absence in other Ophiusini such as *Ophiusa* and *Clytie*

Hübner, 1823 (cf. Leong 2009; Herbison-Evans and Crossley 2021; Mazzei et al. 2021) excludes this feature from the list of putative synapomorphies.

As regards the valval coremata, *Artena* lacks them, in *Ophiusa* they are generally shallow (Holloway 2005), but those of *O. trapezium* (Guenée, 1852) are bigger than those of a poaphiline species such as *Ophisma gravata* Guenée, 1852 (cf. Holloway 1979; and pers. obs.), and the ophiusine *Stenopsis reducta* Mabille, 1880 has long tubular coremata (De Prins and De Prins 2011–2021) not dissimilar from those of some Poaphilini in the so-called *Parallelia*-complex like *Pindara* Moore, [1885] or *Macaldenia* Moore, [1885] (cf. Holloway and Miller 2003; Holloway 2005). Splitting the two groups on this character looks therefore untenable. More promising seemed to be the character of the bloom on pupae, widespread in the Erebininae but apparently absent in the Ophiusini, so that its loss could have served as an autapomorphy delimiting the restricted concept of this tribe. Nonetheless, good illustrations of pupae of *Ophiusa disjungens* (Walker, 1858) and, particularly, *Thyas coronata* (Fabricius, 1775) clearly show that a pupal bloom also occurs in some species of this group, the pupa of the latter being also explicitly stated to be “covered in a white waxy powder” (Herbison-Evans and Crossley 2021).

A further character which has been used to unite the modern Ophiusini is the similarity in pattern, though considering the range of patterns expressed by genera of the Ophiusini and Poaphilini the overall picture is so intermingled that it is debatable that a phylogenetic signal may be traced here. *Tabwecala* itself, which in leg features corresponds to Poaphilini (see description above and comments below), shows the greatest similarity in external appearance to species of *Artena* (Ophiusini), especially members of the *A. rubida* group (cf. Zilli and Hogenes 2004; Zilli and Lourens 2011). Solely upon basis of the habitus it had provisionally been marked by Gaden S. Robinson with “Closest ally *Artena rubida* Walk.”.

Emphasis has also been laid on the widespread acceptance of Euphorbiaceae as hostplants by members of the Poaphilini (Holloway and Miller 2003; Homziak et al. 2016). The host range of Poaphilini is wide in terms of plant families and many overlaps occur with the Ophiusini. Following a recent analysis run on the hostplant data of Robinson et al. (2001), Holloway (2019 and pers. comm.) notes that of the 15 families exploited by the Ophiusini in the Indo-Australian Region, eight are shared with the Poaphilini, while the latter feed on a range of at least 35 plant families (Phyllanthaceae being then still subsumed into the Euphorbiaceae), though the Euphorbiaceae take the lead. This feature seems therefore quite well embedded into the poaphiline lineage, especially in the *Parallelia*-complex studied by Holloway and Miller (2003). However, (A) the existence of several poaphilines feeding on other plant families or at least not known to feed on Euphorbiaceae, (B) the diffuse polyphagy by some species which also exploit euphorbs (Robinson et al. 2001, 2021; Holloway and Miller 2003) and (C) the varying rate of their acceptance, indicate that such habit has to be better considered as a ‘syndrome’ rather than a synapomorphy uniting the whole Poaphilini. For example, out of 35 hostplant associations recently recorded by Staude et al. (2020) for *Achaea* in South Africa, 34.3% were Fabaceae, 14.3% Anacardiaceae, 8.6% each Combretaceae and Rhamnaceae, 5.7% each Myrtaceae, Ochnaceae and Zygophyllaceae, and only 2.9% each (1 record) Euphorbiaceae, Malvaceae, Phyllanthaceae, Plumbaginaceae, Sapindaceae and Sapotaceae. Euphorbs are also known to enter the larval diet of many genera of Erebininae outside of the Ophiusini + Poaphilini clade, e.g. *Asota* Hübner, [1819], *Cosmophila* Boisduval, 1833, *Homodes* Guenée, 1852, *Hypocala* Guenée, 1852, *Tamba* Hübner, [1823], *Ugia* Walker, 1858 (cf. Robinson et al. 2021), thus also this feature appears to be a symplesiomorphy. There is also an indication that

Ophiusa sp. may feed on *Hevea brasiliensis* Müll. Arg. (Euphorbiaceae) in Malaysia (Robinson et al. 2001, 2021; Holloway 2019 and pers. comm.), though such records are drawn from a time when the use of this generic concept among applied entomologists may have been different from the current one (e.g., Rao 1965), even comprising poaphiline taxa such as members of *Achaea*. For instance, *A. janata* (Linnaeus, 1758) (= *melicerta* Drury, [1773]), highly polyphagous and especially feeding on Euphorbiaceae, has long been recorded in the past under *Ophiusa* (e.g., Ridley 1904; Lefroy 1908; cf. Waterhouse 1993).

Apparently good characters to differentiate between the two groups remain those outlined by Berio (1959, 1965) for his ‘phyla’ of *Anua* (= Ophiusini) and *Achaea* (= Poaphilini), both having from one to three spines on the male forefemur (Homziak et al. 2016 record four in Poaphilini but this also seems a lapsus), but differing in the position of the androteca, on the profemur and mesotibia, respectively. For this reason, the systematic position of *Tabwecala*, with its typical mesotibial androteca, is here considered to be in the Poaphilini. However, even if these characters have a diagnostic role, they are unsuitable in the delimitation of either tribe, being symplesiomorphies shared with other erebine groups. A mesotibial androteca is also typical of the Catocalini and Pericymini (Berio 1959: 289; Kühne 2005: 34), and it cannot therefore be used to circumscribe the Poaphilini, while the proleg type is also found in *Audea* Walker, [1858] and *Crypsotidia* Rothschild, 1901 (Audeini) (Berio 1959; Kühne 2005). *Ulotrichopus* Wallengren, 1860 (Catocalini) may have both types (Kühne 2005, and pers. obs.), in some species (*U. variegata* Hampson, 1902, examined) even showing an unusually oriented bunch of modified setae which overlap from the trochanter onto the femur as in some Ophiusini, e.g. *Ophiusa tirhaca* (Cramer, [1777]) (examined), *O. dilecta* Walker, 1865 and *Stenopsis tumiditermina* (Hampson, 1910) (cf. Berio 1965).

There are several other characters uniting the Ophiusini and Poaphilini. They all have membranous papillae anales without sclerotised strips following up in line with the apophyses posteriores, this being a feature of Catocalini, Audeini and Catephiini (Mitter and Silverfine 1988; Goater et al. 2003; Holloway 2005; Kühne 2005; Homziak et al. 2016), and many species of genera of the two tribes sport a dorsal peak or process on the uncus (= superuncus *sensu auct. nec* Klots, 1956), e.g. *Artena*, *Ophiusa*, *Clytie* (Ophiusini) and *Achaea*, *Ophisma* and *Bastilla* Swinhoe, 1918 (Poaphilini). Similarly, many members of the two groups show the coecum of phallus dorsally upcurved into a ‘foot-shape’, and a basically similar structure of the valva (cf. Berio 1965; Holloway and Miller 2003; Holloway 2005). A broader taxon sampling has therefore to be recommended in future molecular analyses to better refine the relationships within the Ophiusini + Poaphilini clade, the two groups possibly not deserving to be split taxonomically in consideration of the absence of clear autapomorphies supporting each individual group and the molecular evidence corroborating their status of adelphotaxa. In this respect, molecular analysis of taxa showing unusual combinations of characters such as *Tabwecala* would be a priority. Besides the features the new genus has in common with several members of both branches of the Ophiusini + Poaphilini clade, such as the corematous valvae, dorsal process of uncus and upcurved coecum, it also shows traits that are found only in one of the two ‘tribes’, such as a mesotibial androteca (Poaphilini). The subbasal rather than basal dorsal process of the uncus is instead a feature more typical of certain Ophiusini such as *Clytie*, with which *Tabwecala* also shares a remarkable similarity in the main part of the structure.

Most notable are the exclusive features of the new genus. The absence of the dorsal sclerotization of the tuba analis (scaphium) occurs sporadically in the Erebiidae. Following the union with the then families of Arctiidae and Lymantriidae based on molecular evidence (cf. Mitchell et al.

2006; Zahiri et al. 2011), the importance of the scaphium as an autapomorphy characteristic of the Erebidae (cf. Fibiger and Lafontaine 2005; Lafontaine and Fibiger 2006) has been devalued. It may also be present or not within the same infrafamilial grouping. Examples are in the Toxocampinae, species of the *Autophila* group showing a scaphium but not so those of the *Lygephila* group (cf. Ronkay et al. 2014; Pekarsky et al. 2019), or the Omopterini *Zale* Hübner, 1818 and *Matigramma* Grote, 1872, scaphium present and absent, respectively (cf. Blanchard and Franclemont 1982; Franclemont 1986). However, the absence is yet unrecorded in the modern concept of Ophiusini and the Ophiusini + Poaphilini clade, which typically sport a scaphium. In species with a dorsal process of the uncus it even contributes to the characteristic ‘triple beak topping’ of the male genitalia common to many members of the clade. Possibly related to this is the development in *Tabwecala* of a hood-like invagination in the superior part of the tuba analis to form a large scaphial pocket that wraps the tip of uncus to likely prevent damages to the rectum. This configuration is more similar to that of the distantly related Hypeninae than to the small rugulose invagination distal to the scaphium, essentially serving the same function, that occurs in Calpinae and other Erebininae (cf. Lödl 2000; Goater et al. 2003).

Legs of *Tabwecala* offer a plethora of unusual features, starting from the distribution of spines on tibiae. The combination of “♂:000; ♀:010” (where 0/1 = absence/presence in pro-, meso- and metatibia, respectively), that corresponds to Berio’s (1959, 1965, 1992) grade VII of spinosity, has not been recorded by Berio in any ophiusine or poaphiline. Berio did not record in all Erebininae he studied any grade VII species with male profemoral spine(s) like instead *Tabwecala* has. The remarkably short, teardrop-shaped male metatibiae bearing a dorsal scent pencil oriented posteriorly are unique, possibly in the whole Erebidae. Noteworthy modifications in male metatibiae to support a scent function are known in other erebids, e.g. *Ascalapha* Hübner, [1809] (Müller 1877; Barth 1951), but their configuration is totally different from that of *Tabwecala*.

In the female, the sterigma surrounding the ostium bursae that projects ventrally and posteriorly into a free lamella and the simultaneous presence of a post-ostial midventral sclerotization from intersegmental membrane A7–A8 to sternum A8, so that technically the new species shows two “lamellae postvaginales”, is also unusual but reviewing details of this area in the specialised literature is difficult because of the practice of not removing sternum A7 (lodix) during preparation of the female genitalia.

Regarding the remarkable variation in wing venation shown by *Tabwecala*, little can be said other than confirming that topology of veins should be always carefully checked on more specimens. Venational patterns were very much used in the past for systematic purposes, but their value has greatly been downscaled (Kristensen 2003), also in the light of remarkable intraspecific variability. This was long known to be common in the more basal lepidopteran lineages but is has also been shown to occur in the most derived families (Alberti 1954; Sotavalta 1964; Albrechts and Kaila 1997; Nath and Sevi 2009), venational patterns being subject during morphogenesis to many regulatory mechanisms that can modulate expression (cf. Shimmi et al. 2014). Nonetheless, topology of wing venation still remains much employed in systematics (e.g., Souza Moraes et al. 2021).

Conclusions

The discovery in a wildlife sanctuary such as the montane forests of the Tabwemasana range in Espiritu Santo (Vanuatu archipelago) of a new species of Erebidae that could not be systematically

placed into any genus known to date shows how partial our knowledge about the diversity of one of the richest families of Lepidoptera remains. Such diversity is not just in terms of species, but also involves genes, morphological traits and eco-ethological adaptations, like those represented by the leg modifications of male *Tabwecala* and their likely role in scent emission and in courtship. The scent organ shown by *Tabwecala* also raises issues about the evolutionary context behind such innovation, given that this insular endemic has a systematically and biogeographically fairly isolated position, so that it does not seem to face any risk of mating mistakes with sympatric relatives. The male scent apparatus seems therefore not to have evolved to promote a species isolating role from any close allies but to enhance the recognition and synchronization of the two sexes in an insular context (cf. Zilli 1993, for a discussion on alternative hypotheses).

Pointing to areas where to look for putative relatives of *Tabwecala* is highly speculative. On the one hand, following an analysis of a major database of plant generic distributions, the tightest phytogeographical links of Vanuatu have been found with eastern archipelagos such as Samoa, Fiji and Tonga (Holloway 1979: 44), locations where no similar groups to the new genus have been found. On the other hand, the geographical range of numerous Lepidoptera species pertaining to the so-called New Caledonian and Fijian elements place the Vanuatu at the crossroads between those two distribution patterns (Holloway 1979). The New Caledonian Lepidoptera have extensively been surveyed, but the moth faunas of the Solomon and Bismarck archipelagos, that is the most western islands comprised within the New Caledonian element (Holloway 1979), still require proper insights and might reveal groups linking to *Tabwecala*.

Interestingly, the most endemic lepidopteran fauna of Vanuatu is from the island of Espiritu Santo, e.g. there are 33 single island endemic macrolepidoptera compared to 51 overall according to the counts by Robinson (1976), and so *Tabwecala robinsoni* is no exception. Besides its area, largest among the Vanuatu islands, the elevation and ecological heterogeneity (Bouchet et al. 2011), including its older age (Tennent 2004), evidently played a role in promoting endemism in Espiritu Santo, with some taxa known only from middle to high elevation of the Tabwemasana range, e.g. *Tiracola tabwemasana* Holloway, 1979. After a study of the species assemblages across his sampling sites on this island, Robinson (1975: 76) identified a cluster of species corresponding to a “montane forest element”, to which *Tabwecala robinsoni* clearly also pertains.

A review of characters of the new genus with respect to putatively related groups provided the opportunity to show that the separation of tribes Ophiusini and Poaphilini of the Erebinæ is still morphologically unsubstantiated and solely based on molecular evidence, which calls for further analysis on these lineages. Poorly explored areas of the southern hemisphere such as the montane forests of Mt Tabwemasana and other major islands are likely to host representatives of other most unusual lineages of Erebidæ and other Noctuoidea, which calls for the deployment of adequate measures ensuring their protection.

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Cyclic abundance fluctuations in a completely isolated population of *Euphydryas maturna*

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Abstract. A highly isolated and the last autochthonous Czech Republic population of the endangered *Euphydryas maturna* (Lepidoptera: Nymphalidae) is monitored since 2001 by larval nests counts. The 20 years' time series displays remarkable abundance fluctuations with peak-to-peak period 11 years, peak numbers >150 and bust numbers <15 larval nests (arithmetic and harmonic means: 92.6 and 36.3). Establishment of more favourable management of the site probably heightened and prolonged the boom phase but did not alter the overall pattern. We attribute the cycling to pressures of natural enemies. Climatically unfavourable years appear deepening the bust phase. Species displaying such fluctuations cannot be conserved within a single site, which is being addressed by ex-situ breeding of the Czech stock and recent reestablishment of two additional populations, with the aim to achieve asynchronous dynamics of the local populations and eventually stabilise the regional metapopulation.

Introduction

Interannual abundance fluctuations are familiar phenomenon in Lepidoptera (Myers 1988; Peltonen et al. 2002; Bungten et al. 2009), including the much studied Melitaeinae checkerspot butterflies (Nymphalidae) (Ford and Ford 1930; McLaughlin et al. 2002; Ehrlich and Hanski 2004; Gros 2012). Irregular fluctuations are attributable to abiotic factors, e.g. weather (Stange et al. 2011; Csóka et al. 2018). More regular abundance changes may be caused by regularly occurring disturbances, such as felling and regrowth at woodland clearings, to which sun-demanding species react by vacating and recolonising suitable sites (Warren 1987). Finally, regular fluctuations independent on the sites' dynamics may result from pressures of natural enemies, such as predators, parasitoids or diseases, lagging after the dynamics of their hosts (Berryman 1996; Dwyer et al. 2004).

Detecting the latter phenomena requires long-term monitoring data (Johns *et al.* 2016) and may be obscured by migrations of individuals among local populations, which may display mutually independent local dynamics (Myers 2000). Here, we report a case of cyclic abundance changes in a population of an endangered woodland checkerspot butterfly, to which immigration has been practically impossible due to its complete isolation.

Euphydryas maturna (Linnaeus, 1758) is an Eurosiberian species, distributed from eastern France across Central Europe and southern Scandinavia to Urals and eastwardly to Baikal region (cf. Rakosy *et al.* 2012). It is threatened in all occupied European countries due to association with open-canopy broadleaf woodlands with species-rich herb layer, which considerably declined across the continent with the cessation of such historical uses as forest pasture or coppicing (Konvička *et al.* 2005; Freese *et al.* 2006; Fischer *et al.* 2017; Mayer 2020). The butterfly is protected under EU Habitat Directives, and increasing number of states pursue active conservation measures, including government-funded restoration of historical forestry practices (Dolek *et al.* 2018). Its decline was particularly severe in the Czech Republic, where it was historically recorded from 29 (out of 675) grid mapping squares but currently survives at a single locality. The past distribution included open canopy structures in floodplain forests along major rivers and sparse oak-hornbeam woodlands in colline altitudinal belt (Benes and Konvicka 2002). The severity of the decline is attributable to complete abandonment of coppicing management in the country during 20th century and ensuing darkening of the woodlands (cf. Chytry 2012). The species was even considered nationally extinct by late 20th century (Vrabec 1994), when Vrabec (1998, 2001) discovered a hitherto unknown population, situated ≈ 12 km from a historically known and then already unoccupied locality. In this population, a mark-recapture study in 2002 estimated alarmingly low adult numbers, ≈ 200 (Konvička *et al.* 2005). Since then, the population has been monitored annually by larval nests counts. Particularly low counts in 2008 and 2009 (Čížek and Konvička 2009) prompted issuing a Species Action Plan [SAP], which strives to improve habitat conditions by transferring the current habitat, high forest with transient clearings, towards more open canopy structure (AOPK ČR 2011). Vrabec *et al.* (2018, 2019) attributed the subsequent population increase to these management measures. The SAP also provided for establishing two ex-situ populations, based on stock from the last locality and intended for eventual reintroductions, or reinforcements.

By early 2021, the larval nests time series covers 20 seasons (2001–2020), which is enough for elucidating the temporal population dynamics.

Methods

The studied population inhabits a single woodland reserve, Dománovický les [= Dománovice forest], Central Bohemia (50.11N, 15.34E, altitude: 247 m, area 75 ha), situated amidst intensive farmland of Elbe river alluvium. It was established in 1989 to protect floristically rich oak-hornbeam forest on base-rich soils. Following the discovery of *E. maturna* population (Vrabec 1998), the reserve, expanded to 355 ha (it exceeds *E. maturna* distribution area) and became a site of European community interest, targeting conservation of this species (AOPK ČR 2011).

The life history of *E. maturna* in Central Europe (e.g., Gros 2002; Straka 2014; Fischer *et al.* 2017; Mayer *et al.* 2020), including the Czech site (AOPK ČR 2011), is known in much detail. The species is univoltine (late May – June), females oviposit batches of several hundred eggs at fresh *Fraxinus excelsior* leaves; rarely used alternative host plants are *Ligustrum vulgare* and

Viburnum opulus (Dolek et al. 2013). Larval feeding begins in communal silken nests. Larvae from these primary nests sometimes merge with others to form secondary nests (Vrabec 2001), and in the 3rd instar (late July – August), they disperse solitarily and enter quiescence and hibernation. In March – April, following the overwintering, they finish feeding first on forest floor herbs (with regionally differing preferences: Rakosy et al. 2012) and then at budding *F. excelsior*. Elsewhere in its wide distribution range, the ecology may considerably differ. For instance, mainly herbs are consumed by larvae in Finland (Wahlberg 2001), whereas *Fraxinus angustifolia* subsp. *pannonica* is used for pre-hibernation larval feeding in Pannonian basin (Rakosy et al. 2012).

The annual monitoring targets the primary larval nests, present from mid-July to mid-August depending on the season. Experienced persons equipped with binoculars systematically survey the site, using the knowledge of the nests' distribution in previous years. They systematically survey forest clearings, open canopy patches, track verges and edges, checking *F. excelsior* saplings and low-hanging (<12 m) branches of taller trees. The alternative host plants are also surveyed. For each nest detected, GPS coordinates are recorded. Each year, the map of the spatial distribution of nests is created to advice woodland managers. It takes 6–10 person-days to survey the entire locality.

In four seasons (2002, 2016, 2017, 2019), adult numbers were estimated by mark-recapture procedures (details: Vrabec et al. 2019). We relate here the adult number estimates to larval nests numbers in the same season.

Results

During the 20 monitoring seasons, two population peaks occurred, both followed by busts (Figure 1). In the peak years, the population reached 164 (2006) and 202 (2017) larval nests. The peaks were preceded by three (2003–2005) or five (2013–2016) seasons with nest numbers >100. Each peak was followed by a season with diminished but still quite high numbers (2007, 2018), and then by a bust, with the nest numbers merely ≈8% of the peaks. The lowest nest numbers observed were

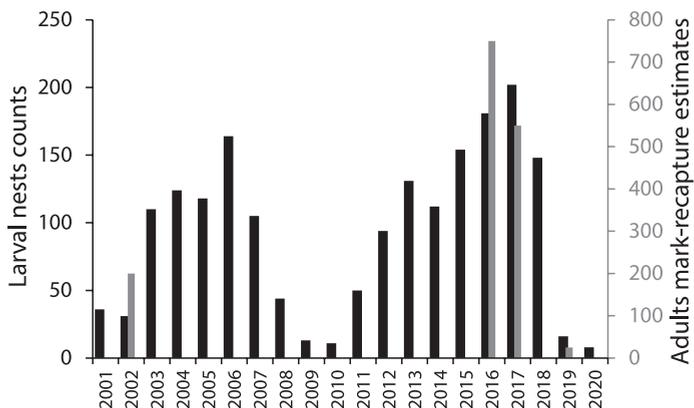


Figure 1. Abundances of *Euphydryas maturna* larval nests in its last Czech Republic population, as detected by annual monitoring surveys, and adult numbers estimates based on mark-recapture surveys. The adult estimates are from Konvička et al. (2005) – 2002, Vrabec et al. (2019) – 2016, 2017, and unpublished data by AOPK ČR 2019.

11 (2010) and 7 (2020). This resulted into a great discrepancy between arithmetic ($=92.6 \pm 61.92\text{SD}$) and harmonic ($=36.3$) means of yearly numbers. Whereas the length of the first cycle cannot be ascertained from the existing data, the peak-to-peak length of the second cycle was 11 years.

Semiquantitative observations of adults and larval nests exist also for the years 1996–1998, following the discovery of the population. Then, the population appeared abundant (Vrabec and Jindra 1998), contrasting with the low numbers in the 2001–2002. Due to a smaller area then examined, the 1996–1998 data cannot be used for direct comparison. Still, they indicate that the monitoring in 2001 started while the population was recovering from a preceding bust.

Based on the four year with mark-recapture data available, the adults : nests ratio is 3.7 (± 2.10 SD), implying that ≈ 4 adults are necessary to produce one larval nests. The lowest ratio, 1.6, was found in the bust year 2019, and highest, 6.5, in the bust year 2002, so the ratios probably had little in common with the stage of the population cycle.

Notably, the development of nests numbers followed identical trajectory of increase, boom and bust prior to 2011, when the site was not actively managed for the species, and after 2011, under active management. Favourable management might had contributed to the longer plateau of nests number >100 during the second cycle and to the higher amplitude of the second peak. On the other hand, the second cycle displayed a steeper decline (90% reduction from 2018 to 2019).

Discussion

An isolated population of *Euphydryas maturna* in the Czech Republic undergoes cyclic abundance changes with ten-fold abundance difference between booms and busts and 11- years period. Such fluctuations were observed by previous authors, e.g., in Salzburg, Austria (Gros 2012), Steigerwald, Germany (M. Dolek, personal communication of unpublished data) and Hungary (Pecsenye *et al.* 2017a, b). Whereas the Austrian data reveal amplitude and period of the fluctuations very similar to the population monitored by us, the fluctuations in Steigerwald display less regular pattern of peaks and busts, but similar magnitude of declines during the busts, $\approx 10\%$ of peak numbers. Such remarkable abundance changes are seriously diminishing the effective population size (Vucetich and Waite 1999), augmenting genetic threats to this endangered species (Pecsenye *et al.* 2017a). They also explain the elusive character of past distribution in the Czech Republic and elsewhere, with the species being repeatedly “lost” and “rediscovered” by recorders (cf. Vrabec 1994, 1998). The period of the fluctuations reported here is rather long, but falls within the range known for cyclically fluctuating woodland moths, which spans from 3–8 years, e.g., in *Lymantria dispar* (Linnaeus, 1758), to 12–20 years, e.g., in *Choristoneura freemani* Razovski, 2008 (Myers 1988; Hlasny *et al.* 2016; Johns *et al.* 2016).

Although we can only speculate on drivers of the pattern, arm-race with natural enemies, frequently mentioned for woodland defoliating insects' abundance cycles (Berryman 1996; Dwyer *et al.* 2004), is the obvious suspect. The communal *E. maturna* eggs and larvae attract large numbers of predators (Vrabec and Jindra 1998) and parasitosis (Dolek *et al.* 2006; Straka 2014; Fischer *et al.* 2017; Mayer 2020); microbial or fungal infections are also possible. Until recently, rarity and legal protection of the species precluded quantifying infestation levels by experimental rearing of parasitoids, or DNA screening of entire larval nests. An indirect support for role of natural enemies is provided by spatial patterns of the larval nests distribution in peak and bust years (Figure 2). During the peaks, the nests tend to be distributed evenly across the inhabited forest, with concentration at appropriate open-canopy patches, whereas during bust phase, majority of the nests were



Figure 2. Examples of the GPS-recorded positions of *Euphydryas maturna* larval nests (yellow dots), shown for 2018, a year with still rather high nests numbers, and 2020, a year with the lowest count ever. Thin green line is the border of Dománovický les nature reserve [= PR], green, thin red line is the border of the Dománovický les Site of community interest [= EVL]. The nests are visibly concentrated in the centre of the occupied area in 2018, while proportionally more nests occur in peripheral positions in 2020.

found in marginal positions. Threats acting as contagions, including natural enemies or diseases, affect populations from centroids of their distributions towards peripheries, while the peripheries are more likely spared (Channel and Lomolino 2020). A complementary explanation for this spatial pattern may follow from biology of the natural enemies, for which it may be more difficult to locate peripherally situated hosts. For the butterfly, a trade-off may exist between development in a half-shaded mature forest, likely suboptimal microclimatically (Freese et al. 2006) but less exposed to natural enemies, and development at microclimatically suitable but infestation-exposed clearings (cf. Rothman and Roland 1998). Finally, a cyclical variation of the host plant chemical defences, complementary with fluctuations of parasitoids and known to affect, e.g., defoliating geometrid moths (Ossipov et al. 2014), may warrant investigation.

Despite the harmonic shape of the fluctuations (Figure 1), the dramatic population drop 2018/19 deserves attention. Besides of the cyclical pressures discussed above, unfavourable weather could have played a role. In the ex situ breeding, a third of larvae (≈ 70 out of ≈ 200 ; more precise counts would intolerably disturb the individuals) produced by 2018 spring adults (eclosed unusually early, during first half of May) pupated and produced 25 adults in September 2018. *Euphydryas maturna* thus produced a partial second (captive) generation. The rearing conditions were similar to the natural locality (a garden 18 km aerial distance apart, identical altitude, open-walled roofed structure). The year 2018 was exceptionally warm, historically the hottest ever. In natural conditions, such late-season adults would perish due to scarcity of nectar, honeydew and larval diet in advancing

autumn. Regrettably, we did not check for late-season adults in situ. Too fast development above some thermal thresholds and ensuing risk of lost autumn generations (Van Dyck *et al.* 2015) may even determine the geographic range of *E. maturna*, which copies the nemoral woodlands but does not reach to warmer regions of southern Europe. The mild 2018 winter was followed by Arctic spell in May 2019, which killed a half of the pupae during a dozen of nights with -0°C temperatures, suggesting a lack of pupal cold hardiness in this species.

Regardless the causes, the fluctuating pattern resolves the contradictions in previous reports, which were based on shorter time frames. Warnings based on the low counts in 2002 (Konvicka *et al.* 2005) and again in 2009 (Cizek and Konvicka 2009) appeared as unnecessarily alarmist shortly thereafter (Krása and Pavlíčko 2014; Vrabec *et al.* 2018). However, these alarm calls accelerated the adoption of more favourable site management (Vrabec *et al.* 2019), which possibly contributed to the high numbers during the 2016–2017 peak (Figure 1). They also propelled the establishment of the ex situ rearing in 2017 (from two larval nests: John 2020).

The low busts numbers emphasize the importance of metapopulation dynamics, both within the woodland (with individual openings viewed as inhabitable patches: Cizek and Konvicka 2005) and at a larger scale. Until recently, the bulks of annually produced larval nests concentrated at a few momentarily available clearings (Figure 2), although more even distribution may be achieved by active management actions. This is already under way, as forest managers added 7 ha of sparse canopy growths recently. Further 5 ha of this structure, plus 3 ha of active coppice, are planned for near future. Even with these measures, however, the appropriately managed area will remain much smaller than in the successfully managed *E. maturna* woodlands in Steigerwald, Germany (Dolek *et al.* 2018) and smaller than it was planned in Species Action Plan (AOPK ČR 2011).

The extremely low numbers in 2019 and 1920 testify that efforts to preserve strongly fluctuating insects within single sites are doomed in a long term (McLaughlin *et al.* 2002). Understanding this, the progeny of ex-situ populations was recently used to re-establish a population at a past site, 11 km distant Libice forest. In this 440.4 ha alluvial forest reserve, currently mostly in mature high forest state, a 1.5 ha clearing with abundant *Fraxinus excelsior* saplings was used to release 190 pre-pupation larvae in June and 3700 3rd instar larvae in July 2018; further 920 and 2320 4th instar larvae were released in June 2019 and 2020; respectively. Search for egg batches in 2019 yielded 24 of them, sixteen larval nests were recorded in 2020. Yet another transfer, planned for 2021, will target Žiželice forest (57.6 ha) situated 800 m apart (edge to edge distance) from Dománovice forest; a reserve was established there in 2017 and open canopy structure is being restored. If needed, the captive stock may also be used to support the donor Dománovice forest population.

A potential threat is represented by the ongoing ash dieback, caused by the fungus *Hymenoscyphus fraxineus* (cf. Skovsgaard *et al.* 2017). Decline of ashes is apparent at all the discussed Czech Republic sites. Planting of ash saplings, plus increasing the abundance of the alternative host *Lonicera nigra*, are considered as possible rescue measures.

If everything goes well, all the remnant deciduous woodlands in the Elbe river alluvium will be re-settled by *E. maturna* again, forming a regional metapopulation with individual woods, rather than clearings within the woods, functioning as local colonies. This assumes gradual adoption of forestry methods more favourable for the species (AOPK ČR 2011; Utínek 2014; Dolek *et al.* 2018). As the metapopulation theory predicts (Hanski 1999), such colonies should achieve mutually asynchronous abundance dynamics, stabilising the entire system against extinction via transfers of individuals (Heino and Hanski 2001). In Steigerwald, Germany, asynchronous local

dynamics plus migrations probably creates the irregularities in populations cycling (M. Dolek, personal communication). Similarly, eventual restoration of functional metapopulation in Czechia should stabilise the species' regional survival either via spontaneous migrations, or by occasional transfers carried out by the managers (cf. Porter and Ellis 2011; Kuussaari et al. 2015).

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Contribution to knowledge of the Balkan Macroheterocera: new and rare species for Bulgaria, North Macedonia and Albania

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Abstract. The Balkan Lepidoptera fauna is still not comprehensively known. We present here some new records for three Balkan countries. *Polymixis xanthomista* (Hübner, [1819]) is confirmed for the Balkan Peninsula from Albania, *Eriogaster inspersa* Staudinger, 1879 is reported new for the Republic of North Macedonia (second locality in Europe), and *Mythimna languida* (Walker, 1858) is new for Bulgaria. Some other species (*Ctenoplusia accentifera* (Lefèbvre, 1827), *Anchoscelis luteoigrisea* (Warren, 1911), *Griposia bouveti pinkeri* (Kobes, 1973) and *Egira anatolica* (Hering, 1933)) are confirmed for these countries. We provide illustrations of the species and their genitalia when necessary for confirmation.

Introduction

The Balkan Peninsula is one of the biodiversity hotspots in Europe (Griffiths et al. 2004) and is very rich in butterflies and moths (Varga 2014). On the Balkan Peninsula there are 13 countries, which have been unequally investigated for their Lepidoptera, especially as regards the nocturnal species. Bulgaria is perhaps one of the best explored countries and new additions to the national list are becoming increasingly difficult to find (Beshkov 2017). Northern Macedonia is less explored and new species for this country are still easily found. Albania is still poorly investigated, and in fact about 50 new species for the country have recently been recorded in a single publication only (Beshkov and Nahimić 2018a). The poorly known faunas of such countries are mostly due to the paucity of local lepidopterists, little use of modern collecting methods and lack of through the year research (cf. “winter moths” in Beshkov 2018). For these reasons much of the research has been carried out by Bulgarian and west European workers (Beshkov 2014; Tóth 2019; Plant et al. 2020). Here we present some of the results from the years 2003–2020 and corrected data for a specimen of *Eriogaster inspersa* Staudinger, 1879 treated in Beshkov and Gashtarov (2014).

Methods

The collecting methodology involved two or three portable light traps with an 8W BL 368 black light and 8W BL812 black light tubes, both powered by 12V 9Ah batteries: a Finnish “tent trap” with a 160W mercury vapour bulb at the top of the pole and a 20W BL368 mini-lynx black light compact lamp over the catching pot below. An additional 20W BL368 mini-lynx black light com-

light trap was also positioned about 70 m from the tent trap. The distance between the Finnish “tent trap” and the light traps, as well as between the light traps themselves, was sometimes more than 1 km, as they were deployed in different habitats and conditions wherever possible. All traps ran throughout the night.

After dissection and staining with a 2% Merbromin solution (Mercurochrome), the genitalia were fixed on glass slides in Euparal mountant. All genitalia slides were photographed with a Zeiss stereo microscope Stemi 2000-C with AxioCam ERc 5s digital camera. The moths and collecting sites were photographed with a Sony DSChX400v digital camera. The habitat of *Eriogaster inspersa* was photographed with an Olympus SZ-20 digital camera. The genitalia slides were prepared by S. Beshkov and are part of collection of S. Beshkov, which is part of the Museum collection (National Museum of Natural History, Sofia (NMNHS)).

In the case of the genus *Agrochola* sensu auct. we follow the taxonomic arrangement proposed by Ronkay et al. (2017).

Results and discussion

Results from years 2003 to 2020 are summarised. Most records are relatively new (2019–2020), and the only revised material is from an earlier period (2003–2013). We provide here data for seven species that are very rare in or new to Balkan countries.

List of the species

Lasiocampidae

Eriogaster inspersa Staudinger, 1879

Beshkov and Gashtarov (2014) reported and illustrated a single aberrant male of *Eriogaster rimicola* ([Denis & Schiffermüller], 1775) caught in March. This specimen was collected in Northern Macedonia (that time known as the former Yugoslav Republic of Macedonia), at Middle Vardar river valley near Demir Kapiya town, 130 m, 41°24'12"N, 22°17'19"E, 08.iii.2013 (Fig. 1). The habitat is pseudomachus with *Quercus coccifera* L., *Quercus* sp., *Paliurus spina-christi* Mill. and *Platanus orientalis* L., on limestone soil (Fig. 2). The specimen has incompletely developed hind wings and the forewings have a black elongate discal spot, not the round white spot exhibited by typical *E. rimicola*. According to Beshkov and Gashtarov (2014) perhaps low temperatures during the overwintering of the pupa were the reason for the black coloration of the discal spot. They did not dissect the specimen, remarking that the flight period was an anomaly. At that time *E. inspersa* was unknown from Europe. The specimen has now been dissected (gen. prep. 1/08.xi.2020 S. Beshkov) and we have established that it is *E. inspersa* Staudinger, 1879. Examination of the black discal spots shows that the black coloration is the result of leaked and dried haemolymph. Such a small black patch is also present on one of the hind wings. The male genitalia (Fig. 3) are very distinctive and correspond well to those of *E. inspersa* illustrated in de Freina (1988, as *E. nippei*) and Zolotuhin (2007). In fact, this species was illustrated and described as new by de Freina (1988) as *Eriogaster nippei* de Freina, 1988, later placed as a synonym of *E. inspersa* (see Zolotuhin 2007). Based on our record and information from Zolotuhin (2007), we confirm that specimen identified as *Eriogaster rimicola inspersa* Staudinger, 1879 in de Freina (1999) is not that species but a different taxon with autumn appearance



Figure 1. *Eriogaster inspersa*, male. North Macedonia, near Demir Kapiya, 08.iii.2013. Scale bar: 1 cm.



Figure 2. Collecting locality of *Eriogaster inspersa*. North Macedonia, near Demir Kapiya, 08.iii.2013.



Figure 3. *Eriogaster inspersa*, male genitalia. North Macedonia, near Demir Kapiya, 08. iii.2013. Scale bar: 1 mm.

that differs in the genitalia. The male genitalia of *E. inspersa* have a flattened, broad, plate-like vinculum (Zolotuhin 2007) whereas in *E. rimicola* the vinculum is narrow and short.

Eriogaster inspersa was reported as new for Europe from Greece by Rosenbauer and Theimer (2016). The specimen captured in North Macedonia is more than 300 km distant and the spot in the Vardar valley near Demir Kapiya is hence the most northern and western point of the range of this species. As far as we know, there is no other similar *Eriogaster* species with a spring flight period known from the Balkans.

Noctuidae

Ctenoplusia accentifera (Lefèbvre, 1827)

SW Bulgaria, Struma river valley, rocky hill above the fishpond near Levunovo village, Sandanski district; ca 120 m, 41°29'29"N, 23°16'07"E, 18–20.x.2020, V. Gashtarov leg., 1 male (Fig. 4).

In Bulgaria *C. accentifera* was known only from a single specimen from the Rhodopi Mts, camp site below Trigrad village, Devin district, ca 800 m, 26.vi.1995, R. Radev leg., at light (Beshkov 2000). This is the second record for Bulgaria from a different region of the country, elevation and habitat.



Figure 4. *Ctenoplusia accentifera*, male. Bulgaria, near Levunovo, 18–20.x.2020. Scale bar: 1 cm.

Anchoscelis luteogrisea (Warren, 1911)

N Macedonia, Prilep Region, Babuna Planina, Pletvar Pass, 960 m, 41°22'12"N, 21°40'11"E, 27.ix.2019, marble stony area with *Artemisia* spp., *Quercus trojana* Webb, *Ulmus* spp. etc., S. Beshkov & A. Nahirnić leg., 1 male (Fig. 5), genitalia examined; SW Bulgaria, between S Pirin and Alibotush Mts, "Izvara" Spring above Petrovo village, ca 640 m, 41°24'58"N, 23°33'3"E, 29.x.2019, S. Beshkov & A. Nahirnić leg., 1 male, genitalia examined; SW Bulgaria, Pirin Mts, Vlahi village, 556 m, 41°44'27"N, 23°13'46"E, 27.x.2020, S. Beshkov leg., 1 male, genitalia examined.

Anchoscelis luteogrisea is reported here for the second time from both North Macedonia and Bulgaria. In North Macedonia it was known only from Velestovo near Lake Ohrid and in Bulgaria only from Kresna Gorge (Beshkov 2016; Beshkov and Nahirnić 2018b). *Anchoscelis luteogrisea* is a late autumn species, only recently identified from Bulgaria, North Macedonia, Serbia and Albania. Because of small differences there is a possibility of misidentification with the closely related species *A. litura* (Linnaeus, 1758) (Beshkov and Nahirnić 2020).

Griposia bouveti pinkeri (Kobes, 1973)

SW Bulgaria, Pirin Mts, Vlahi village, ca 560 m, 41°44'27"N, 23°13'46"E, 27.x.2020, S. Beshkov leg., 1 male (Fig. 6), genitalia with everted vesica examined (Fig. 7).



Figure 5. *Anchoscelis luteogrisea*, male. North Macedonia, Pletvar Pass, 27.ix.2019. Scale bar: 1 cm.

This is the second record of this species for Bulgaria, about 40 years after the first and from a fairly close location. In Europe *G. bouveti pinkeri* is known only from a few localities in Greece (Beshkov and Wegner 2004; Wegner 2002; Wegner 2011; Speidel et al. 2016), these two in Bulgaria, and from European Turkey (Ronkay et al. 2001). Misidentification with *G. aprilina* (Linnaeus, 1758) (= *G. wegneri* Kobes & Fibiger, 2003) is possible, but the genitalia, especially the aedeagus and vesica are very distinctive (Figs 7, 8). Differences in the clasper are easy to see after brushing the end of the abdomen. One of us (SB) checked a great number of specimens from Southern Bulgaria, Albania and North Macedonia, but all of them were *G. aprilina*, indicating that *G. bouveti pinkeri* may be very rare and local from those areas.

***Polymixis (Xanthomixis) xanthomista* (Hübner, [1819])**

S Albania, Gjirokaster County, Mt. Lunxhërisë, between Mal Çajup and Erind Village, ca 1010 m, 40°10'57"N, 20°09'58"E, mountain steppe with *Quercus* spp., *Carpinus orientalis* Mill., and *Acer* spp. trees on limestone, 02.x.2019, S. Beshkov and A. Nahirnić leg., 1 female (Fig. 9), genitalia examined, gen. prep. 1./23.xi.2020, S. Beshkov (Fig. 10).

To date, the only two specimens of this species known from the Balkan Peninsula have been recorded from Bulgaria: one from Iskarski Prolom Gorge, Tscherepisch Railway Station and one from Lakatnik Railway Station (Slivov and Lukov 1976 [1977]). According to Beshkov (2000), there are two females of *P. xanthomista* in the Slivov collection at the Institute of Biodiversity and Ecosystem Research of the Bulgarian Academy of Sciences, one labelled "Lakatnik, 14.10.1965, Al. Slivov" [=Lakatnik Railway Station] and the other "Tscherepisch, 13.10.1965, Al. Slivov". However, we doubt that these specimens are either correctly labelled or from Bulgaria. We suggest that they were received without labels and subsequently labelled, or that the labels were changed. Kolev (2002) and Ignatov et al. (2013) have described the doubt regarding the data of Alexander



Figure 6. *Griposia bouveti pinkeri*, male. Bulgaria, Vlahi Village, 27.x.2020. Scale bar: 1 cm.



Figure 7. *Griposia bouveti pinkeri*, male genitalia with everted vesica. Bulgaria, Vlahi Village, 27.x.2020. Scale bar: 1 mm.

Slivov and why a number of his records should be treated as doubtful. This is supported by the fact that above Lakatnik Railway Station one of us (SB) collected many times in the autumn without being able to confirm *P. xanthomista* from the area.



Figure 8. *Griposia aprilina*, male genitalia with everted vesica. Bulgaria, S Black Sea Coast, Ropotamo, 18.x.2005. Scale bar: 1 mm.



Figure 9. *Polymixis xanthomista*, female. Albania, Mal Çajup - Erind Village, 02.x.2019. Scale bar: 1 cm.

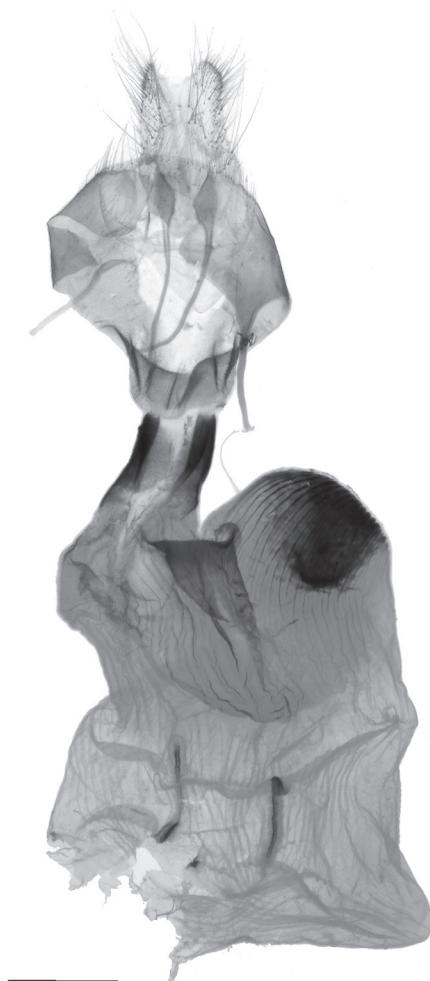


Figure 10. *Polymixis xanthomista*. female genitalia. Albania, Mal Çajup - Erind Village, 02.x.2019. Scale bar: 1 mm.

Egira anatolica (Hering, 1933)

Albania, Mt. Thanës, near Bulqizë town, above Plani i Bardhë village, 833 m, 41°28'47.3"N, 20°9'12.2"E, 06.iv.2019, S. Beshkov and A. Nahirnić leg, 2 males, genitalia examined; Albania, Shkodra County, Stara village, Hot district, ca 500 m, 42°22'15"N, 19°28'13"E, 05.iv.2019, limestone area with *Quercus* spp., *Carpinus orientalis*, *Juniperus oxycedrus* L., *Fraxinus ornus* L., *Paliurus spina-christi* and clearing, S. Beshkov and A. Nahirnić leg, 1 male, genitalia examined. Second record for Albania, previously known from Qafa e Mollës near Tirana (Beshkov and Nahirnić 2020). SW Bulgaria: Struma valley, Skrinski Prolom Gorge, St. Todor Church near Boboshevo, 08.iv.2007, slopes with *Astragalus* spp., *P. spina-christi*, etc. S. Beshkov leg., 2 males, gen. preps 5–6./09.iv.2008, S. Beshkov, male genitalia with everted vesica on glass in euparal; Struma Valley, Kresna gorge, Kresnensko Hantche, ca 220 m, 41°46'59"N, 23°09'18"E, 02–04.iv.2003, S. Besh-

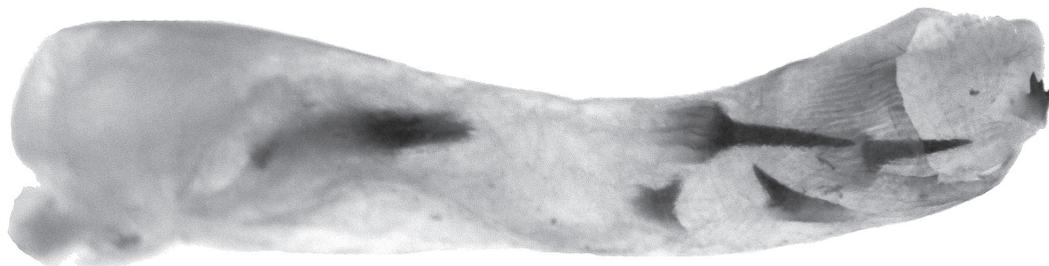


Figure 11. *Egira anatolica*, aedeagus. Albania, near Bulqizë town, 06.iv.2019. Scale bar: 1 mm.



Figure 12. *Egira conspicillaris*, aedeagus. Albania, Tirana Region, Dajti Mt, Qafmolla Pass, 04.iv.2019. Scale bar: 1 mm.

kov and M. Langourov leg., 3 males, genitalia examined, in micro vials in Glycerol; Struma Valley near Kamenitza village 200 m, 41°38'43"N, 23°09'59"E, 25.iii.2017, Maquis, S. Beshkov and B. Zlatkov leg, 1 male, genitalia examined, 04.iv.2003, S. Beshkov, M. Langourov, K. Ivanov & D. Tchobanov leg; S Pirin Mts, Malinova Burchina near Kalimantzi Village, 350 m, 41°27'58.6"N, 023°29'56.5"E, 09.iv.2005, Maquis, S. Beshkov, G. Petranyi and T. Harz leg.

Egira anatolica flies in early spring and is found in Bulgaria (Beshkov 2000), Macedonia (Beshkov 2014) and Serbia (Beshkov 2015). In Bulgaria it was known only from Rhodopi Mts, three localities reported in Zlatkov and Beshkov (2008) and from Belassitza Mts (Beshkov 2011), and it is reported here from more localities. The lack of records may be because of its early flight period and possible misidentification with other *Egira* species. Identification without examination of genitalia is generally easy, but for those with insufficient experience, dissection or at least checking of external genitalia after brushing with a fine brush is recommended. However, dissection is preferable as the size and number of the cornuti in the vesica are another differentiation between *E. anatolica* (Fig. 11) and *Egira conspicillaris* (Linnaeus, 1758) (Fig. 12).

***Mythimna (Morphopoliana) languida* (Walker, 1858) (= *consanguis* auct. nec Guenée, 1852)**

SW Bulgaria, Struma river valley, rocky hill above the fishpond near Levunovo village, Sandanski district; ca 120 m, 41°29'29"N, 023°16'07"E, 19.xi.2020 (Fig. 13), V. Gashtarov leg., 1 male (Fig. 14).

New to Bulgaria. In Macedonia it was known from Kicevo, 02.v.1981 (Pettersson 1990; Rezbanyai-Reser and Hausmann 2000). Recently reported as new for Albania in several coastal localities (Beshkov 2018; Beshkov and Nahirnić 2019). It has spread also recently in the rest of Europe: e.g. Germany (Heinicke 1997); Italy (Rezbanyai-Reser and Hausmann 2000); Spain (Yela and De Vrieze 2002), Sweden (Gustafsson and Malm 2021) or in Denmark (Karsholt and Nielsen 2013). In the Balkans known also from Central Greece and the Peloponnese (Hacker 1989). *Mythimna languida* is a palaeotropical-subtropical species known in Europe from the Mediterranean coast with some dispersal inland. In Bulgaria, as well as in the only locality in North Macedonia, the records are presumably due to migration. *Mythimna languida* has been found in the same locality with *C. accentifera*, another palaeotropical-subtropical species reported here.



Figure 13. Collecting locality of *Mythimna languida*. Bulgaria, near Levunovo, 19.xi.2020.

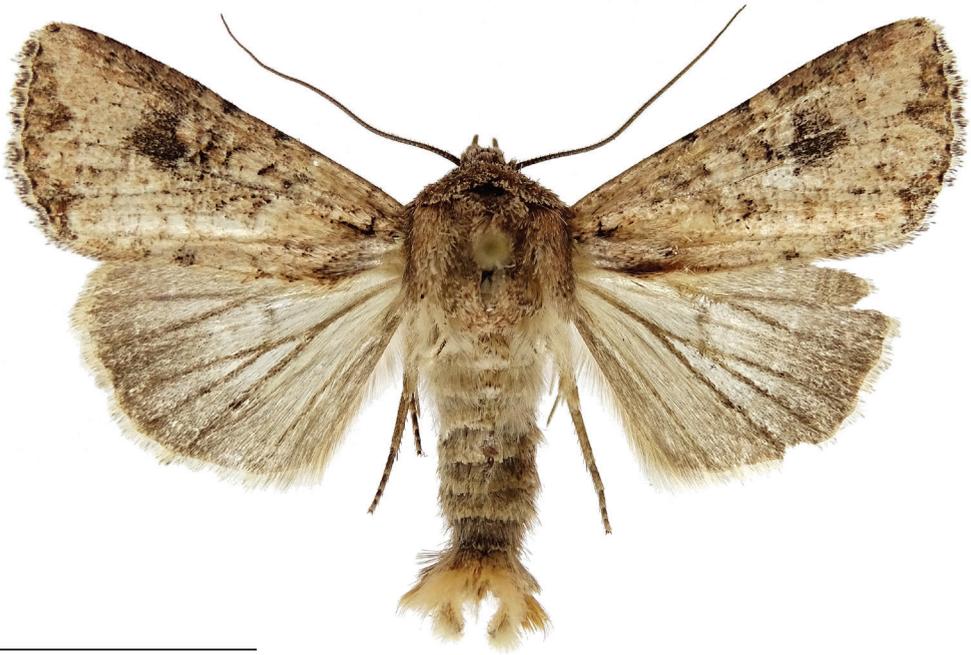


Figure 14. *Mythimna languida*, male. Bulgaria, near Levunovo, 19.xi.2020. Scale bar: 1 cm.

Conclusion

In the Balkan Peninsula and within certain Balkan countries is still possible to find a species new to Europe, since the Balkans are insufficiently investigated, even for Macrolepidoptera. Some species, such as *Anchoscelis luteogrisea*, *Griposia bouveti pinkeri* and *Egira anatolica*, may be overlooked because for confirmation of the identification, full examination of genitalia is necessary. Most of the species reported here are on the wing in the early spring (*Eriogaster inspersa*, *Egira anatolica*) or late autumn (*A. luteogrisea*, *G. bouveti pinkeri* and *Polymixis xanthomista*) when collecting is sometimes problematic due to weather conditions. For some other palaeotropical-subtropical species found recently in the most southern and warmer locations of Bulgaria, such as *Ctenoplusia accentifera* and *Mythimna languida*, we are of the opinion that they have spread as a result of climate change. Similarly, some other species with palaeotropical-subtropical range previously recorded in Bulgaria from the southernmost area of the country have recently extended their range and have started breeding in the central parts of Bulgaria, e.g. *Lindenia tetraphylla* (Van der Linden, 1825) (Odonata) (Kolev and Boudot 2018) and *Lethocerus patruelis* (Stål, 1855) (Hemiptera) (Grozeva et al. 2013). In our opinion certain species with Atlantico-Mediterranean ranges such as *P. xanthomista* and *Menophra japygiaria* (O. Costa, 1849) colonised the Balkans from the Central Apennines to the Albanian coast directly, and not along the Adriatic coasts of Italy and Dalmatia (cf. Racheli and Zilli 1985; Schmitt and Varga 2012; Sucháčková Bartoňová et al. 2021).

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A new species of *Eupithecia* Curtis (Lepidoptera, Geometridae) from the Andes of northern Chile

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<http://zoobank.org/56CFE7C5-114A-4C05-BD32-6B0D4762E50D>

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Abstract. *Eupithecia copaquillaensis* sp. nov. (Lepidoptera, Geometridae, Larentiinae, Eupitheciini) is described and illustrated. Adults of this new species were discovered using a light trap in the Copaquilla ravine, at about 2800 m elevation on the western slope of the Andes of northern Chile. The morphology of the genitalia of *E. copaquillaensis* resembles that of *E. atacama* (Vojnits, 1985), which is also Chilean. However, the shape of the smaller cornutus and the signa in the male and female genitalia respectively enable accurate differentiation of the two species. DNA barcodes are used to associate male and female *E. copaquillaensis*.

Introduction

The widespread moth genus *Eupithecia* Curtis, 1825 (Larentiinae, Eupitheciini) is the most speciose of the family Geometridae (Lepidoptera), with more than 1300 species listed in the latest world catalogue (Parsons et al. 1999). Despite this impressive number, new species continue to be discovered in different parts of the world (e.g. Ferris 2007; Mironov and Ratzel 2012; Mironov and Galsworthy 2014; Skou et al. 2017; Seven et al. 2019).

Based on the study of the Palearctic, Nearctic and Oriental fauna, Mironov and Galsworthy (2012) redefined *Eupithecia* and indicated a combination of some key features in the male genitalia for distinguishing the genus from the morphologically closely related genera of Eupitheciini: uncus broadest basally and hook-like distally with one or two tips, juxta “hourglass shaped” with a bilobed calcar, anterior arm of labides curved with a setose finger-like papilla at apex, and sternum VIII modified with patches of sclerotization. Furthermore, recent molecular phylogenetic studies that included Old World representatives of *Eupithecia* suggest that the genus represents a monophyletic group (Öunap et al. 2016; Brehm et al. 2019).

About a fourth of all the known species of *Eupithecia* are recorded in the Neotropical Region (Herbulot 2001). It has been suggested that the moist environments of the Andes are the most species-rich for this genus in the world (Brehm et al. 2019), based on the high species richness revealed in recent studies performed in the moist forests of the Ecuadorian Andes (Brehm et al. 2016). In contrast, the species richness of *Eupithecia* appears to be lower in the arid environments of South America (Rindge 1987).

Parsons et al. (1999) listed 61 species of *Eupithecia* with type locality in Chile; four others were added later (Parra and Ibarra-Vidal 2002; Vargas 2011). Most of the Chilean *Eupithecia* occur in the central and southern zones of the country (Vojnits 1985, 1992, 1994; Rindge 1987, 1991). In contrast, only five species have been recorded in the extremely arid environments of the northernmost part, at about 18–19°S, only one of which is known to occur in the highlands of the Andes (Rindge 1987; Vargas 2011). Adults of a second high-elevation species were recently collected in northern Chile. The examination of their genitalia revealed that the moths represent an undescribed species, whose description is provided here. DNA barcodes of one female and one male were used to confirm conspecificity.

Material and methods

The studied specimens were collected using a light trap in December, 2020 in the Copaquilla ravine (18°23'55"S, 69°37'49"W) at about 2800 m elevation on the western slopes of the Andes. Their abdomens were removed, cleared in hot KOH 10% for a few minutes, stained with Eosin Y and Chlorazol black and slide-mounted with Euparal. Images were captured with a Sony CyberShot DSC-HX200V digital camera attached to a Leica M125 stereo microscope and a Micropublisher 3.3 RTVQImaging digital camera, attached to an Olympus BX51 microscope. The distribution map was generated using SimpleMappr (Shorthouse 2010). Specimens will be deposited in the “Colección Entomológica de la Universidad de Tarapacá”, Arica, Chile (IDEA).

Genomic DNA was extracted from legs of one female and one male using the QIAamp Fast DNA Tissue Kit, following the manufacturer’s instructions, and sent to Macrogen Inc. (Seoul, South Korea) for purification, PCR amplification and sequencing of the barcode region (Hebert et al. 2003) using the primers (LEP-F1 and LEP-R1) and following the procedures described in Hebert et al. (2004). The sequences were aligned with ClustalW in MEGA X (Kumar et al. 2018) to search for variable sites and were analyzed using the BOLD Identification System (Ratnasingham and Hebert 2007).

Results

DNA barcodes

Two identical DNA barcode sequences of 658 base pair length were obtained, confirming the conspecificity of the male and the female analyzed (GenBank accessions MZ821652, MZ821653, respectively). The nearest match in BOLD (98.6% similarity) was with one sequence of *Eupithecia* from Antofagasta, Chile, at “Private” status. The following nearest match (93.9%) was with “*Lepidoptera* sp. 049 PS-2011” from Ecuador.

Eupithecia copaquillaensis sp. nov.

<http://zoobank.org/A4BD2F1B-22C7-4CBF-9A89-138C7D3B9058>

Figs 1–7

Type material. *Holotype*, male, CHILE: Chile, Parinacota, Copaquilla, 2800 m.; December 2020; light trap; H.A. Vargas leg.; IDEA-LEPI-2021-007; genitalia slide HAV-1415. Specimen and genitalia slide deposited at IDEA.

Paratypes, CHILE. Three males, IDEA-LEPI-2021-008, IDEA-LEPI-2021-009, IDEA-LEPI-2021-010, genitalia slide 1408, 1409, 1473, respectively, three females IDEA-LEPI-2021-011, IDEA-LEPI-2021-012, IDEA-LEPI-2021-013, genitalia slides 1410, 1417, 1434, respectively, same data as for holotype. Specimens and genitalia slides deposited at IDEA.



Figure 1. Male paratype of *Eupithecia copaquillaensis* sp. nov. in dorsal view. Scale bar: 5 mm.

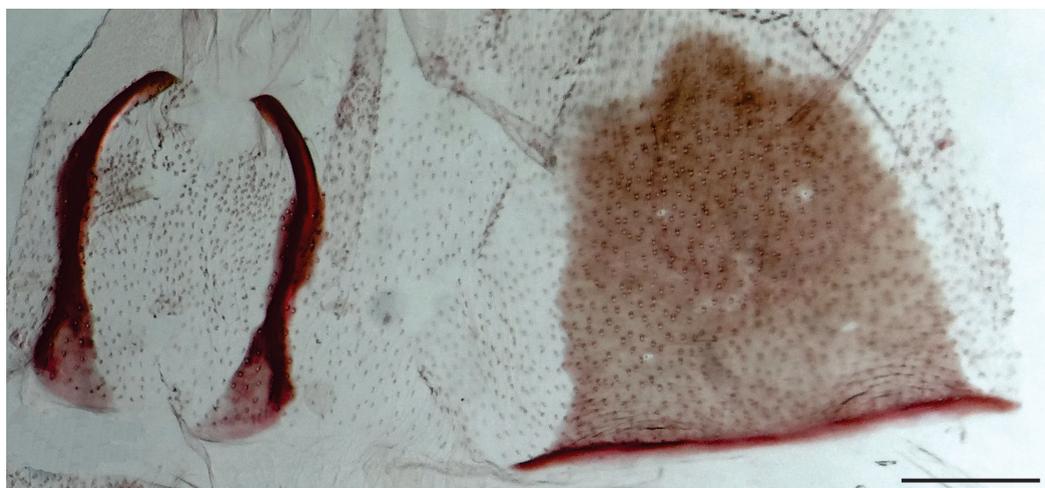
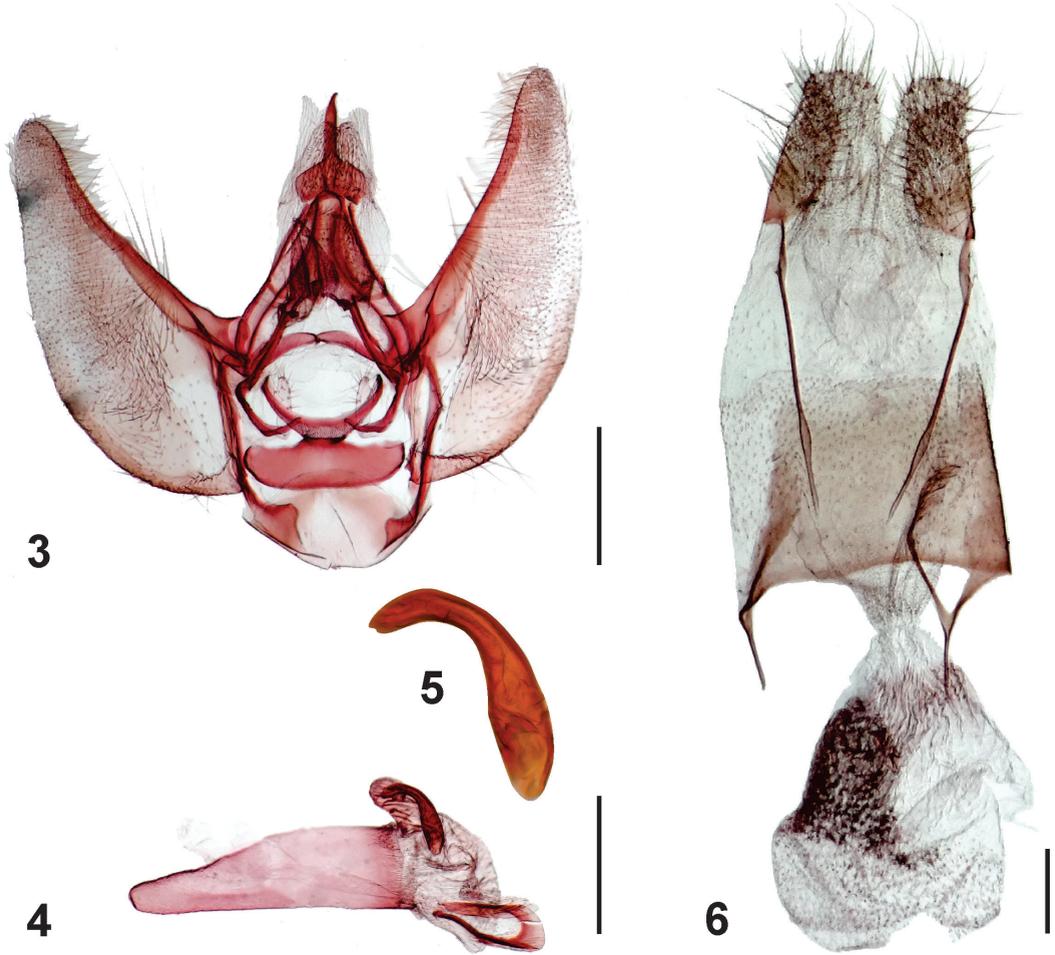


Figure 2. Male abdominal segment VIII of *Eupithecia copaquillaensis* sp. nov. Sternum (left) in ventral view; tergum (right) in dorsal view. Scale bar: 0.2 mm.

Diagnosis. The morphology of the genitalia of *E. copaquillaensis* sp. nov. (Figs 3–6) closely resembles that of *E. atacama* (Vojnits, 1985) (Figs 8–11), with type locality near Freirina village in the Huasco Province of northern Chile, also recorded in a few localities of the Coquimbo Province (Vojnits 1985). *E. atacama* was originally described in *Heteropithecia* Vojnits, 1985, a monotypic genus synonymized with *Eupithecia* by Rindge (1987). This synonymy has been followed in



Figures 3–6. Genitalia of *Eupithecia copaquillaensis* sp. nov. **3.** Male genitalia in ventral view, phallus removed; **4.** Phallus in lateral view; **5.** Smaller cornutus; **6.** Female genitalia in ventral view. Scale bar: 0.4 mm.

subsequent studies (Rindge 1991; Parsons et al. 1999), including the redefinition of *Eupithecia* by Mironov and Galsworthy (2012). The males of *E. copaquillaensis* sp. nov. and *E. atacama* have two cornuti on the vesica, the larger of which is a narrow horseshoe-like piece with asymmetrical arms. However, the smaller cornutus is sub-cylindrical and curved on the distal half in *E. copaquillaensis* sp. nov., while it is depressed, squat and concave in *E. atacama*. The females of the two species have a mainly membranous corpus bursae with small teeth-like signa. However, the signa are grouped in a dense semicircular patch in *E. copaquillaensis* sp. nov., while those of *E. atacamae* are arranged in longitudinal stripes.

Description. Male (Fig. 1). Forewing length 9.9–10.1 mm.

Head. Frons and vertex creamy white with brownish gray scattered scales. Labial palp concolorous with frons and vertex. Antenna filiform, creamy white dorsally, ciliated ventrally, cilia longer than flagellomere diameter.

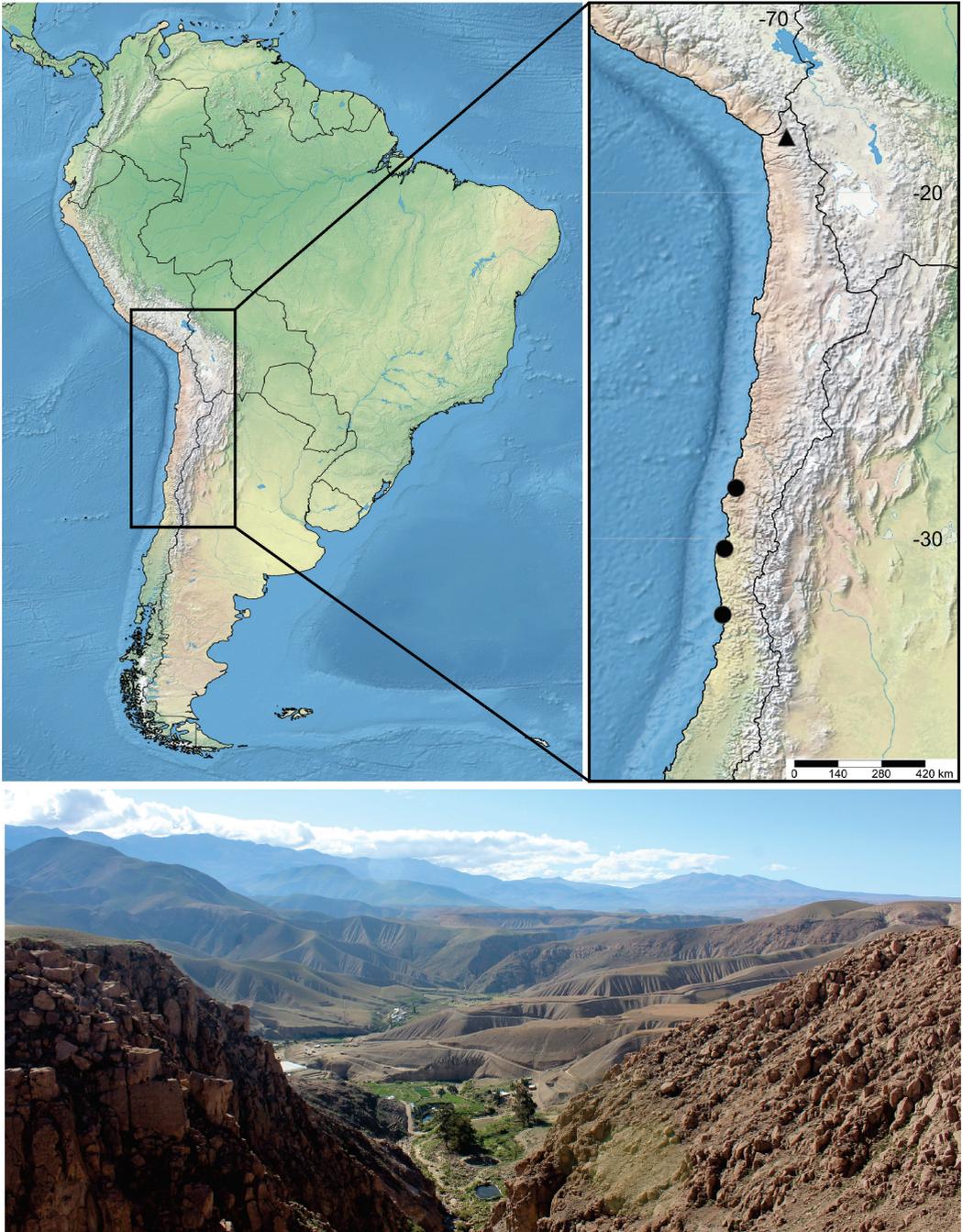


Figure 7. Geographic distribution of two morphologically close species of *Eupithecia* of northern Chile: *E. copaquillaensis* sp. nov. (triangle) and *E. atacama* (Vojnits, 1985) (circles). Lower box shows the type locality of *E. copaquillaensis* sp. nov., the Copaquilla ravine, on the western slopes of the Andes of northern Chile.

Thorax. Mainly creamy white with brownish gray and yellowish brown scattered scales. Fore-leg mainly brownish gray with creamy white scattered scales. Mid- and hindleg mainly creamy white with brownish gray scattered scales; tibial spurs creamy white. Forewing mainly creamy white with abundant brownish gray and a few yellowish brown scattered scales; poorly differentiated brownish gray transverse stripes broader and darker near costal margin, narrower and lighter towards posterior margin. Hindwing mainly creamy white with poorly differentiated brownish gray transverse stripes near posterior wing margin and brownish gray scattered scales on distal half.

Abdomen. Mainly creamy white with brownish gray and yellowish brown scattered scales. Tergum VIII (Fig. 2) square-like; anterior margin straight, distinctly sclerotized, shortly projected laterally; posterior margin with short semicircular projection in the middle. Tergum VIII (Fig. 2) as two separate longitudinal rods depressed anteriorly, medially curved posteriorly.

Male genitalia (Figs 3–5). Uncus broad, depressed basally, narrow, spine-like distally, with pointed apex. Tegumen narrow, left and right parts completely separated. Saccus broadened ventrally, posterior margin broadly rounded. Juxta as a transverse ellipsoid stripe, calcar broadly U-shaped. Transtilla as a transverse stripe. Labides with anterior arm medially curved, bearing an apical finger-like papilla with short setae on distal half; posterior arm straight, bearing a semicircular slightly sclerotized papilla. Valva elongated, broader basally, narrowing distally, apex rounded, costal sclerotized band not reaching apex, sacculus slightly sclerotized. Phallus sub-cylindrical, anterior apex rounded, broadening distally; vesica with two cornuti, larger cornutus a narrow horseshoe-like piece with asymmetrical arms, smaller cornutus a sub-cylindrical piece curved on distal half.

Female. Forewing length similar to male. Antenna with cilia shorter than flagellomere diameter. Wings slightly lighter than those of male, with less brownish gray and more yellowish brown scales.

Female genitalia (Fig. 6). Papilla analis lobe-like, slightly sclerotized near anterior margin, with hair-like setae. Posterior apophysis narrow, rod-shaped, about twice the length of papilla analis. Anterior apophysis narrow, rod-shaped, about half the length of papilla analis; ventral arm about same length as papilla analis, distally depressed and slightly broadened. Antrum broad, membranous. Ductus bursae short, membranous. Corpus bursae mainly membranous, with longitudinal striations, small teeth-like signa grouped in a dense semicircular patch. Ductus seminalis at apex of a narrow, finger-like appendix bursae near the base of corpus bursae.

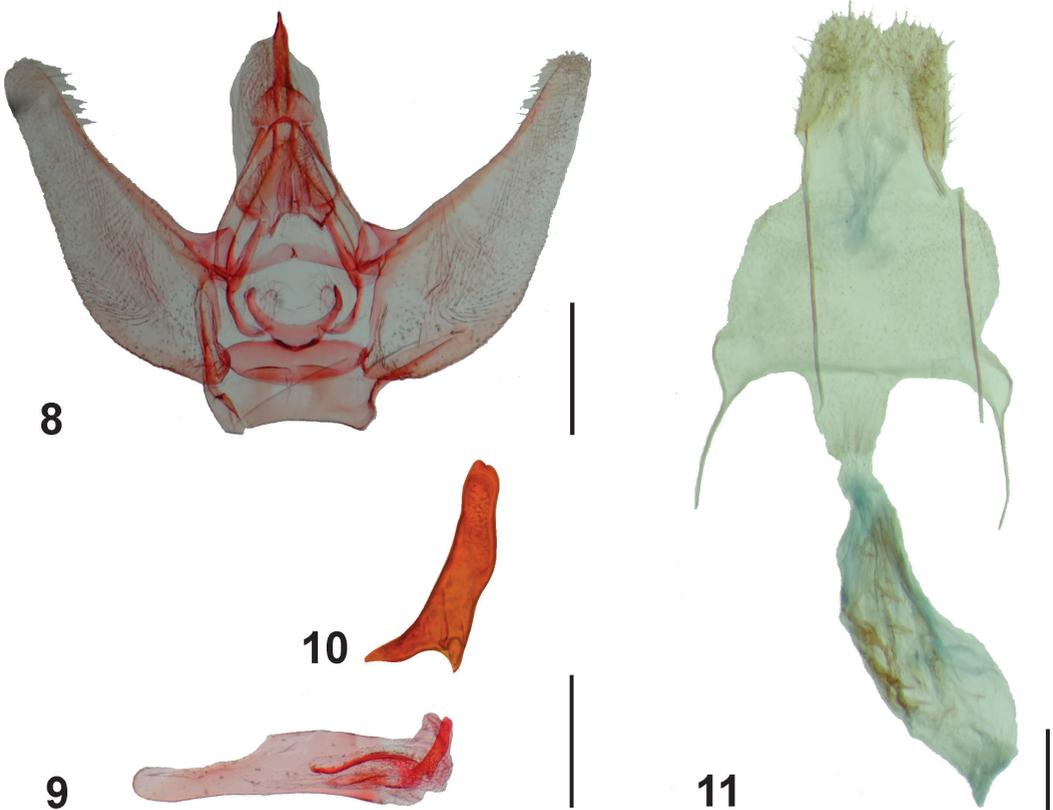
Etymology. The specific name is derived from the type locality.

Distribution (Fig. 7). Based on the type material, *E. copaquillaensis* sp. nov. is known only from the type locality, the Copaquilla ravine (18°23'55"S, 69°37'49"W), at about 2800 m elevation on the western slopes of the arid Andes of northern Chile. The high similarity (98.6%) of the barcode of *E. copaquillaensis* sp. nov. to a congeneric sequence from Antofagasta, Chile found in BOLD suggests a broader geographic range, reaching to about 400 km south of the type locality. However, the exact sampling site of the BOLD sequence is unknown.

Biology. Adults of *E. copaquillaensis* sp. nov. were collected using a light trap in December 2020. Host plants remain unknown.

Discussion

Eupithecia copaquillaensis sp. nov. is the second species of the genus known to occur in the arid highlands of the western slopes of the Andes of the northernmost part of Chile. The only con-specific previously recorded in the same area is *E. tarapaca* Rindge, 1987, whose larvae feed on



Figures 8–11. Genitalia of *Eupithecia atacama* (Vojnits, 1985). **8.** Male genitalia in ventral view, phallus removed; **9.** Phallus in lateral view; **10.** Smaller cornutus; **11.** Female genitalia in ventral view. Scale bar: 0.4 mm.

flower buds of *Balbisia microphylla* (Phil.) Reiche (Vivianiaceae) (Vargas 2016). However, the two species are easily separated based on morphology, because in the latter the male sternum VIII is a narrow piece with two short apical arms, the larger cornutus is a broad piece slightly shorter than the phallus and the smaller cornutus is a C-shaped piece, all of which remarkably contrast with the morphological pattern of *E. copaquillaensis* sp. nov.

Rindge (1987) arranged the species of *Eupithecia* of Chile in two Sections, namely 1 and 2, with the latter subdivided into four Groups named A to D, based on the morphology of the male segment VIII and male and female genitalia. The tergum fully sclerotized and the sternum as two separate longitudinal rods in the male segment VIII, the elongated valva, uncus with single apex and vesica with two cornuti in the male genitalia, and the corpus bursae with longitudinal striations in the female genitalia suggest that *E. copaquillaensis* sp. nov. is related to the species of Section 1, in which Rindge (1987, 1991) included the morphologically close *E. atacama* and four others: *E. atacamaensis* Rindge, *E. guayacanae* Rindge, 1991, *E. osornoensis* Rindge, 1987 and *E. seatacama* Rindge, 1987. However, the monophyly of this species group, as well as the phylogenetic relationships of all the Neotropical fauna of *Eupithecia*, must be reassessed using modern procedures.

Perhaps discouraged by the extremely arid conditions, surveys for geometrid moths have been scarce on the western slopes of central Andes. For instance, in the case of *Eupithecia*, the holotype

of *E. tarapaca* was until a few years ago the only specimen reported in the scientific literature from above 3000 m in the northernmost part of Chile (Vojnits 1985, 1992, 1994; Rindge 1987, 1991). In accordance with recent additions to other genera of Geometridae (Palacios et al. 2020; Vargas et al. 2020; Vargas 2021), the discovery of *E. copaquillaensis* sp. nov. confirms the need for further studies to characterize better the overlooked fauna of geometrid moths harbored by the high elevation environments of central Andes.

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In Memoriam: Peter Hättenschwiler 26.09.1927–17.08.2021

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At the age of 93, Peter Hättenschwiler (Fig. 1) passed away on August 17th 2021 at Uster (Switzerland). He is well known to the readers of this journal as a leading specialist of the Bagworm moths, in German “Sackträger” (Psychidae). Some of his most important publications appeared in the “Nota Lepidopterologica”, e.g. all papers “Zum System der paläarktischen Psychiden” (1991, 1999, 2004), written together with Prof. Dr. Willi Sauter (1928–2020) which are still of tremendous meaning for Psychidae research. Since 1977 Peter was an ordinary member of Societas Entomologica Europaea and became honorary member in 2007.



Figure 1. Portrait Peter Hättenschwiler, 1998 (Photo: Author unknown).

Peter was born on September 26th 1927 at St. Gallen (Switzerland). After school, he started an apprenticeship as a precision mechanic at the former Zellweger AG at Uster (ZH). He remained closely associated with this town during his whole life. Peter worked on the development of machines for testing yarns, especially of silk, and on the establishment of quality standards, which are still relevant today as the “Uster Statistics”. Due to his professional activities as a customer consultant, he visited many countries and on these occasions he took advantage of many opportunities to collect Bagworm moths. Later on he advanced to become the company’s chief technology officer and continued to work with silk until after his retirement.

The fact that Bagworm moths became his lifelong passion probably is closely connected with his decades-long friendship with Prof. Dr. Willi Sauter. Sauter received his doctorate in 1956 with a thesis on the morphology and systematics of the Swiss species of the genus *Solenobia* auct. (= *Dahlica* Enderlein) with Prof. Dr. Jakob Seiler (1886-1970) at ETH Zurich. Later he was considered one of the best European psychid experts. He encouraged and supported Peter in 1977, based on the knowledge gained together, to describe the first three new taxa, later followed by many others. One of these (*Dahlica sauteri*) he dedicated to his friend.

Already about 30 years ago, I (TS) was fascinated during my first contacts with Peter by his careful way of handling his collection objects. Packages which I received from him were small works of art, showing accurately placed different stamps; small jars filled with a special mix of alcohol and formalin containing the wingless females of the Psychidae were individually wrapped in pink tissue paper and packed in absorbent cotton. It was only later during visits to Uster that we got to know each other personally.

It was Peter’s warm-heartedness and willingness to help which deeply impressed me (TS). He supported me with literature, exactly and precisely pinned psychid specimens and expertise, which he freely shared without any reservation. Thus, over time, a friendly collaboration developed. Peter was a family man. His family supported Peter’s entomological work with the careful rearings, travel companionship and their own collections during their holiday trips. He was married to his wife Ruth for 65 years. They have three children, seven grandchildren and two great-grandchildren. At Christmas time, Peter’s annual summaries written jointly with Ruth, were eagerly awaited by our family. (Fig. 2)

On our silver wedding in 2016 my wife Ute and me (TS) took a trip to New Zealand to the Bay of Islands. We also searched for *Scoriodyta* species there and were successful. As a small episode on the side, it may be noted that I noticed after our return that Peter had collected *Scoriodyta* at that same place almost 35 years earlier for his revision of that genus. When I shared this with him, he reported with a smile that the occasion of his trip was also his silver wedding anniversary.

Peter’s kindness of heart was almost proverbial. When I (WRA) met Peter in 1974 as a young entomologist on the occasion of my first small essay about Bagworm moths in the “Entomologische Zeitschrift”, he literally bound me to the psychids, eventually with his extensive experience and knowledge as well as with the already described and excellently pinned specimens which he always generously exchanged. Hence, Peter’s support was one reason that I have remained faithful to psychids until today.

One of his mentors was the well-known Austrian psychid expert Leo Sieder (1887-1980). When I (WRA) visited Leo in Klagenfurt in 1975 he told me that Peter had a very close personal relationship with him which went far beyond the regular exchange of Bagworms and expertise. In the 1960th Sieder gave his large psychid collection to the Karlsruhe Natural History Museum due to health reasons. Because he missed his work with his beloved Psychidae, shortly thereafter he fell



Figure 2. Peter with his wife Ruth in his study in Uster, Seeblickstraße, approx. 1990 (Photo: Sereina Parpan-Hättenschwiler).

into a deep psychological crisis. It is characteristic for Peter's empathy that he was able to convince the old man to start collecting Bagworms again to overcome his problems. The result was several more boxes of valuable material and Sieder's health improved over the years. Similarly, after the death of my son Christian in 2000, followed by a difficult time of grief, I (WRA) was convinced by Peter to resume my entomological activities, of course with an extensive package with literature and Psychidae from him.

Besides some essays on silk and yarn production, Peter's entomological publications are significant. They deal exclusively with the Psychidae over a period of 50 years. He published more than 50 papers, 20 of them in the "Nota Lepidopterologica". The faunistic treatment of the Psychidae in the Swiss "Schmetterlinge und ihre Lebensräume" (Hättenschwiler 1997) is to be emphasized as a good example of the profound research on this family with aids for species determination and equipped with excellent photos. (Fig. 3)

Peter introduced the family group names of Placodomininae (Sauter & Hättenschwiler 1991) and Scoriodytinae (Hättenschwiler 1989). Altogether he described 31 taxa, but it is difficult to identify his main focus or special interests in the Psychidae, because Peter's publications cover a wide range. Due to his enormous notoriety as a leading Bagworm specialist, many entomologists have turned to Peter with their questions. Thus, a very broad spectrum of different publication themes has resulted over time, with descriptive taxonomy probably accounting for the largest proportion.

Travels took him to many countries in Europe and other continents, for example to the USA, China and New Zealand.



Figure 3. Peter determining Psychidae (2005) (Photo: Franz Lichtenberger).

As a very active member, he was the soul of the Entomological Society of Zurich and its president from 1968 to 1974 and he became honorary member in 1979. Peter was associated with all important Psychidae specialists worldwide, for example Dr. Wolfgang Dierl (1935-1996) in Munich, Dr. Jean Bourgogne (1903-1999) in Paris, Leo Sieder in Klagenfurt, Dr. Donald R. Davis (*1934) in Washington, Dr. Gaden Robinson (1949-2009) in London and Prof. Toyohsei Saigusa (*1937) in Japan. But he was also in contact with specialists of other Lepidoptera families, e.g. with Dr. Chunsheng Wu from China, Ole Karsholt (*1948) in Copenhagen, Erik van Nieukerken (*1952) in Leiden and many others. The type specimens of the species described by him and also other specimens are deposited in numerous museums and private collections. He greatly supported the psychid research of many other lepidopterists and these achievements are evident by the acknowledgements in numerous publications.

After his move to the Tertianum “Residenz Brunnehof” in Uster in 2017 Peter transferred his entire collection of about 40,000 specimens (mainly Psychidae) and associated archival materials to the Entomological Collection of ETH Zurich.

With the passing of Peter Hättenschwiler, lepidopterology has lost an outstanding specialist. All who knew him will miss his friendly manner, his helpfulness and his competent professional advice.

We sincerely thank his daughter Sereina Parpan-Hättenschwiler (Uster) for her support and information about Peter’s life. We would also like to thank Don Davis for reviewing the manuscript and linguistic corrections.

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- Hättenschwiler P, Dewhurst C, Nyaure S, Bonneau L (2013) New bagworms (Lepidoptera, Psychidae) from oil palm plantations in Papua New Guinea. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 86: 253–260.

Described taxa

Subfamilies

- Placodomininae Sauter & Hättenschwiler, 1991
 Scoriodytinae Hättenschwiler, 1989

Species

- Dahlica sauteri* (Hättenschwiler, 1977) (*Solenobia*)
Dahlica simplonica (Hättenschwiler, 1977) (*Solenobia*)
Dahlica ticinensis (Hättenschwiler, 1977) (*Solenobia*)
Dahlica rianella Hättenschwiler, 1981
Reisseronia magna Hättenschwiler, 1982
Leptopterix himalayalta Hättenschwiler, 1985

- Oreopsyche dellabrunai* (Hättenschwiler, 1985) (*Standfussia*)
Scoriodyta dugdalei Hättenschwiler, 1989
Scoriodyta rakautarensis Hättenschwiler, 1989
Scoriodyta sereinae Hättenschwiler, 1989
Scoriodyta virginella Hättenschwiler, 1989
Scoriodyta suttonensis Hättenschwiler, 1989
Scoriodyta patricki Hättenschwiler, 1989
Typhonia christenseni (Hättenschwiler, 1990) (*Melasina*)
Proutia chinensis Hättenschwiler & Chao, 1990
Dahlica vaudella Hättenschwiler, 1990
Pseudobankesia casaella Hättenschwiler, 1994
Pseudobankesia contractella Hättenschwiler, 1994
Montanima aurea Hättenschwiler, 1996
Ptilocephala piae Hättenschwiler, 1996
Sciopetris karsholti Hättenschwiler, 1996
Eumasia brunella Hättenschwiler, 1998
Eumasia ziegleri Hättenschwiler, 1998
Typhonia beatricis Hättenschwiler, 2000 (syn. zu *Typhonia melana* Frivaldski, 1838)
Oiketicoides jamaicana Hättenschwiler & Rezbanyai-Reser, 2003
Phalacropterix fritschi Hättenschwiler, 2003
Acanthopsyche muralis Hättenschwiler, 2004
Amicta sericata Hättenschwiler & Alemansoor, 2006
Manatha conglacia Hättenschwiler, Dewhurst & Nyaure, 2013
Amatissa bilomia Hättenschwiler, Dewhurst & Nyaure, 2013
Amatissa nava Hättenschwiler, Dewhurst & Nyaure, 2013

Patronyms

- Peloponnesia haettenschwileri* Hauser, 1996
Placodoma haettenschwileri Sobczyk, 2013