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# Alpine Entomology

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## Alpine Entomology

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### Photo

The cover picture shows habitus of *Hypera temperei* Hoffmann, 1958. See paper of Germann C *Hypera temperei* Hoffmann, 1958 – first discovery of the western alpine element in the Swiss Alps with biological details, and new morphological insights (Coleoptera, Curculionidae).

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# First report of *Cooka incisa* (Beekey, 1937) from Europe (Diptera, Scatopsidae)

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## Abstract

*Cooka incisa* (Cook, 1956) is recorded from several wooded localities in southern Switzerland (canton of Ticino). This is the first European record of this species, as well as the first record of the otherwise Nearctic genus *Cooka* Amorim, 2007 in the Palaearctic region as a whole. The possibility of an accidental introduction of *C. incisa* in Europe is discussed.

## Key Words

Scatopsidae, faunistics, Palaearctic, Nearctic, Switzerland

## Introduction

In 2015–16 an extensive faunistic survey employing different trapping methods was conducted in the area initially proposed for the Swiss National Park of Locarnese, near Locarno (Ticino, southern Switzerland). Among the many Diptera found, midges of the family Scatopsidae were caught in significant numbers, revealing the presence of several interesting species, some of them still under study (Haenni and Pollini in prep.). The unexpected discovery among this material of a Nearctic species never before recorded in Europe is presented here.

## Material and methods

The samples were collected by Lucia Pollini (LP) and †Michele Abderhalden during a 2015–16 faunistic survey in the area of the planned Swiss National Park of Locarnese, using Malaise traps, aerial Malaise traps (SLAM traps) and three slightly different beer/wine traps. This material, sorted by LP, is preserved in 70%

alcohol in the collection of the Museo cantonale di storia naturale in Lugano (MSNL) and was identified by Jean-Paul Haenni (JPH).

Additional specimens of *C. incisa* were discovered in material sent for identification to JPH by Gerhard Bächli (Dietikon) and preserved in his collection (CGB) (now partly in the collection of the Muséum d'histoire naturelle de Neuchâtel (MHNN)). This material originates from two biodiversity programs, namely a general faunistic survey of Switzerland conducted by Peter Duelli (WSL, Birmensdorf) from 1999 to 2006, using “Kombi-fallen” (window traps combined with yellow pans), and the national research program BiodiverCity conducted by Thomas Sattler (WSL, Birmensdorf) using “Kombi-fallen” and pitfall traps in 2006 in urban landscapes of three Swiss cities (Lugano, Luzern, Zürich). The dipteran material, originally preserved in 70% alcohol, was later sorted and partly dry-mounted by G. Bächli. Some specimens were cleared in KOH, dissected and slide-mounted for description and production of figures. Morphological nomenclature follows Haenni (1997), nomenclature and faunistics Haenni (2013).



**Figures 1–4.** *Cooka incisa* (Cook): **1.** Habitus, male, lateral view. **2.** Wing, male. **3.** Tip of abdomen and genital capsule, male, ventral view; inset a. Genital capsule, dorsal view (true ventral, as genitalia rotated through 180°). **4.** Tip of abdomen, female, lateral view.

## Faunistics

### *Cooka incisa* (Cook, 1956)

Figs 1–5

*Rhexoza incisa* Cook, 1956: Ann. Ent. Soc. Am. 49: 6, figs 2A, 2G, 3B.

Cook in Stone & al., 1965: Cat. Dipt. N. Amer.: 240.

Cook, 1975: Pan-Pac. Entomol. 51: 66, figs 13, 24–25.

Cook, 1981: Manual of Nearctic Diptera 1: 315, figs 20–22.

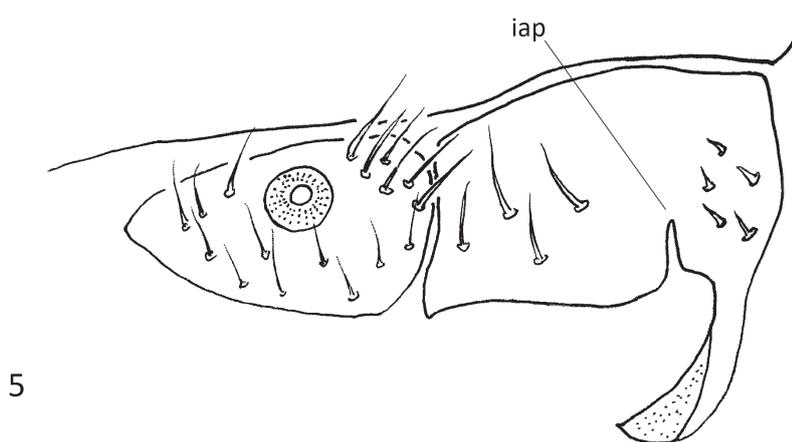
*Cooka incisa* (Cook, 1956): Amorim 2007: Zootaxa 1640: 48.

**Material studied** (12♂♂, 4♀♀). SWITZERLAND, TI: Bolle di Magadino, [Gordola, Reviscài], 199 m, 710.121/114.037 [46°10'07.685"N, 8°51'52.248"E], forest, mid June-end July 2000, 1♂; same locality but mid June-end July 2001, 3♂♂ 1♀; same locality but mid June-end July 2004, 2♂♂; same locality but mid June-end July 2005, 2♂♂, all P. Duelli leg., CGB, MHNN; Lugano, 24.VI–5.VIII.2006, 1♂, Th. Sattler leg., MHNN; Losone, Arcegno, Collina di Maia, 420 m, 701.151/113.376 [46°09'51.337"N, 8°44'53.687"E], ARC1, 21–28.VII.2015, birra bianca, 2♀♀; same, but 7–18.VIII.2015, 1♂ 1♀; same, but 411 m, 701.013/113.741 [46°10'03.240"N, 8°44'47.535"E], ARC2, 28.VII–7.VIII.2015, vino, gialla,

1♀; same, but, 366 m, 701.307/113.196 [46°09'45.434"N, 8°45'00.812"E], ARC3, 7–26.VII.2016, birra bianca, 1♂, all L. Pollini & M. Abderhalden leg., MSNL.

**Diagnosis.** Body, elongate (Fig. 1), dull in general appearance, except for contrasting, shining tergite 7 and basally sub-shining sternite 7 in male. Wing venation (Fig. 2) very similar to that of *Rhexoza* species and of the cosmopolitan *Coboldia fuscipes*. Tergite 7 (Fig. 3) with median posterior projection broad, sternite 7 deeply incised medially, genital capsule (Fig. 3) with elongate, pointed, posteriorly directed lateral projections, aedeagus short. Female (Fig. 4) with tergite 8 deeply incised medially, sternite 8 broadly divided in two basally broad, apically pointed lateral lobes.

The Swiss material perfectly agrees with the description and figures of North American specimens of this species, especially regarding the very characteristic shape of the male genital capsule (Cook, 1981: fig. 20.22, and present paper, Fig. 3). *Cooka incisa* will run to *Rhexoza* in the key to the Palearctic genera of Scatopsidae (Haenni 1997), but can be differentiated from the four known European species of *Rhexoza* by the features given in the diagnosis. Furthermore, the pregenital segment of *C. incisa* is shiny, strongly contrasting with the other abdominal tergites in



**Figure 5.** *Cooka incisa* (Cook), male, anteprepronotum and anterior spiracular sclerite (iap: indentation of anteprepronotum).

the male, which are dull (pregenital segment only partly shining in female). All tergites are dull in *Rhexoza*.

**Distribution.** *Cooka incisa* was described by Cook (1956) (as *Rhexoza incisa*) from the Great Lakes region (USA: Iowa, Illinois, Minnesota; Canada: SE Ontario). It is recorded here for the first time from Europe and the Palaearctic region as a whole. In Europe it is presently known only from the Swiss canton of Ticino in the localities cited above.

**Biology.** “The larvae of this species have been collected from beneath the bark of dead American elm [*Ulmus americana*], box elder [*Acer negundo*] and cottonwood [*Populus* spp.] trees” in the USA (Cook 1956: 8), where this species is bound to wet areas. One of the Swiss localities, namely Bolle di Magadino, is a riverine forest which presents similar characteristics (main tree species are *Alnus glutinosa*, *Fraxinus excelsior*, *Quercus robur*, *Ulmus* spp., *Salix alba* and *Populus* spp., while *Acer negundo* is also present in the region). In Arcegno, on the other hand, *C. incisa* was caught in a forest consisting of chestnut (*Castanea sativa*) together with oak (*Quercus petraea*, *Q. pubescens*, *Q. robur* and *Q. rubra*) [“castagneto con querce”].

## Discussion

The genus *Cooka* Amorim, 2007 (with *Scatopse similis* Beekey, 1938 as type-species) is one of the most derived genera of the Swammerdamellini, as well as of the subfamily Scatopsinae as a whole. It was erected by Amorim (2007) for six species previously placed within *Rhexoza* Enderlein, 1936 *sensu lato* (Cook 1956, 1975). *Cooka* can be distinguished from *Rhexoza* mainly by the structure of male genitalia, the unsclerotized abdominal sternites 1–4 (only 1–3 unsclerotized in *Rhexoza*) and the shape of anteprepronotum, which is deeply indented ventrally in *Cooka* (Fig. 5). Until now, the distribution of *Cooka* was considered purely Nearctic (Amorim 2007), thus the discovery of one species in Europe could be of special interest from zoogeographical and phylogenetic points of view. However, the indigenous status of *C. incisa* in Europe cannot

be ascertained at present. Indeed, there are some cases of scatopsid species with Holarctic distribution: these include *Arthria analis* Kirby, 1837, *Pharsoreichertella simplicinervis* (Duda, 1928), *Scatopse lapponica* Duda, 1928 and *Thripomorpha borealis* (Cook, 1955), but all these species, however, exhibit more or less marked boreal affinities, with a circumpolar distribution. *Ectaetia clavipes* (Meigen, 1846), on the other hand, has a wide distribution both in Europe and in North America. The case seems different for *Cooka incisa*, whose only European records are those presented here from the canton of Ticino, in a region characterized by comparatively mild, warm Insubrian climatic conditions. Its absence from older faunistic surveys in Ticino is puzzling (first known capture in the year 2000), while its recent discovery in various forested environments within a relatively limited area (all five localities lie within a radius of only about 20 km) could indicate an alien origin for this species. The possibility of an accidental introduction of *C. incisa* from North America cannot be immediately discarded. Hopefully, future observations of this species from other parts of Europe or the discovery of additional material in collections may bring an answer to this question.

## Conclusion

Although one of the richest in Europe, the fauna of Scatopsidae of Switzerland still remains incompletely known, as shown by the discovery of *Cooka incisa* presented here, regardless of an indigenous or alien origin of this species. This demonstrates the importance of including poorly documented taxonomic groups in regional or national faunistic surveys of biodiversity.

## Acknowledgements

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# *Hypera temperei* Hoffmann, 1958 – first discovery of the western alpine element in the Swiss Alps with biological details, and new morphological insights (Coleoptera, Curculionidae)

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## Abstract

Since its description based on a single female from the Maritime Alps in France, no other localities of this enigmatic alpine species have become public. In a scree slope in the Valais at high montane altitude *Hypera temperei* Hoffmann, 1958 was discovered for the first time elsewhere, in Switzerland. The species' biology is unravelled, its habitat is described, and photographs of the male, larvae and pupa are presented. The re-investigation of the species morphology revealed that *Hypera temperei* is closest to *H. postica* (Gyllenhal, 1813), and not to *H. viciae* (Gyllenhal, 1813) as previously supposed. A revision of specimens in collections revealed that *H. temperei* is distributed even more eastern in the alpine Arc in Grisons at high montane to high alpine altitudes. Hence the species shows a considerably wider distribution in the Alps than supposed before.

## Key Words

Hyperinae, alpine species, new record, host plant, biology

## Introduction

The Swiss weevil fauna (Curculionoidea) comprising 1083 taxa is well explored, with a regularly updated checklist (Germann 2010a, 2011a, 2013a, 2017, 2019). But especially regarding alpine species with restricted distributions, some unexpected and thus surprising discoveries have been made in the past. In the Entiminae, *Otiorhynchus grischunensis* Germann, 2010 was such an unexpected discovery (Germann 2010b, 2012), still only known from four localities in the canton of Grisons. In Cyclominae, *Dichotrachelus sondereggeri* Germann, 2011 from Val Poschiavo is another example, where an investigation of the whole species-complex of *D. augusti* F. Solari, 1946 is likely to result in further discoveries of isolated populations at high alpine altitudes (Germann 2011b; Germann et al. 2017). Or the records of the apionid *Loborhynchapion amethystinum* (Miller, 1857) in the Binntal in Valais by Giusto and Germann (2015), a remarkable species with a distribution from Central Asia

to the Alps, with solely small and isolated populations towards the West.

In the present contribution, the subfamily Hyperinae bears such an unexpected discovery, on which I report in the following. Hyperinae are represented in Switzerland with 31 species out of the genera *Brachypera* Capiomont, 1868, *Coniatus* Germar, 1817, *Donus* Jekel, 1865, *Limobius* Schoenherr, 1843 and *Hypera* Germar, 1817, where the latter genus includes eleven species, the presently recorded *H. temperei* included. All Hyperinae show an ectophagous lifestyle, which is rather exceptional in Curculionidae. At first sight, the larvae of Hyperinae are morphologically more similar to caterpillars of Lycaenidae than to typical larvae of other Coleoptera, and can be determined to species level using chaetotaxy (Skuhrovec 2004, 2006, 2007; Skuhrovec and Bogusch 2016), but in several cases also based on their colouration and characteristics of their cuticula (Dieckmann 1989). Often these larvae are more easy to find and breed than searching for adult beetles. This was the case in the present discovery, where details are given in the following.

## Material and methods

The live photos were taken with an Olympus T4 tough camera partly in the field and partly in the lab. The mounted specimens and their genitalia were photographed with a Keyence 6000 photosystem at the NMB. All given coordinates in decimal degrees within square brackets should be understood as approximates of the localities written on the labels. The collected specimens of *Hypera temperei* from Valais, Zinal are conserved in the collections of the author, at the Naturhistorisches Museum Basel (NMB), and The Natural History Museum London (NHML). For subsequent DNA extraction two specimens are conserved in alcohol. Additional specimens were found and/or examined in the following collections: cCG – collection Christoph Germann, Rubigen. NMBE – Naturhistorisches Museum Bern. NMSO – Naturmuseum Solothurn.

## Results

### Excursions and breeding of larvae

During a first excursion to Zinal [46.13365°N, 7.62454°E], canton of Valais on the 2<sup>nd</sup> of July 2020, six larvae of at least two different larval stages (based on different sizes) of an unknown species of Hyperini were collected from *Astragalus leontinus* Wulfen growing along a path (Figs 1–3). The locality is situated at the bottom of an alpine scree slope facing towards east at 1650 m a.s.l. Three of those larvae (Figs 4–6) reached the stage of the last larval instar and built a net cocoon, whose colour reached from transparent-whitish (Figs 8–10) to slightly brownish (Fig. 11), where they pupated in the following 5 days. After 16–18 days the three adults, one female and two males, hatched. After 1 or 2 additional days, they showed a characteristic dark colouration (Figs 12–14).

On the 22<sup>nd</sup> and the 23<sup>rd</sup> of July 2020 a second excursion to the same place was taken in order to estimate the size of the whole habitat, the abundance of the host plant *Astragalus leontinus* (Figs 1–3) and to test for suitable surrounding habitats. The scree slope is surrounded by a *Larix-Picea* forest. The host plants are restricted to an artificial path which was broken through the scree slope in north-south direction. The host plants grew on both sides of the path in finer crushed rocks, likely an ideal substrate for the plant (Fig. 1). Along the scree the habitat consists the path (along 60 m), where more than 120 individual plants were counted. In the surroundings of the scree, in the forest and in the scree itself (on or between the rocks) no further plants could be detected. Hence, it can be supposed that at least in closer vicinity to the detected habitat no other suitable habitats are present. Under the host plant, also two adults could be found from the old (hibernated) generation (see sternite IX Fig. 20, in specimens which hatched in the same year, the sternite remains thin and feebly sclerotized for a longer time). In the leaves of an *Astragalus leontinus*, a cocoon with a

not yet pupated larva was found. Another 12 larvae (from totally 21 counted larvae) were taken home for breeding. Moreover, a search more southern in a flood plain (Les Plats de la Lé) along the rivulet La Navisence revealed three additional larvae – also from *H. temperei* which could be confirmed after successful breeding – collected from *Astragalus penduliflorus* Lam. Despite of the tested 30 specimens of the plant not more larvae were found.

### Morphology

The subsequent morphological comparison of the adults from Zinal with the description of *Hypera temperei* by Hoffmann (1958), the addition by Tempère and Péricart (1989) and a critical check (see comments below) of the identification key including a photo of the female holotype (Skuhrovec 2009) allowed its determination. Hence, the *Hypera* found in Zinal was definitely conspecific with *H. temperei*. Hoffmann (1958) described *Hypera temperei* in a short note of a first supplement of the Faune de France volume on page 1747 based on a single female collected by Gaston Tempère on the 24<sup>th</sup> July of 1956 at the Col de la Cayolle (2300 m a.s.l.) [44.2591°N, 6.7439°E] in the southwestern Alps. *Hypera temperei* was compared with its supposed sister species *H. viciae* (Gyllenhal, 1813) (Figs 29, 34, 35), from which *H. temperei* differed in the following characters: i) darker brownish colour, ii) rostrum bigger, iii) antennae and legs (mainly tibiae and tarsi) reddish, iv) bifid scales on elytra finer, v) those in middle of pronotum simple, vi) white bristles on elytra longer and somewhat elevated, vii) striae well visible. The addition on the species variation by Tempère (1961) can be confirmed. The integument of the elytra is more maculate, which concerns the odd intervals including sutural interval (Figs 12–14, 15) than in the type specimen. The white bristles in the punctures of the striae, and those longer ones on the intervals are well visible. The penis (Figs 30, 31) is similar to the hand drawing provided by Tempère (1961) and reprinted in Tempère and Péricart (1989), where the mentioned (lateral) constriction in the apical part is well visible (Fig. 30, arrow).

However, a thorough comparison with the common and widespread *Hypera postica* (Gyllenhal, 1813) (Figs 17, 19, 24, 26, 28, 32, 33), which also reaches altitudes up to 1800 m a.s.l. (e.g. Hoffmann 1954, and own unpublished data), was a first decisive result. Based on its morphology, *H. temperei* indeed looks much more similar to *H. postica* than to *H. viciae*, and can easily be confused with it, especially when the coloration patterns are more contrasting, as expressed in the Swiss specimens shown here. Even the larva looks much more like the ones of *Hypera postica* (Fig. 7), although all larvae of *H. temperei* had a dull surface (Figs 4–6), whereas those of *H. postica* are shining (Fig. 7). Dieckmann (1989: 101) characterised the larva of *H. viciae* as follows: “Larve durch zahlreiche schwarze Körnchen in der gelb-weißen



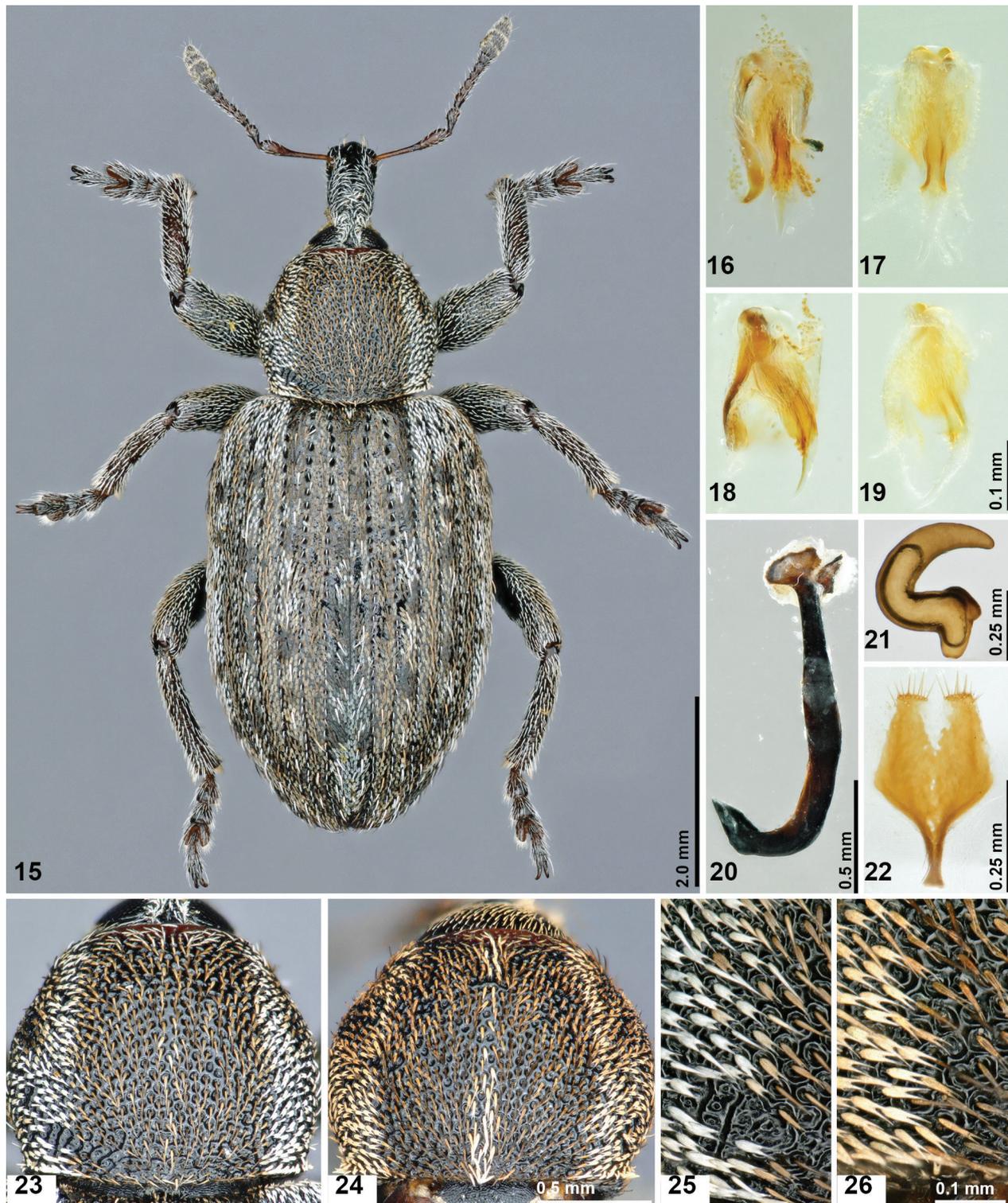
**Figures 1–3.** Habitat in a scree slope near Zinal. **1.** The arrows point at the microhabitats of *Hypera temperei* where *Astragalus leontinus* grows. **2, 3.** Host plant *Astragalus leontinus* where larvae, a cocoon and adults of *H. temperei* were found (Photos: C. Germann).

Haut grau bis grauschwarz aussehend...” which is clearly not the case in *H. temperei*. Concerning the adult weevil, the character of the rostral length used by Skuhrovec (2009) in the key to separate the “group *postica*” from the others is difficult or – in the case of *H. temperei* – not really possible to use. On the one side the rostrum is “short and robust” which leads to the *postica* group, on the other side the rostrum is “long and slender”,

which leads to *H. temperei* among others. It is even more difficult, if one of the typical traits of *H. temperei* is the longer rostrum, as mentioned above. Hence I here provide additional traits compared to the key by Skuhrovec (2009) that help separating *H. temperei* from *H. postica*, namely by: i) Its slightly more slender habitus, where the humeral calli are weakly pronounced (more pronounced in *H. postica*); ii) Colouration much



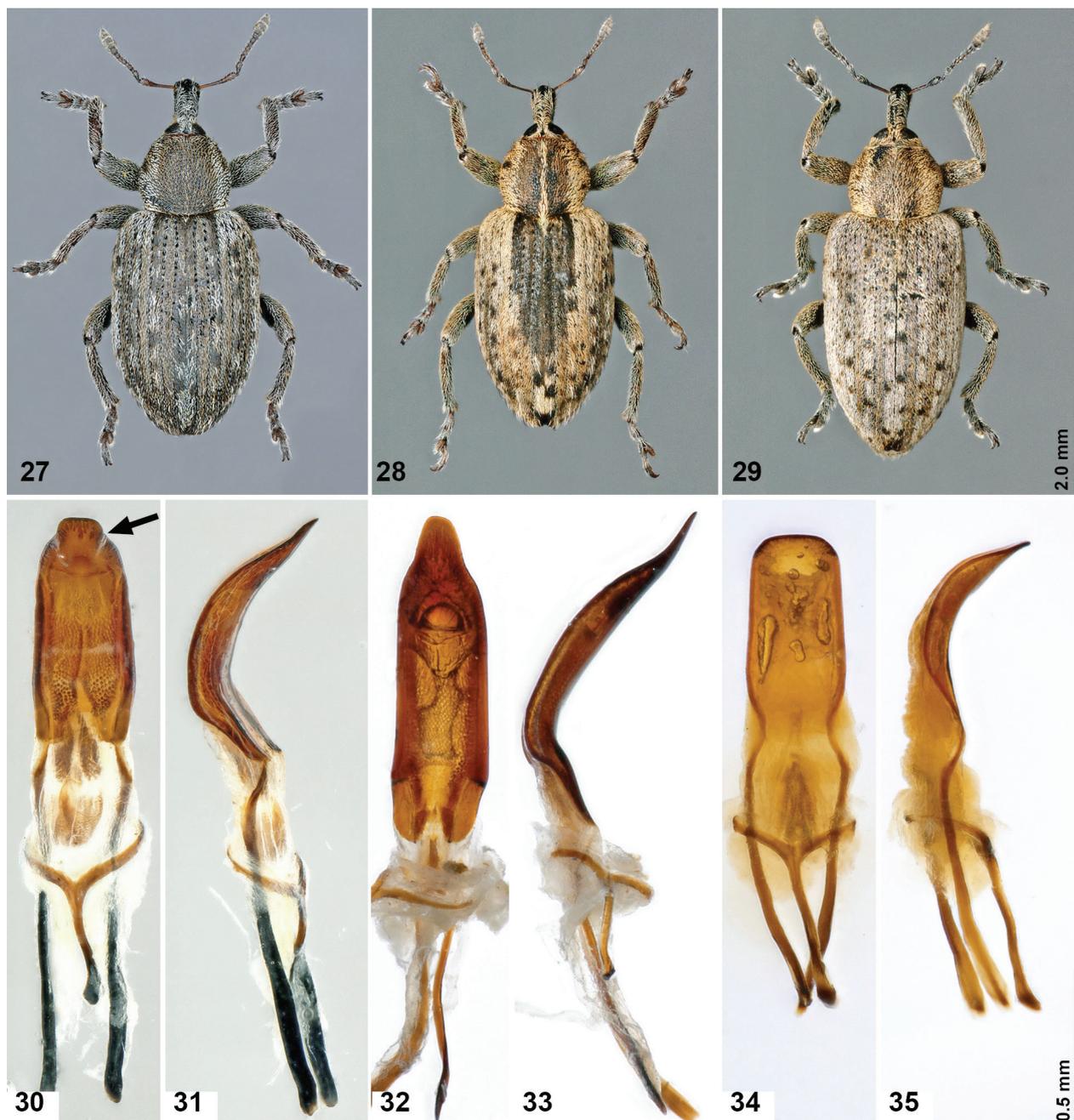
**Figures 4–14.** Different life stages of *Hypera temperei*. **4.** Young larva shortly after first moulting. **5, 6.** Older larva on leaves and flowers of *Astragalus leontinus*. **7.** Larva of *Hypera postica* for comparison. **8.** Larva spinning a net cocoon. **9.** Larva lying in the finished net cocoon. **10.** Ventral view on pupa in an opened cocoon. **11.** Freshly hatched adult. **12, 13.** Freshly emerged adult males with contrasting colouration, the white bristles are well visible. **14.** Ditto darker coloured male (Photos: C. Germann).



**Figure 15–26.** 15. Habitus of *H. temperei*, dorsal view. 16, 18. Internal sclerites of penis of *H. temperei* in dorso-ventral, and lateral views. 17, 19. Ditto of *H. postica*. 20. Male sternite IX; rather thick of a hibernated specimens from the last year generation. 21. Spermatheca. 22. Female sternite VIII. 23, 25. Scales on pronotum of *H. temperei*. 24, 26. Ditto of *H. postica* (Photos: C. Germann).

darker (beige to light brown or yellowish in *H. postica*); iii) Pronotum and elytra with whitish scales of the lateral bandings less deep cut, about to one third of a scale (Figs 23, 25) – this shape of the scales is most similar to those of *H. viciae* – in *H. postica* the yellowish to beige coloured scales are deeper cut, to one half of a

scale (Figs 24, 26); iv) Scales of the dark middle band on pronotum in general simple in *H. temperei*, almost all bifid ones (deeply cut) in *H. postica*; v) Shape of the penis (Figs 30, 31) with a short and basally constricted tip (Fig. 30, arrow), in lateral view more rounded in *H. temperei*, where the penis is more elongated, with apex longer and



Figures 27–35. 27–29. Habitus dorsal of males of 27. *Hypera temperei*. 28. *H. postica*. 29. *H. viciae*. 30–35. Penis ventral and lateral views of 30, 31. *H. temperei* (arrow indicates typically constricted tip). 32, 33. *H. postica* (Baden-Württemberg). 34, 35. *H. viciae* (Baden-Württemberg), Photos: C. Germann.

flattened in *H. postica* (Figs 32, 33); vi) Internal sclerites (= internal sac) of the penis are rather similar in both species, the paired sclerite is more strongly sclerotized in *H. temperei*, and the single sclerite in the middle is narrower and more sword-like (Figs 16, 18) compared with the broader and tube like one of *H. postica* (Figs 17, 19). As the habitus of *H. temperei* is more gracile, the hind wings were examined in all of the collected adults with the result that in all specimens the hind wings were rudimental. This last character is very likely not unique in the case of *H. temperei*, and was therefore checked on specimens of *H. postica* collected at higher

altitudes: 1720 m a.s.l. at Tschier, Chasuras in Grisons (cCG), from Tschlin [46.87657°N, 10.42957°E], lower Engadine at 1500 m a.s.l. in Grisons (NMSO), and from Griesalp [46.54745°N, 7.76217°E], Kiental at 1400 m a. s. l. (NMB) where again in all specimens only short rudiments were perceptible. However, such differences in hind wing length in *H. postica* (where flight capability is widespread and thus long and functional hind wings are developed in certain populations) had already been documented (e.g. Hsiao and Hsiao 1985), and can vary between geographically close populations, even at low altitudes in the Netherlands.

## Data from collections

The search for more specimens of *H. temperei* from Switzerland, but also elsewhere in the Alps, hidden under the common *H. postica*, resulted in the following specimens and localities (in chronological order): 1 male: “Suisse GR Samedan [46.53982°N, 9.86773°E] 15.7.1975 [above 1700 m a.s.l.], [leg.] P. Scherler» (NMBE). – 2 males: «SCHWEIZ, GR, Ftan, Umgb., N813.000 /E186.000 [46.79127°N, 10.22890°E], 1700 m, 19.6.2006, leg. Germann, *Hypera postica* det. C. Germann 2007» (cCG). – 2 males: «SCHWEIZ, GR, Ftan, Piz Clünas [46.81956°N, 10.24457°E], S-exp. Hang, 2500–2700 m, GS Pflanzenstreue Felsbänder, 10.8.2011, e.l. an Fabaceae (undetermined), leg. C. Germann, *Hypera postica* det. C. Germann 2012” (cCG, NMB).

Additionally, one single female from the following locality was examined, and could be only assigned with doubts to *H. temperei*: “Suisse BE Rothorn [46.78701°N, 8.04596°E] Brienz 11.8.2000 [assumed altitude 2300 m a.s.l.], Mousses sol [sifted from], [leg.] P. Scherler” (NMBE). Male specimens are needed to definitely confirm that record.

## Host plants

All present records of larvae, and two adults from two excursions were collected from *Astragalus leontinus*. Only three additional larvae were collected from *A. penduliflorus*. The breeding of the larvae was mostly successful. The larvae were held in small plastic boxes (for details see Germann 2021). The larvae fed on leaves but also on the flowers of the plant. The hatched adults fed on their cocoons, but did not feed on the plant leaves during the first days. Then small roundish holes were fed into the host plant’s leaves. When Tempère (1961) rediscovered *Hypera temperei* at the type locality on 21 July 1958, he added a potential host plant (*Oxytropis montana* L., now *Oxytropis jacquinii* Bunge), however without any proof of a development: “L’insecte vit, très probablement, sur *Oxytropis montana* D. C., Papilionacée montagnarde, sous les touffes serrées de laquelle j’ai trouvé une bonne partie des individus. « (Tempère 1961: 94).

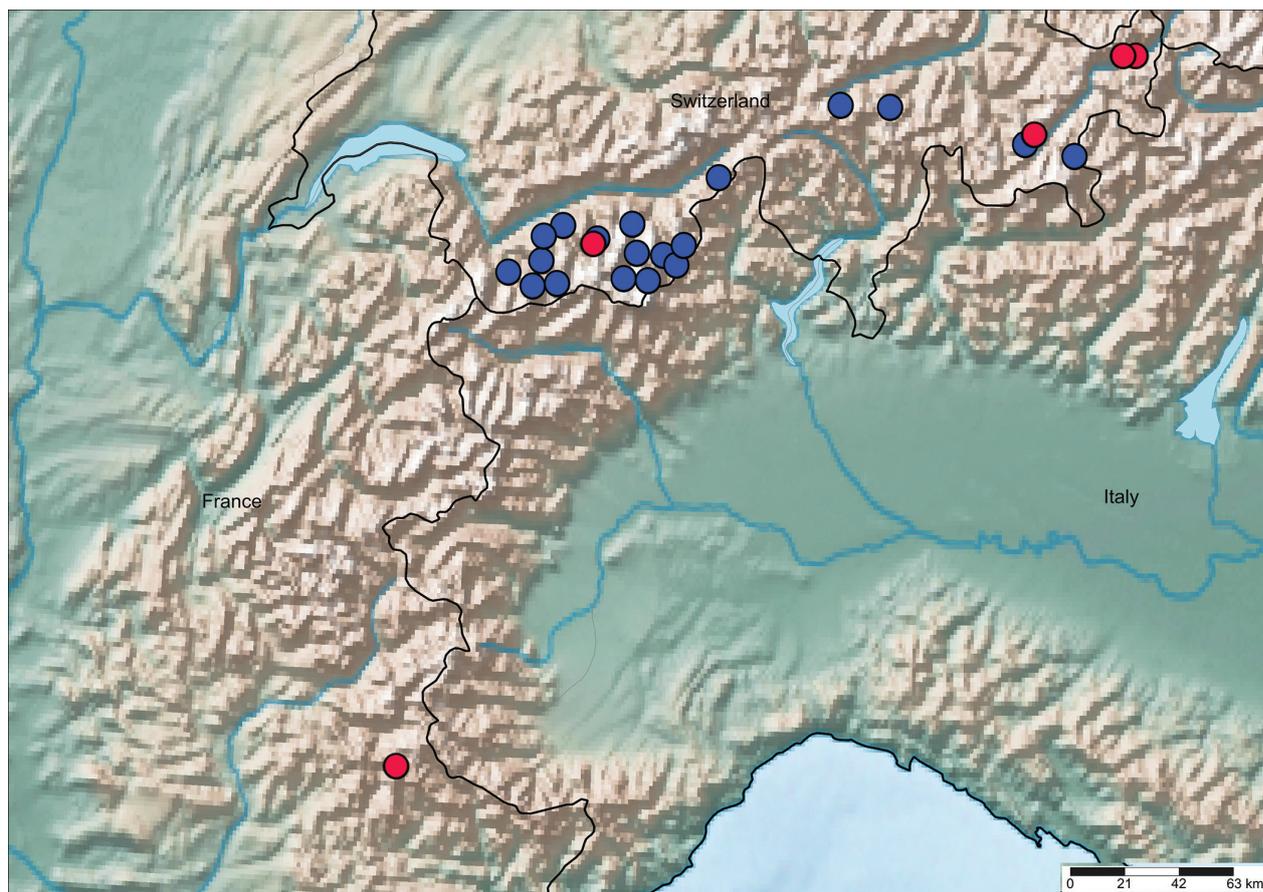
## Discussion

Focarile (1988) once mentioned *Hypera temperei* in an article on the Coleoptera collected in Val Piora, canton of Ticino in the south of Switzerland. As this record was quite a surprise then, since the French locality was still the only known one for this enigmatic species, I personally asked him in 2012 whether a revision of the determination of the specimen would be possible, and he agreed. Rather disappointingly, the specimen was of a misidentified *Hypera plantaginis* (De Geer, 1775), a widely distributed, often misinterpreted species (Germann 2013a, 2013b). However, a possibility of occurrence of *H. tem-*

*perei* in the Swiss Alps remains, now corroborated with discoveries of this western alpine element in southern Valais and in Grisons.

The herein presented morphological re-investigation may help substantially to recognise *Hypera temperei* in the field and in collections, if male specimens are present; the female genitalia did not provide relevant differences when compared (Figs 21, 22). The possibility exists that *H. temperei* is more often present in collections, but hidden among misidentified *Hypera postica* from sub-alpine or alpine localities. However, in most collections visited, only *Hypera postica* was found. The records from Piz Clünas above 2500 m a.s.l. show that the species can also be expected at high alpine altitudes in Switzerland. The hereby presented characteristics, clearly show that *H. temperei* is morphologically most similar to *H. postica*, and not to *H. viciae* as originally proposed by Hoffmann (1958), followed by Tempère (1961), Tempère and Péricart (1989), and Skuhrovec (2009). The only remaining similarity shared with *H. viciae* is the shape of the scales on elytra and pronotum, reported and shown above (Figs 23, 25). Despite the hereby facilitated morphological recognition of the species, at least when male specimens are available, a subsequent molecular investigation should be made, to test the sister group relationships of *Hypera temperei*, and to evaluate if a certain genetic isolation is visible regarding its low mobility and rather big distance from the type locality in the Maritime Alps, in the hope that fresh samples from the type locality in France are still available 62 years after the last specimens were collected. However, a thorough investigation of the whole *Hypera postica*-species complex seems necessary and even a precondition before focusing on *H. temperei*, which is obviously part of this complex. This because of other taxa as e.g. *H. transsilvanica* (Petri, 1901), or *H. ornata* (Capiomont, 1868) which show close affinities to *H. postica*. The morphological background, which proofs the existence of such a species complex around *Hypera postica*, was already set by Petri (1901), and then re-mentioned by Dieckmann (1989). Based on experiences with the barcode sequence COI used for possible species discrimination in the *H. nigrirostris*-species group, including the species *H. nigrirostris* (Fabricius, 1775), *H. ononidis* (Chevrolat, 1863) and *H. melarynchus* (Olivier, 1807) – where no separate clades resulted likely due to recent speciation and incomplete lineage sorting (Germann et al. 2017), it might be wise to use a broader set of molecular markers.

The plant on which Tempère (1961) found specimens of *H. temperei* (*Oxytropis jacquinii*) may i) either have been confused with the somewhat similar looking *Astragalus leontinus* (which is recorded from around the Col de la Cayolle (<https://www.tela-botanica.org/bdt-fx-nn-8107-repartition>), or ii) the *Oxytropis* only served as hiding plant for *H. temperei*, or iii) the species develops on several species around the genera *Astragalus* and *Oxytropis*. The latter hypothesis is based on knowledge of host plants of other *Hypera*-species, which are mostly



**Figure 36.** Map with records of *Hypera temperei* (red dots) and potential localities (blue dots) where the host plant *Astragalus leontinus* grows (only validated records from the southern side of the central Alps were included, taken from Info Flora; <https://www.infoflora.ch/de/flora/astragalus-leontinus.html>). Map background by [www.simplemappr.net](http://www.simplemappr.net).

oligophagous (Skuhrovec 2005), and only in three species a monophagy may occur, as far as they were yet subject of any feeding tests. This should be considered in further searches for other populations, hence different plant species of the genera mentioned should be tested for occurrences of *H. temperei*. The hereby reported and validated host-plant *Astragalus leontinus* and its records might serve as first search-aid (Fig. 36) to locate more populations of this exceptionally rarely collected alpine weevil. Although the finds of additional larvae on *Astragalus penduliflorus* already show that more species are accepted by *H. temperei*, and from the additionally listed specimens from collections no specific host plant, but at least an undetermined species of the genus *Astragalus* was listed from the locality Piz Clünas in the lower Engadine (Germann 2012: 52). However, it was surprising that not more larvae could be found on the large plants of *A. penduliflorus* nearby Zinal despite of the effort of 30 plants tested. This may indicate that *H. temperei* shows certain preferences (thus prefers *A. leontinus* over *A. penduliflorus*), and/or that the microclimatic conditions were more favourable in the habitat of the scree slope presented. What contributes further to certain preferences regarding its microhabitat is also the observation that despite of numerous occurrences of *Astragalus leontinus* in the area

of Chalbermatten close to Zermatt (1800–2000 m a.s.l.) a thorough search for *Hypera temperei* in September 2020 remained unsuccessful. The place's ground substrate beneath the plants consists of dense stone split, which may be hardly accessible for the adults to hide themselves.

## Acknowledgements

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# Two males, one female: triplet-style mating behaviour in the Darwin wasp *Xorides ater* (Gravenhorst, 1829) (Hymenoptera, Ichneumonidae, Xoridinae) in the Swiss Alps

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## Abstract

The Darwin wasp *Xorides ater* is a solitary idiobiont ectoparasitoid of wood-boring beetle larvae. It occurs across the Palaearctic, and in Switzerland seems to be restricted to areas above 980 m altitude. Very little is known about its biology and behaviour. We here report three separate instances of a female *X. ater* mating simultaneously with two males, observed on the same occasion on a *Picea abies* woodpile near Lenk, Switzerland. Only two copulae that involved one male and one female were observed at the same time, which might indicate that this mating mode is rather common in *X. ater*. We illustrate our observations with photo and video material and compare it to mating behaviour known from other species of Darwin wasps.

## Key Words

Altitudinal distribution, Copulation stance, Phenology

## Introduction

Hymenoptera have a haplo-diploid reproductive mode (Crozier 1975) and, although thelytoky is not uncommon in the order, most species reproduce sexually through union between a haploid male and a diploid female. The latter then lays eggs that are either haploid (male-producing) or diploid (female-producing) through her ability to control access of sperm to the egg as it passes down the oviduct and past the spermatheca (Gerber and Klostermeyer 1970; Cole 1981; Strand 1989). Female hymenopterans are thus able to produce viable offspring without having to mate, although the offspring then would only be of the male sex. This mode of sex determination, known also as arrhenotokous parthenogenesis, is believed to have had a great bearing on the success of the order (Gauld and

Bolton 1988; Heimpel and De Boer 2008). It is especially through the ability of mated females to control the sex of the eggs they lay that the ensuing complex behavioural and evolutionary ecology of parasitoid Hymenoptera has been so well-studied, albeit in a very limited number of species (Godfray 1994; Wajnberg et al. 2008).

Detailed courtship studies have been made only in a minute fraction of Darwin wasp species, but it is usual for female parasitoid Hymenoptera to be receptive to mating for only a short time following their emergence (Quicke 1997). Courtship is typically rather brief but can involve elaborate cues. It is usually initiated by volatile pheromones emanating from females (Quicke 1997; McClure et al. 2007) and may then involve wing-fanning “songs” (Bredlau and Kester 2019), male-male struggles over access to females (Eggleton 1991), or the transfer of contact

pheromones from the antennae of the male to those of the female (Steiner et al. 2010).

It is by no means unusual for several males of a range of parasitoid wasps to simultaneously court a female, and aggregations of competing males are commonly observed, especially in parasitoids of wood-boring insect larvae such as Pimplinae (*Theronia maculosa* Kreiger, 1906, M. Giannota observations) and Rhyssinae (Eggleton 1991). However, to the best of our knowledge, only a single male has ever been observed to achieve copulation at any one time, even though females are sometimes receptive to repeated matings with the same or a different male for a short time afterwards (Quicke 2015; M. R. Shaw observations). With the exception of a very brief mention of *Rhyssa persuasoria* Linnaeus, 1758 being observed with two males apparently attached, though this was under conditions of disturbance whereby a large courting aggregation was being deliberately dismantled (Baker 1992), we have not encountered reports of more than one male achieving simultaneous copulation (whether ejaculation or not) with a single female in any species of Ichneumonoidea. We have never observed it ourselves during many decades of extensive rearing and field observations and, on that basis, we presume that it is highly unusual for it to occur.

It was therefore a surprise to observe three instances of a female of the xoridine ichneumonid *Xorides ater* Gravenhorst, 1829 in copula with two males, and apparently comfortably so for a prolonged time. During the same observation period, we observed only two standard pairings in the same location. In this brief report, we describe and illustrate these observations.

## Study species

*Xorides ater* (Fig. 1) is a member of the putative sister group to all other Darwin wasps, the subfamily Xoridinae (Klopfstein et al. 2019; Bennett et al. 2019). By analogy with congeners *X. brachylabis* Kriechbaumer, 1889 and *X. irrigator* Fabricius, 1793 (Chrystal and Skinner 1931), and *X. corcyrensis* Kriechbaumer, 1894 (Sharifi and Javadi 1971), *X. ater* can safely be presumed to be an idiobiont parasitoid (i.e., one that kills or permanently paralyzes its host at the time of oviposition) whose solitary larva develops on the body of its beetle larva, prepupa or pupa host. The parasitoid would pass the winter in its cocoon; however, neither the host range nor the developmental biology of *X. ater* is properly understood, nor is there any report of its courtship and mating behaviour.

## Materials and methods

### Circumstances of observations

During a period of general collecting of Ichneumonoidea near Lenk in the Swiss Canton of Bern, we came across an exposed woodpile of cut and partly split spruce logs

(*Picea abies*), originally up to about 20 cm diameter before being split. The woodpile was located just below Läheweid, about 600 m NW of the cable car station Bettelberg, Stoos (46°26'40"N, 7°25'31"E) at about 1510 m altitude. The observations took place on 3.vii.2019 in the early afternoon from 13.00 hrs to 15.00 hrs of a humid and intermittently sunny day. The dimensions of the woodpile, which had a corrugated iron cover, was approximately 10 × 2 × 1 m and ran length-ways from West to East with one side in shade (at 23 °C) and with the majority of insect activity observed on the shaded side. From the insect species seen on the woodpile and their activity, we deduced that it had been present for at least two years.

Photographs and short video recordings were taken with an Olympus EM-5 Mark II with a 60 mm macro-Olympus lens and later viewed and processed in Adobe Photoshop 2020 and Adobe Illustrator 2020. The composite video was edited in iMovie 10.2.3.

## Results

### Activity and mating observations

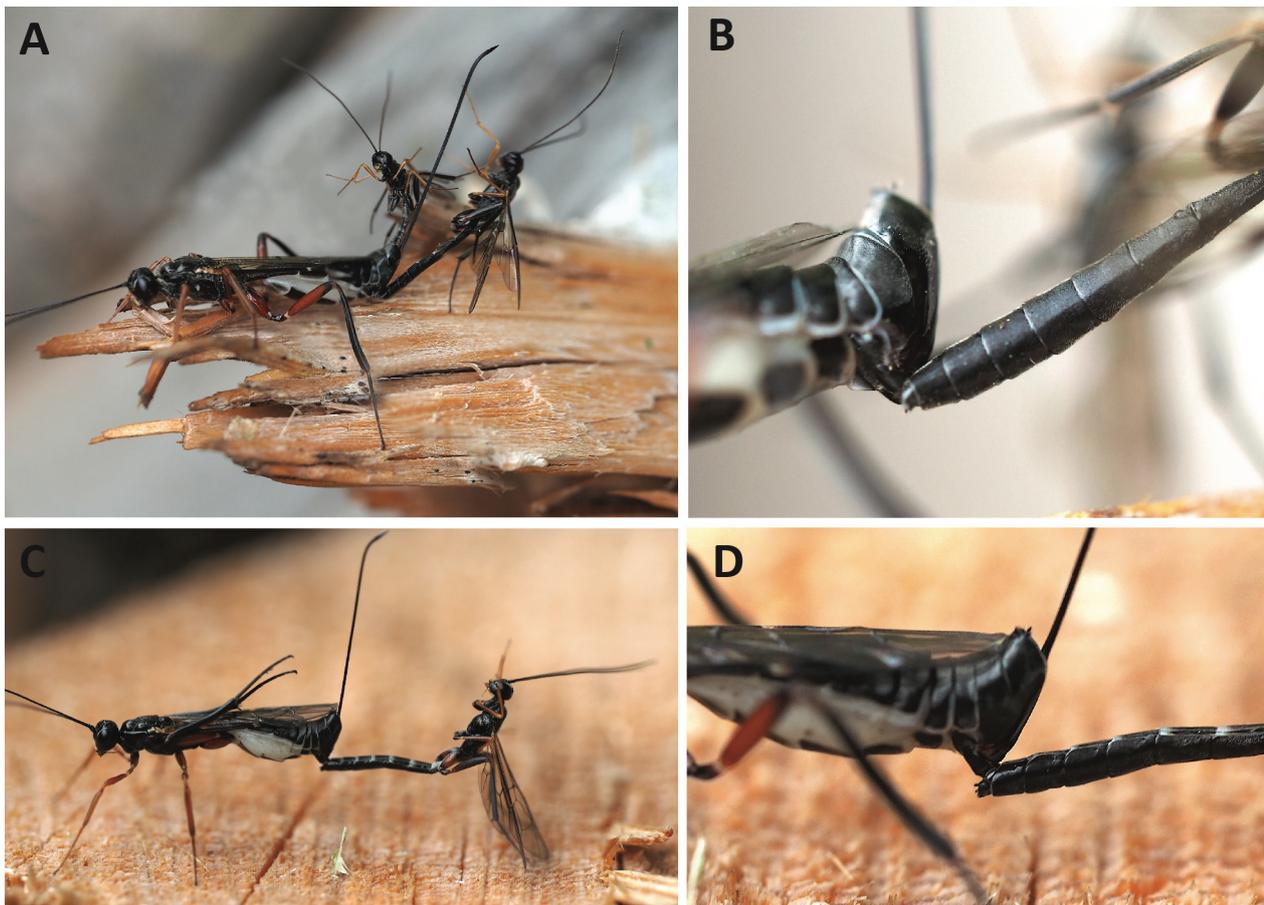
Arriving at the woodpile, we immediately observed a very high level of Ichneumonoidea activity, at one point counting more than 40 males in flight in front of the shaded side of the woodpile. Not only males but also females were present, and closer examination revealed that most of the individuals belonged to the ichneumonid *X. ater* (Fig. 1) with fewer of the similarly sized (but koinobiont endoparasitoid) braconid *Helcon nunciator* Fabricius, 1793. At least some of the females of *X. ater* present were clearly freshly emerged, as matings were occurring, though there were also some females resting without being courted that may or may not have already mated. A few males of *X. ater* were observed at rest but more often they were flying close to the woodpile and apparently in search of females, although without evident aggregation. Although some adult parasitoids were seen on the sunny (southern) side of the woodpile, insects there were too highly active to be easily observed or collected, and most of our observations were made on the shaded (northern) side, where insects were more abundant and easier to observe.

In the braconid *H. nunciator*, we observed about three matings, each between one male and one female. In *X. ater*, on the other hand, over a period of about two hours we saw three instances of a female *X. ater* with two males attached in apparent mating mode (Fig. 2A, B; Suppl. material 1: Movie 1). Only two copulations involving a single individual of each sex by this species were observed during the same period (Fig. 2C, D; Suppl. material 1: Movie 1). Unfortunately, no courtships or commencements of copulation were seen, so whether the attachment of the two males in the triplets happens simultaneously or sequentially is unknown.

In addition to the fact that the triplet-style matings appeared to happen rather easily and possibly even



**Figure 1.** *Xorides ater* female. Freshly eclosed female resting on a *Picea abies* woodpile in the Swiss Canton of Bern.



**Figure 2.** *Xorides ater* mating behaviour **A** Adult female (left) in copula with two attached males (right). [For greater clarity, figure 2A has been edited to create a stacked composite image of two less-focused images. The original raw files are available in Suppl. material 2: S.Fig. 1A and S.Fig. 1B]; **B** Close up of genitalic attachment points – left paramere of male (right) attached to the sixth sternite of female (left). Parameres of second male (background) are obscured from view; **C** Adult female (left) in copula with single male (right). Only the hind legs of the male are in contact with the wood; **D** Close up of genitalic attachment points – left paramere of male (right) attached to the sixth sternite of female (left).

regularly, several things struck us. In the first place, the union seemed to be satisfying all three participants as, overall, the assemblages were as quiescent as the two normal copulae seen at the same time and appeared to persist for an equivalent period (at least 5–10 minutes, with separation occurring only as we collected them). Second, there was no evident jostling or attempt by one male to dislodge the other; indeed, they seemed extremely relaxed, with legs twitching and often held outstretched and clear of everything (usually at least one hind leg touched the substrate, but sometimes all legs were completely free). The females, too, seemed unperturbed and made no attempt to dislodge either male. Third, the positioning of the genitalia appeared to be normal, although the precise mechanism of attachment of males to the female's sixth sternite (hypopygium) in the triplets could not be investigated in any detail. However, the single paramere (= harpe, sensu Schulmeister 2001) that was visible appeared to be normally deployed (Fig. 2B) and was presumably attached to the female's sixth sternite by means of the usual pincer action of the cuspis and digitus of the volsella. The other side of the male external genitalia was not visible, and how it was deployed or indeed whether insemination would be possible, could not be deduced.

## Ecological observations

In addition to copulation behaviour, some information on the ecology of *Xorides ater* can be given here. First, we were interested in the altitudinal distribution of the species in Switzerland and thus obtained data from museum collections (Table 1). All 71 specimens found were collected

above 980 m altitude, and the narrow flight time from late June to early August indicates that *X. ater* is univoltine. Furthermore, three out of the 26 collection events included at least a dozen males, while females were always only collected one or two at a time, adding support to our observation of high male abundance (Table 1).

The few and mostly unconfirmed host records that can be found for *X. ater* in the literature all include cerambycid beetles in conifers (Hilszczański 2003; Sheng and Wen 2008). The only suitably sized adult beetles seen at our site were the three species of *Callidium* (Coleoptera: Cerambycidae) that occur in Switzerland: *Callidium aeneum* De Geer, 1775, *C. coriaceum* Paykull, 1800, and *C. violaceum* Linnaeus, 1758. However, there was no direct evidence that any of these was serving as host.

While the females of *X. ater* seen were rather uniform in size, males were substantially more variable in that respect, suggesting that hosts of different sizes had been accepted, but whether of the same or different host species is unknown.

## Discussion

### Copulatory position in *X. ater* and other Hymenoptera

In the majority of Hymenoptera, the male genitalia are orthandrous, resulting in a mating stance whereby the male is mounted on the top of the female, the same way up and with head-to-head orientation and the apex of his metasoma curled below that of the female (Schulmeister 2001). The major exception is the Tenthredinoidea and

**Table 1.** Collection data from 71 individuals of *Xorides ater* collected in Switzerland.

Canton.	Locality	Date	N, E	Altitude	Males	Fem.	Legator	Collection <sup>1</sup>
BE	Adelboden	13 Aug.1922	46°29.54, 7°33.35	1340	0	1	T. Steck	NMB
GR	National park	22 Jul.1923		>1400	1	0	A. Barbey	MZL
GR	National park	26 Jul.1926		>1400	3	1	A. Barbey	MZL
GR	Somvix, Val Sumvitg	25 Jul.1891	46°40.80, 8°58.08	1200	0	1		NMBE
GR	Versam	9 Jul.1898	46°47.50, 9°19.49	908	1	0		NMBE
GR	Zerne, Il Fuorn	21 Jul.1949	46°39.85, 10°12.6	1794	0	1	J. de Beaumont	MZL
GR	Zerne, Val dal Spöl, Praspöl	5 Jul.1922	46°39.47, 10°9.40	1800	2	0	C. Ferrière	BNM
GR	Zerne, Val dal Spöl, Praspöl	5 Jul.1922	46°39.47, 10°9.40	1800	12	2	C. Ferrière	BNM
SG	Pfäfers, Vättis	12 Jul.1912	46°54.40, 9°26.03	980	0	1	T. Steck	NMBE
VS	Agettes, Les, Les Mayens-de-Sion	Aug.1946	46°12.05, 7°22.67		0	1	J.L. Nicod	MZL
VS	Ayer, Zinal	26 Jul.1926	46°7.94, 7°37.19	1675	0	1		NMBE
VS	Champéry, Col de Bretolet	18 Jul.1964	46°8.60, 6°47.80	1920	0	1		MZL
VS	Evolène	7 Aug.1933	46°6.33, 7°29.42	1371	0	1	T. Steck	NMB
VS	Evolène	8 Jul.1911	46°6.33, 7°29.42	1371	1	0	T. Steck	NMBE
VS	Evolène	7 Jul.1911	46°6.33, 7°29.42	1371	12	1	T. Steck	NMBE
VS	Evolène	12 Jul.1911	46°6.33, 7°29.42	1371	13	1	T. Steck	NMBE
VS	Evolène, Les Haudères	27 Jun.1915	46°4.71, 7°30.20	1550	0	1	T. Steck	NMB
VS	Evolène, Les Haudères	1 Jul.1925	46°4.71, 7°30.20	1550	1	0	T. Steck	NMB
VS	Grimentz	16 Jul-5 Aug 1942	46°10.81, 7°34.56	1600	2	1	J. de Beaumont	MZL
VS	Grimentz	16 Jul-5 Aug 1942	46°10.81, 7°34.56	1600		1	J.F. Aubert	MZL
VS	Lötschental	16 Jun.1919	46°25.18, 7°49.73	1700	1	0	T. Steck	NMB
VS	Saas	Jul.1938			1	0	J. de Beaumont	MZL
VS	Saas Fee	Aug.1912	46°6.27, 7°55.03	1798	1	1		NMB
VS	Vissoie	22 Jun.1921	46°12.80, 7°34.87	1200	0	1	T. Steck	NMB
VS	Vissoie	24 Jun.1921	46°12.80, 7°34.87	1200	1	0	T. Steck	NMB
VS	Vissoie	23 Jun.1921	46°12.80, 7°34.87	1200	1	0	T. Steck	NMB

<sup>1</sup>Collection abbreviations are as follows: BNM – Bündner Naturmuseum, Chur; MZL – Musée de Zoologie, Lausanne; NMB – Natural History Museum Basel; NMBE – Natural History Museum Bern.

Xyelinae, in which the male genitalia are strophandrous (twisted through 180°), resulting in a coplanar end-to-end stance with the two sexes looking in opposite directions (or positioned co-ventrally), as is typically seen in Lepidoptera. The database Taxapad (Yu et al. 2016) gives references to some 333 papers in which courtship and/or mating in Ichneumonoidea is at least mentioned, but it is beyond the scope of this work to attempt a detailed review of these, and we restrict ourselves to an outline of the most usual copulatory stances seen, and a more detailed comparison between species of *Xorides*.

In most Ichneumonoidea, especially when the sexes are of comparable size so that the heads can be more or less adjacent, the male is usually mounted on top of the female and holds her with his legs (Fig. 3A). In this position, some degree of antennal contact during mating is usual. Indeed, the antennae of males are furnished with tyloids in species of approximately ten subfamilies of Darwin wasps (Quicke 2015), which appear to play a role in antennal communication during courtship and mating (e.g., Bin et al. 1999; Bordera and Hernandez-Rodriguez 2003; Steiner et al. 2010); an extreme example of this is seen in the diplazontine *Syrphoctonus tarsatorius* Panzer, 1809 (Fig. 3B; Steiner et al. 2010). In other cases, the male may slip back, foregoing antennal contact (Fig. 3C; also see Benelli et al. 2019 for the campoplegine *Campoplex capitator* Aubert, 1960). When the sexes are dissimilar in size, the male is usually the smaller and, because he is necessarily further back, antennal contact is often literally out of reach during copulation itself. In such cases, the male might start by climbing onto the female's back to perform antennal courtship, then sliding back as the female signals receptiveness, as we have seen in the rhyssine *Rhyssa perusatoria* (Fig. 3D; S. Klopstein observations).

Once genital attachment is achieved, it seems not unusual for males, particularly in species with a large sexual size difference, to fall further back and flip through 180° so that the orientation changes to one with the heads looking in opposite directions, and the male on his back with respect to the female (Fig. 2C). In such cases, there is usually little advantage in the male using many of his legs to hold onto the substrate, and they are sometimes all left free, with only his genitalia attached to anything (Suppl. material 1: Movie 1). This orientation of the male's body was seen in both of the normal copulae (Fig. 2C) and all three triplets (Fig. 2A). It has been reported also in the tryphonine subgenus *Netelia* (*Netelia*) Gray, 1860 (Vance 1927) although, in another species of the same subgenus, Shaw (2001) recorded a more normal male-on-top stance, suggesting some degree of plasticity or variation in the group. Recently, we have seen a similar stance to that encountered in *X. ater* in an unidentified species of the ophonine genus *Enicospilus* in Australia (Fig. 3E), though in this case the male did twist round to grasp the substrate rather than hang free.

Mating behaviour has been described for two other species of *Xorides*, in both cases from captive material in the laboratory. Chrystal and Skinner (1931) observed several pairings of *X. brachylabis*, noting that in courtship the male stroked the female's antennae with his own

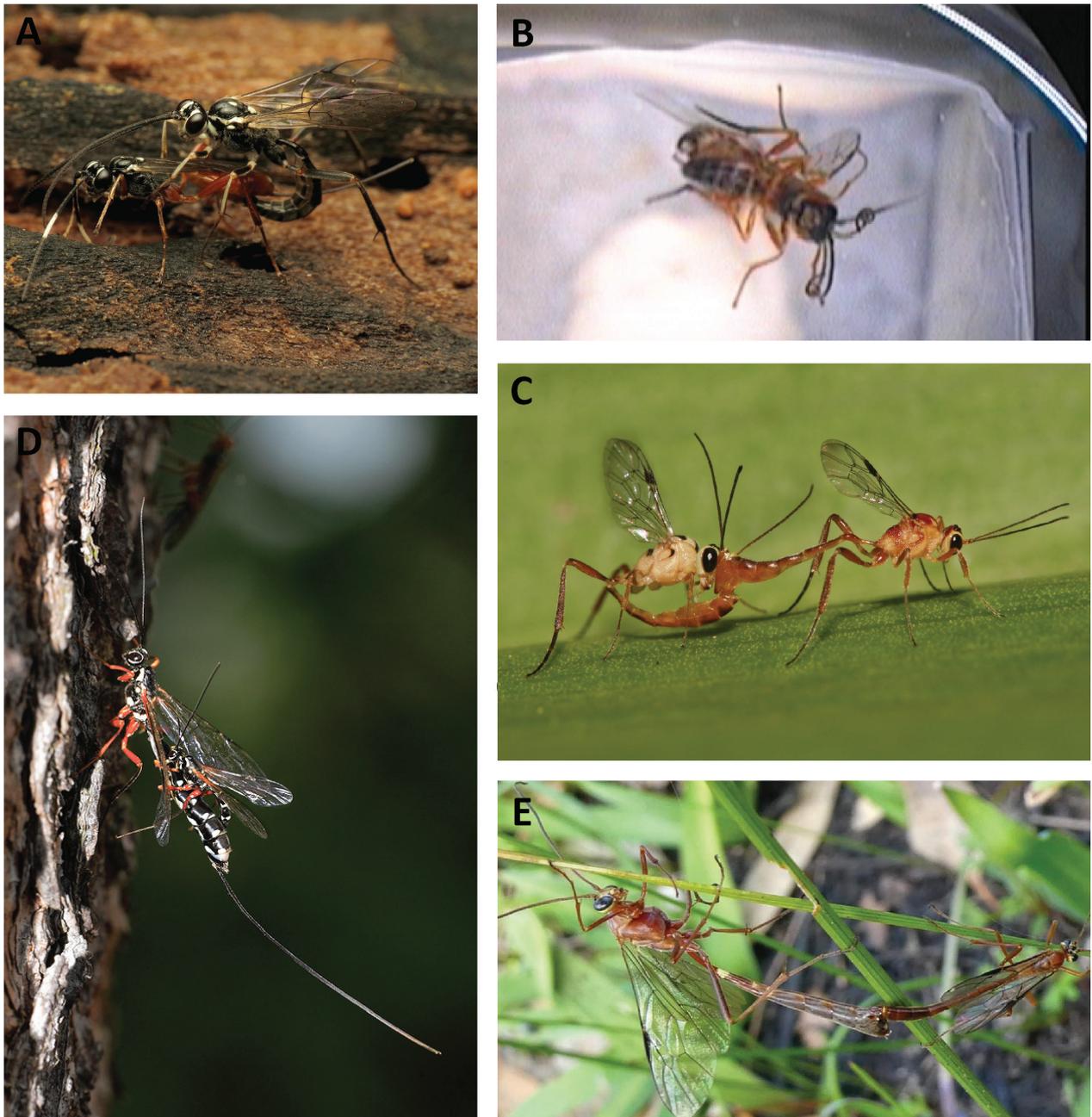
and, having approached slowly, mounted the female and grasped her with all six legs while stroking her thorax with his antennae throughout the copulation, which lasted from 15 to 40 minutes. This head-to-head alignment with the male mounted on top corresponds to our Fig. 3A. The mating behaviour of a single pair of *Xorides corcyrensis* described by Sharifi and Javadi (1971) differs in several respects but the male, although perhaps a little further back, was also essentially mounted head-to-head on the female. During copulation the mounted male placed his fore and mid legs on the female's mesoscutum and scutellum, with the fore legs sometimes suspended in the air.

Although unfortunately we did not witness the initiation of copulation, the position finally arrived at by *X. ater* in the copulations we observed, whether involving one or two males, differed markedly from these literature descriptions of union in other *Xorides* species. As in the case of *Netelia* mentioned above, this indicates that uniformity within a genus should not necessarily be expected. It is possible that the copulatory position of *X. ater* may be one factor facilitating matings involving two males, as more space around the female's external genitalia is exposed than in a male-on-top stance. However, additional mating observations under natural circumstances are needed to assess whether triplet-style matings are common in the genus or whether they are restricted to *X. ater*.

### Are triplet-style matings of adaptive significance or just a side-effect of scramble competition?

Although males certainly predominated, we were able to find several females of *X. ater* on the woodpile that were not mating and that did not seem to attract much attention at all from the numerous males. Although they were not necessarily receptive, some females did appear freshly emerged, judging from the distended membranous separation of metasomal tergites from sternites and from particles of wood dust on them not yet cleaned away. There is thus no reason to believe that the triplet-style mating was a unique result of particularly high male density and a shortage of females, and we did not observe anything resembling scramble competition among the many males present.

Whether or not insemination was taking place in the triplets and, if so, whether it was from one or both of the males, are key questions that unfortunately we are not able to resolve at present. There are, however, several interesting considerations pertaining to this that can be briefly summarised here. If sperm transfer from both males takes place, is it a fitness strategy of the female to permit or even encourage simultaneous mating by two males, perhaps thereby ensuring a higher genetic mix for her progeny, or offsetting her risk of mating with an infertile male? By decreasing mating time while simultaneously maximising overall sperm transfer, a triplet-style mating strategy may lower the cost (for example the increased risk of predation, or simply the



**Figure 3.** Various mating positions, and orthandrous attachment, of the Ichneumonidae **A** Cryptinae sp. exhibiting a common mating stance. Female – left, male – right. Image Credit: Katja Schulz; **B** Copulation in *Syrphoctonus tarsatorius* (Diplazontinae), with the male antennae coiled round those of the female (ventral view, taken from video sequence in Steiner et al. 2010); **C** Anomaloniinae sp. exhibiting a common mating stance. Male – left, female – right. Image Credit: Muhammad Mahdi Kahrim; **D** *Rhyssa persuasoria* (Rhyssinae) mating pair. The significantly smaller male (right) is seen clinging to female’s metasoma (left). The pair is not yet engaged in copulation. Image Credit: Reto Burri; **E** *Enicospilus* sp. (Ophioninae) in copula. Male – right, female – left. Image credit: Len van der Waag.

time investment) that would be associated with mating successively with more than one male. From the male side, is it just an unintended consequence of the scramble competition between males frequently observed in parasitoids of wood-inhabiting insects (e.g. Eggleton 1991), or is there a trade-off in avoiding conflict? Is there more than just passive sperm competition? Or, if insemination does not occur (in spite of the female’s presumed belief and subsequent behaviour), and if triplet-style sterile matings are common, does it constitute

a fitness impediment carried by *X. ater* by producing a higher proportion of males than would be optimal?

It would be interesting to know of additional observations of similar behaviour, whether in Xoridinae or in other ichneumonoid or hymenopteran groups. Further work is needed to elucidate whether or not sperm transfer from one or both males was successfully achieved in the triplets that evidently occur in *X. ater* at least on occasion, and possibly regularly, and any morphological modifications that might facilitate it.

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## Supplementary material 1

### Movie 1

Authors: Mark R. Shaw, Madalene Giannotta, Andrés F. Herrera-Flórez, Seraina Klopstein

Data type: multimedia

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Link: <https://doi.org/10.3897/alpento.5.64803.suppl1>

## Supplementary material 2

### Figure S1

Authors: Mark R. Shaw, Madalene Giannotta, Andrés F. Herrera-Flórez, Seraina Klopstein

Data type: Raw Images

Explanation note: Two raw images used to generate the stacked composite image, Fig. 2A, in the manuscript.

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Link: <https://doi.org/10.3897/alpento.5.64803.suppl2>

# First observation of an ant colony of *Formica fuscocinerea* Forel, 1874 invaded by the social parasite *F. truncorum* Fabricius, 1804 (Hymenoptera, Formicidae)

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<http://zoobank.org/90CA22B2-A9EA-43E1-93B4-132D57C57B0A>

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## Abstract

In the northern Alps of Switzerland we observed a mixed ant colony of *Formica truncorum* Fabricius, 1804 and *F. fuscocinerea* Forel, 1874 at the foot of a schoolhouse wall in the built-up centre of the small town of Näfels (canton of Glarus). Based on the fact that the habitat is favorable only for *F. fuscocinerea* and that *F. truncorum* is a notorious temporary social parasite, we conclude that in this case a colony of *F. fuscocinerea* must have been usurped by *F. truncorum*. This is remarkable, as it is the first reported case where a colony of *F. fuscocinerea* has been taken over by a social parasite. We consider the observed unusually small workers of *F. truncorum* to be a starvation form. This is probably due to the suboptimal urban nest site, as this species typically occurs along the edge of forests or in clearings.

## Key Words

Central Europe, northern Alps, social insects, temporary social parasitism, urban ecology

## Introduction

Parasitism is an extremely common life history strategy. Adopting a broad definition – obligate feeding on a living organism without (at least immediately) causing the death of the host – about half of all animal species can be considered parasites (Poulin and Morand 2000, 2004). In social insects (namely some ants, bees and wasps), however, there is a very particular mode of life called interspecific temporary social parasitism, in which a parasite species depends on a host species during its colony-founding phase (Forel 1898; Wilson 1971; Hölldobler and Wilson 1990). The host queen is replaced by an invading, freshly mated parasite female, which will then start to lay her own eggs and thus become the queen herself. The host workers will nurse the parasite queen's brood until they gradually die off. With the death of the last host worker, the found-

ing phase of the parasite colony ends. By this time, there is a large population of the parasite's own offspring available to run the nest (Kutter 1968; Buschinger 1986, 2009).

There are 24 ant species of the genus *Formica* Linnaeus, 1758 recorded from Switzerland (Neumeyer and Seifert 2005). These species are classified in four subgenera, two of which (*Formica* subgenus *Formica* and *Formica* subgenus *Serviformica* Forel, 1913) are of interest here. While in *Serviformica* the inseminated females of all ten species occurring in Switzerland (Neumeyer and Seifert 2005) can establish a colony independently, those of the other species of the genus *Formica* occurring in Switzerland are incapable of doing so (Kutter 1968, 1977; Seifert 2018). For colony establishment the females of *Formica* subgenus *Formica* either need existing colonies of the same species or those of a species of *Formica* subgenus *Serviformica*. Only females of *Formica truncorum* Fabricius, 1804 may

occasionally also parasitize colonies of *Formica polyctena* Förster, 1850 (Kutter 1968), which belongs to the subgenus *Formica*. But otherwise also females of *F. truncorum* invade colonies of the subgenus *Serviformica*, such as *Formica fusca* Linnaeus, 1758 (Seifert 2018) and probably also *Formica lemani* Bondroit, 1917 (Kutter 1956).

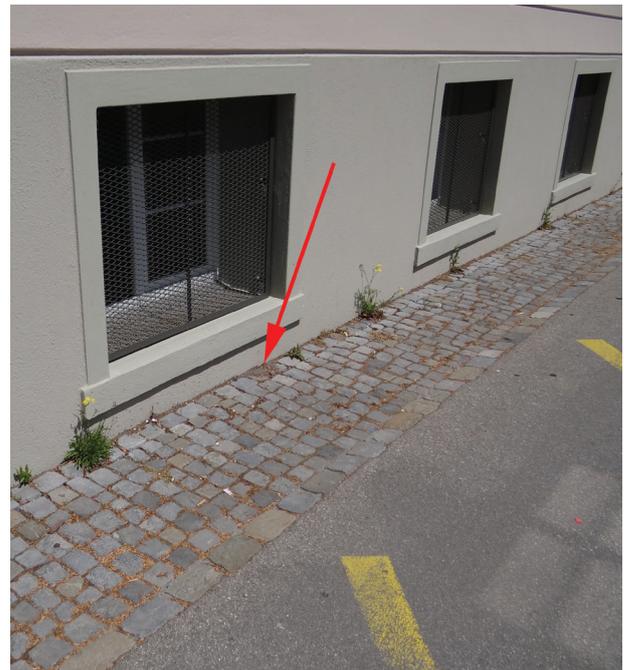
Most species of the subgenus *Serviformica* are predominantly monodomous, that is the population of the whole colony is united in a single nest. These species are generally prone to social parasites (Kutter 1968; Seifert 2018). Only the three representatives (*Formica cinerea* Mayr, 1853; *F. fuscocinerea* Forel, 1874; *F. selysi* Bondroit, 1918) of the *Formica cinerea* group (Seifert 2002) are known for their tendency to form polydomous supercolonies with the population inhabiting several spatially distributed nests (Kutter 1968; Seifert 2018). These species are hardly ever invaded by social parasites. While the widespread species *Formica cinerea* has been reported to serve as a host of socially parasitic ants (Czechowski 2001; Zacharov 2015; Seifert 2018), we are not aware of any case of previously reported social parasitism in *F. selysi* or *F. fuscocinerea*.

## Materials and methods

In the course of inventorying the ants of selected reserves in the canton of Glarus located in the northern Alps of Switzerland, we also tried to locate some of the hitherto missing species from the *Formica cinerea* group in built-up areas not existing in the reserves. We collected the ants by hand or using a small insect aspirator (pooter). The ants were killed and preserved in ethanol (80%). They were examined with the help of a stereo microscope (Olympus SZH10) with ring illumination using magnifications between 10× and 70×. The specimens were identified by Rainer Neumeyer following the key in Seifert (2018). The identification was later confirmed by Bernhard Seifert (Görlitz). Voucher specimens are deposited in the entomological collection of the Senckenberg Museum in Görlitz, Germany. The collection locality of the specimens reported in this article is in the center of the small town of Näfels (population 4000) in the canton of Glarus in Switzerland. The street address is *Im Dorf 14b*, the elevation is 440 meters above sea level and the coordinates are 47.09944°N and 9.06223°E. The colony was found at the cobble foot of the south-facing wall of the school building, erected in 1877 (Fig. 1). Its neighborhood is largely urban, although the outer boundary of the built-up area is only about 200 meters away in north-western direction. In addition, about 400 meters to the west there is a steep forest with interspersed rock faces (<https://s.geo.admin.ch/8dd530cefe>).

## Results

Searching our study area for colonies of *Formica fuscocinerea* we discovered one small colony in sandy soil



**Figure 1.** Location of the only active nest entrance of the examined small colony along the south-facing wall of the school building. Photo: Rainer Neumeyer.

between cobble stones along the building wall. At the nest entrance we not only found workers of *Formica fuscocinerea* (Fig. 2), but also somewhat more numerous ants of the parasitic species *Formica truncorum* Fabricius, 1804 (Fig. 3) on 25<sup>th</sup> May 2020 at 6:30 p.m. After a preliminary identification of some specimens, we returned to the site four days later, on 29<sup>th</sup> May 2020 at 1 p.m. for taking pictures and recording video footage (<https://youtu.be/nSY1wzVkigs>). We collected two voucher specimens of each species emerging from the nest entrance.

The workers of *Formica truncorum* were all below average in size – hardly larger than the workers of the host species *F. fuscocinerea* – and at first sight they resembled small workers of *Formica rufa* Linnaeus, 1761 in terms of their dark pigmentation, especially on the head (Fig. 3). In contrast, in medium and large workers of *F. truncorum*, the whole head is uniformly light reddish brown in the vast majority of cases (Seifert 2018: 134–135).

We observed the nest entrance for 15 minutes in sunny and windless conditions at 21 °C, counting a total of five workers (one *Formica fuscocinerea* and four *F. truncorum*) returning to the colony and eleven (four *Formica fuscocinerea* and seven *F. truncorum*) emerging from the colony. Along the south- and west-facing wall of the school building we found three additional ant species, namely *Lasius emarginatus* Olivier, 1792, *Myrmica sabuleti* Meinert, 1861 and *Tetramorium impurum* (Förster, 1850). When we returned to the site on 17<sup>th</sup> September 2020, the nest entrance had apparently shifted almost a meter to the west in the meantime. However, this does not necessarily mean that the colony had also moved its underground nest chambers.



**Figure 2.** Close-up of a worker of the host species *Formica fuscocinerea*. Photo: Jürg Sommerhalder.



**Figure 3.** Close-up of a worker of the socially parasitic species *Formica truncorum*. Its dark head marking is typical for nanitic workers of this species, but not for normal sized ones. Photo: Jürg Sommerhalder.

## Discussion

All species of *Formica* subgenus *Formica* occurring in Switzerland – including *Formica truncorum* – can establish their colonies as interspecific temporary social parasites of colonies of certain species of *Formica* subgenus *Serviformica* (Kutter 1968). Another potential explanation for our observation would be if *Formica truncorum* was behaving in a dulotic manner, that is hunting slaves from *F. fuscocinerea* to be brought to an already existing *F. truncorum* colony. However, within the genus *Formica*, in Europe so far only *Formica (Raptiformica) sanguinea* Latreille, 1798 is known to behave in this way (Kutter 1968; Buschinger 2009). Thus, we rather assume that at the schoolhouse of Näfels a female of *Formica truncorum* usurped a nest of *F. fuscocinerea* after her nuptial flight. This assumption seems justified given that the built-up habitat is typical only for *F. fuscocinerea* (Kutter 1977; Seifert 2018), a species originally inhabiting alluvial sand and gravel banks, nowadays also anthropogenic habitats such as gravel pits, industrial wastelands and the interior of settlements. *F. truncorum*, on the other hand, is a species typically occurring in habitats such as at the edge of forests or in clearings, moreover, also in bogs developing to heathland and bushy xerothermic grassland (Seifert 2018). Therefore, in this case we exclude the possibility of a daughter colony formation of *F. truncorum* with subsequent dulosis.

As we have seen, common nests of *F. truncorum* and *F. fuscocinerea* are likely to remain the exception, if only because the two species generally colonize different habitats and accordingly encounter each other at most in transitional areas. In addition, *Formica fuscocinerea* is known to form vigorous supercolonies (Seifert 2018), which can be expected to be difficult to approach for any socially parasitic female. However, as Seifert (2018: 312–313) reported, it appears that *Formica fuscocinerea* retained the potential for single-queen colony foundation at least in certain regions. Accordingly, we conclude that the observed nest entrance belonged to a small monogynous (single-queen) or even queenless colony of *Formica fuscocinerea*, when it was taken over by the social parasitic *F. truncorum* female. In fact, we were not able to locate another colony of *Formica fuscocinerea* in the immediate area surrounding the schoolhouse. Given the relatively few host workers left, the colony was most likely taken over already in 2019, if not 2018.

Nanitic workers are somewhat smaller than usual ones. They are rather characteristic of the initial phase of a colony founded claustrally, i.e. by independent colony foundation in a closed cavity (founding chamber) by a single, recently mated female (Hölldobler and Wilson 1990; Seifert 2018). These smaller workers are expected to occur only when food is scarce and needs to be saved (Peeters and Ito 2015). They are therefore perhaps best understood as starvation forms (Dejean and Dejean 1998). Consequently, nanitic workers are less likely to occur after a social parasitic colony takeover, where food-supplying workers of the host species are available from the beginning. Hence, the fact that we nevertheless observed exclusively dwarf workers of *Formica truncorum* suggests that the present colony is starving, probably because the colony is located in an urban setting, an environment that is certainly not ideal for this particular species (Seifert 2018). As suggested by Bernhard Seifert (pers. comm.), it can be expected that the colony will need to relocate to a more favorable habitat to avoid perishing. However, the nearest suitable habitats are at least 400 meters further west in the forest and scree of the steep mountain slopes rising to an elevation of more than 1000 meters above sea level within a distance of about 1200 meters. Several hundred meters is likely to be an insurmountable distance for a relocating colony. At best, it could be covered in a stepwise fashion over the course of several years. Indeed, observations on such a migrating *F. truncorum* population in Finland suggest relocation distances of 95 meters at most per year (Elias et al. 2005). For such a stepwise migration the colony would have to rely on suitable stepping stone habitats such as gardens and meadows with trees.

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# A fungal parasite selects against body size but not fluctuating asymmetry in Swiss subalpine yellow dung flies

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## Abstract

Evidence for selective disadvantages of large body size remains scarce in general. Previous studies of the yellow dung fly *Scathophaga stercoraria* have demonstrated strong positive sexual and fecundity selection on male and female size. Nevertheless, the body size of flies from a Swiss study population has declined by ~10% 1993–2009. Given substantial heritability of body size, this negative evolutionary response of an evidently positively selected trait suggests important selective factors being missed. An episodic epidemic outbreak of the fungus *Entomophthora scatophagae* permitted assessment of natural selection exerted by this fatal parasite. Fungal infection varied over the season from ~50% in the cooler and more humid spring and autumn to almost 0% in summer. The probability of dying from fungal infection increased with adult fly body size. Females never laid any eggs after infection, so there was no fungus effect on female fecundity beyond its impact on mortality. Large males showed their typical mating advantage in the field, but this positive sexual selection was nullified by fungal infection. Mean fluctuating asymmetry of paired appendages (legs, wings) did not affect the viability, fecundity or mating success of yellow dung flies in the field. This study documents rare parasite-mediated disadvantages of large-sized flies in the field. Reduced ability to combat parasites such as *Entomophthora* may be an immunity cost of large body size in dung flies, although the hypothesized trade-off between fluctuating asymmetry, a presumed indicator of developmental instability and environmental stress, and immunocompetence was not found here.

## Key Words

body size, developmental stability, *Entomophthora*, fecundity selection, fluctuating asymmetry, fungal parasite, insect immunity, *Scathophaga stercoraria*, sexual selection, trade-off, viability selection

## Introduction

Systematic quantification of selection has become one of the hallmarks of modern biological research so as to acquire a thorough understanding of the process of natural selection and its evolutionary consequences. Standardized measures of selection have been available for some time (Lande and Arnold 1983; Arnold and Wade 1984a, b; Brodie et al. 1995) and have been applied to many species and situations to foster several comparative (meta-)analyses, which greatly enhanced our understanding of the action of natural selection in the wild (e.g. Endler 1986; Kingsolver et al. 2001; Kingsolver and Pfennig 2004; Cox and Calsbeek 2009). Phenomenological (i.e.

non-behavioural) investigations of selection also are the field method of choice to understand the evolution and population biology of single species and populations in an integrative manner, and to test hypotheses about the evolution of particular traits and patterns (e.g. sexual size dimorphism: Blanckenhorn 2007).

The widespread yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae) is a classic model species for studies of natural and particularly sexual selection (Parker 1979; Borgia 1982). The species prefers cooler climates and populates the entire northern hemisphere up to very high latitudes, being particularly common around cow pastures in north-central Europe, also at high altitudes (Sigurjónsdóttir and Snorrason 1995;

Blanckenhorn 1997; Bauerfeind et al. 2018; Blanckenhorn et al. 2018; Schäfer et al. 2018; <https://www.gbif.org/species/1556243>). In lowland central Europe, each year has a spring (March – June) and an autumn season (September – November), while during the hot midsummer (July and August) the flies largely disappear from the pastures due to their heat sensitivity (Blanckenhorn 2009). Phenomenological studies of our long-term field population in lowland Switzerland have documented temporally variable but on average very strong mating advantages of large males, as well as fecundity advantages of large females (cf. Honek 1993; Jann et al. 2000; Blanckenhorn et al. 2003). Strong sexual selection on male body size likely is the main driver of the untypical male-biased sexual size dimorphism of *S. stercoraria* (Fairbairn 1997; Kraushaar and Blanckenhorn 2002; Blanckenhorn 2007, 2009). Nevertheless, the body size of flies has declined by almost 10% over a 15-year period from 1993–2009, possibly related to our warming climate (Blanckenhorn 2015). Given generally substantial heritability of body size also in this species (Mousseau and Roff 1987; Blanckenhorn 2000), this negative evolutionary response of a trait that is measurably strongly positively selected suggests that we are missing important selective episodes or factors shaping the morphological evolution of yellow dung flies (Merilä et al. 2001; Blanckenhorn 2015; Gotanda et al. 2015). Evidence for selective disadvantages of large body size remains scarce in general, also for yellow dung flies (Blanckenhorn 2000, 2007).

One aspect not well studied in yellow dung flies is size-dependent survival in nature. This is generally the case for small-bodied invertebrates, for which longitudinal field studies are essentially impossible because individuals cannot be as easily marked and followed like larger vertebrates (Merilä and Hendry 2014; Schilthuizen and Kellermann 2014; Stoks et al. 2014; Blanckenhorn 2015). At the same time, laboratory longevity estimates (e.g. Blanckenhorn 1997; Reim et al. 2006b; Blanckenhorn et al. 2007) generally do not well reflect field mortality. We have acquired multiple field estimates of larval survivorship at various conditions suggesting some counter-selection against large body size mediated by their longer development (summarized in Blanckenhorn 2007). However, sex- and size-specific adult survivorship in the field was so far estimated only indirectly by Burkhard et al. (2002) using age-grading by wing injuries, with mixed results. We here add a study of natural selection on morphological traits by the fatal fungal parasite *Entomophthora* spp.

The parasitic fungus *Entomophthora scatophagae* regularly infects yellow dung flies in Europe and North America (Hammer 1941; Steinkraus and Kramer 1988; Maitland 1994; Steenberg et al. 2001). Primarily at humid conditions infections can be occasionally (though unpredictably) epidemic (pers. obs.), in which case infected dead flies can be found prominently exposed near cow pastures on flowers, long grass or fences in a characteristic posture presumably effectively disseminating fungal

spores and/or attracting other flies (Møller 1993; Maitland 1994). Spore transmission may also occur via physical contact, e.g. during copulation (Møller 1993). This type of fungus is highly virulent and effective at infecting and killing insects within few days, and it can be manipulated such that *Entomophthora* species are being considered for biological control of insect pests (e.g. Steenberg et al. 2001; Nielsen and Hayek 2006). We took advantage of an unusually conspicuous fungus epidemic at our field population in Fehraltorf, Switzerland, in 2002.

I here assessed viability, fecundity and sexual selection acting on morphology and fluctuating asymmetry of field-collected yellow dung flies. Morphological traits reflecting body size are often evaluated in selection studies, documenting selective advantages of large size and corresponding evolutionary responses in many vertebrate and invertebrate species (Kingsolver et al. 2001; Kingsolver and Pfennig 2004; Blanckenhorn 2007; Gotanda et al. 2015). Body size is one of the most important quantitative traits of an organism, as it strongly affects most physiological and fitness traits (Calder 1984; Schmidt-Nielsen 1984; Roff 1992) and exhibits several prominent evolutionary patterns in many organisms (e.g. Rensch's Rule, Cope's Rule, or Bergmann clines; Rensch 1950; Fairbairn 1997; Blanckenhorn 2000; Blanckenhorn and Demont 2004; Kingsolver and Pfennig 2004). Depending on the taxon, diverse traits are typically used as surrogates of body size, which are usually highly correlated (i.e. integrated) within individuals due to pleiotropy, epistasis, or gene linkage. Nevertheless, for functional reasons selection on various body parts may vary (e.g. Preziosi and Fairbairn 2000), producing responses in correlated traits and thus generally requiring a multivariate approach (Lande and Arnold 1983). I focused on paired appendages (legs, wings), so I could also assess fluctuating asymmetry (FA; Palmer and Strobeck 1986). Small and random deviations from the a priori perfect symmetry in bilaterally symmetric organisms, i.e. FA, are presumed to reflect heritable developmental instability, such that individuals with good genes and/or living in good conditions can produce more symmetric bodies in the face of environmental or genetic stress, ultimately augmenting organismal fitness. Symmetric individuals consequently should have greater survival prospects (viability selection), or should be more successful at acquiring mates (sexual selection: Møller and Swaddle 1997). However, especially the latter notion, and the evidence, remain controversial (Møller and Thornhill 1997; Palmer 2000; Klingenberg 2003; Polak 2003; Van Dongen 2006; Knierim et al. 2007). In yellow dung flies, Liggett et al. (1993) and Swaddle (1997) found a negative relationship between FA and mating or foraging success, respectively, while Floate and Coughlin (2010) found no evidence for FA being a useful biomarker of environmental stress exerted by toxic livestock medications (ivermectin). Our own previous studies of this species revealed that FA is not heritable (Blanckenhorn and Hosken 2003), that it does not increase with inbreeding (or homozygosity: Hosken

et al. 2000), that it does not affect male mating success in the field while nevertheless being negatively related to energy reserves (Blanckenhorn et al. 2003), but that FA increases at stressfully high developmental temperatures (Hosken et al. 2000). Of central relevance for our study is the hypothesized link between FA and immunocompetence, postulating that more symmetric, but likely also larger individuals are expected to better fend off internal parasites such as *Entomophthora* (e.g. Rantala et al. 2000, 2004, 2007; Yourth et al. 2002, and references therein).

## Materials and methods

### Study species

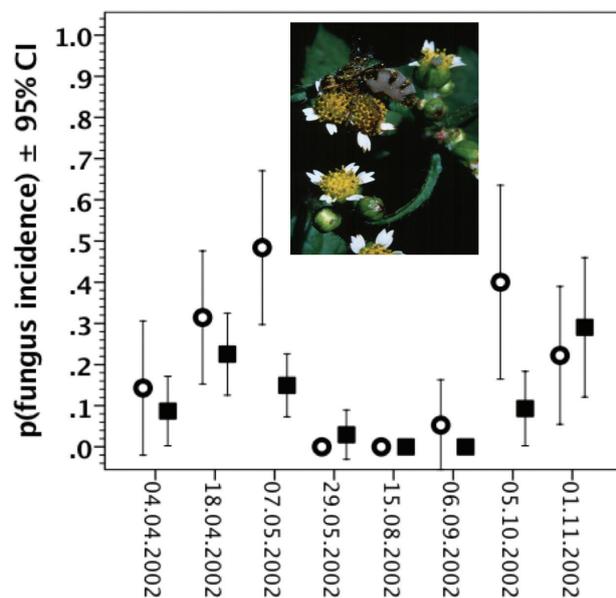
Adult *S. stercoraria* are sit-and-wait predators of small flying insects, from which they extract protein to produce sperm and eggs (anautogeny: Foster 1967). Females spend most of their time foraging for nectar and prey in the vegetation surrounding pastures. About once a week they visit fresh cattle (or other) dung to deposit a clutch of eggs. Larvae feed on and develop in the dung. Multiple males typically wait at fresh dung pats to mate with (stochastically) incoming females. Copulation usually takes place in the surrounding grass or on the dung pat; during the ensuing oviposition the male guards the female against other competitors (Parker 1970). Competition among males for females is strong as the operational sex ratio is highly male biased (Jann et al. 2000). Larvae face unpredictable spatio-temporal variation in local temperatures, dung (i.e. food) quality and quantity, intra- and inter-specific competition, and dung drying, all factors that ultimately largely determine their phenotypic adult body size. Towards the end of the season the flies have to reach the overwintering pupal stage before the first winter frost (Blanckenhorn 2009).

### Fly sampling

I sampled our population in Fehraltorf near Zurich (47°52'N, 8°44'E) roughly once a month between April and November 2002 (8 seasonal samples; total of  $N = 541$  flies). Fly densities permitting, we randomly selected one representative fresh dung pat, collecting all single and paired flies on and ca. 20 cm around the pat to bring them alive to the laboratory. (Else more than one pat were so sampled.) The group composition around any given fresh dung pat technically defines the relevant competitive situation for sexual selection (Arnold and Wade 1984a, b; elaborated below), and is as random as any random sample of flies from the entire pasture or population (Jann et al. 2000; Blanckenhorn et al. 2003). As virtually no unpaired females occur at the dung in the field because competition for mates is so intense, the number of pairs corresponds to the number of females present, and the proportion of paired males corresponds to the operational sex ratio (females / males).

## Laboratory procedures

Although dead flies visibly infected with the fungus were occasionally found on and around the pasture, these were too rare and haphazard to be sampled systematically. Instead, all flies collected were kept alive in the laboratory in single 100 ml bottles with sugar and water for up to two weeks. Infected flies would develop the fungus within few days, first visible in the abdomen but eventually covering the entire fly (Fig. 1), and eventually die; non-infected, recovered or resistant flies, which for all practical purposes here were indistinguishable and hence subsumed as non-infected, would not. Once in the laboratory, all females received dung to oviposit one clutch of eggs, which was counted.



**Figure 1.** Proportion of male (filled squares) and female (open circles) flies infected by the fungus *Entomophthora* over the season 2002, with an infected specimen inset (photo Peter Jann).

After death, work study students measured left and right wing length as well as fore, mid and hind tibia length of each fly. Mean values for these paired traits were subsequently calculated, as well as signed FA as  $(L - R)$ , unsigned FA as  $(|L - R|)$  (both in mm) and unsigned, size-corrected FA as  $(|L - R|) / \text{mean}(L, R)$  in %, as recommended by Palmer and Strobeck (1986). Paired traits were measured twice blindly by the same person to estimate measurement error relative to fluctuating asymmetry (Palmer and Strobeck 1986), and to calculate the repeatability of all trait measurements (Becker 1992). All measurements were taken with a binocular microscope at 16× magnification.

### Statistical analysis

For each monthly sample we calculated standardized viability selection differentials (= gradients) for both sexes

**Table 1.** Overall intensities ( $\beta \pm 95\%$  CI) of female and male adult viability selection ( $N_f = 171$  and  $N_m = 370$ ) exerted by the fungus *Entomophthora*, female fecundity selection (clutch size;  $N_f = 126$ ), and male sexual selection (pairing success;  $N_m = 370$ ) for one Swiss population of yellow dung flies (*Scathophaga stercoraria*) over the season 2002. Significant coefficients are bold ( $P < 0.05$ ).

Trait	Adult viability				Female fecundity		Male mating success	
	$\beta_f$	95% CI	$\beta_m$	95% CI	$\beta$	95% CI	$\beta$	95% CI
Hind tibia length	-0.158	0.305	-0.306	0.252	0.185	0.027	0.259	0.149
Mid tibia length	-0.089	0.310	-0.328	0.277	0.179	0.029	0.228	0.150
Fore tibia length	-0.196	0.304	-0.221	0.251	0.174	0.029	0.226	0.159
Wing length	-0.254	0.307	-0.324	0.248	0.179	0.029	0.267	0.147
Overall PC size	-0.099	0.292	-0.317	0.302	0.184	0.029	0.253	0.136
Hind tibia FA	-0.020	0.333	-0.086	0.258	-0.023	0.045	0.051	0.151
Mid tibia FA	0.204	0.231	0.003	0.219	-0.026	0.041	0.010	0.173
Fore tibia FA	-0.037	0.299	0.224	0.283	-0.024	0.045	0.040	0.180
Wing FA	-0.187	0.321	0.046	0.279	0.037	0.045	-0.041	0.168
Mean FA	0.035	0.284	0.097	0.327	-0.021	0.040	0.071	0.134

(binary variable: dead/alive = infected/uninfected), sexual selection differentials for males (binary: mated/unmated), and (continuous) fecundity selection gradients for females based on their clutch size using standard methods (Lande and Arnold 1983; Arnold and Wade 1984a, b; Brodie et al. 1995). It turned out that almost all females that developed the fungus and eventually died in the laboratory did not lay any eggs, so fecundity selection coefficients only refer to healthy (uninfected or resistant) females. We calculated female and male selection coefficients for each trait separately (4 morphological and 4 asymmetry traits), and additionally for the first principal component (PC) of all (mean) appendages signifying a compound index of body size.

Because the sizes of all appendages were highly positively correlated, and because FA and size are mathematically related (see formulae above), we calculated only univariate linear ( $\beta_{uni}$ ) and corresponding non-linear ( $\gamma_{uni}$ ) selection coefficients. To do so, for each seasonal sample we produced standardized z-scores for trait  $x$  by subtracting the sample mean from each value and dividing by the standard deviation:  $z_i = (x_i - \text{mean}(X))/SD(X)$ . In cases of low density, when more than one pat was sampled, pat identity was entered as random effect. Relative survival or male pairing success was computed as absolute survival or pairing success (1 or 0) divided by the sample proportion of survived flies or mated males, respectively (Brodie and Janzen 1996). We used the univariate model of relative fitness on standardized body size  $w = c + \beta_{uni} \cdot z$  to estimate the linear selection intensities  $\beta_{uni}$ , and the corresponding quadratic model  $w' = c + \beta_1 \cdot z + 0.5\gamma_{uni} \cdot z^2$  to estimate corresponding univariate non-linear selection coefficients  $\gamma_{uni}$  (note that  $\beta_{uni} \neq b_1$ ). These linear coefficients (gradients) reflect the combined effects of direct and indirect selection on body size (Endler 1986). The overall weighted means presented in Table 1 were likewise derived from the overall model with all seasonal samples (and sex, where applicable) as fixed factor(s) and dung pat as random factor (plus any applicable covariates).

The difference of the regression coefficients from a slope of zero (the null hypothesis of no selection) was tested. For estimation of the coefficients least-squares regression was applied, but for tests of significance logistic

regression was used when our measures of success were binary (viability and mating success: Brodie et al. 1995). In general, binary variables were analysed with binomial errors, whereas normally distributed errors were analysed using normal errors, if necessary after (log- or square-root) transformation.

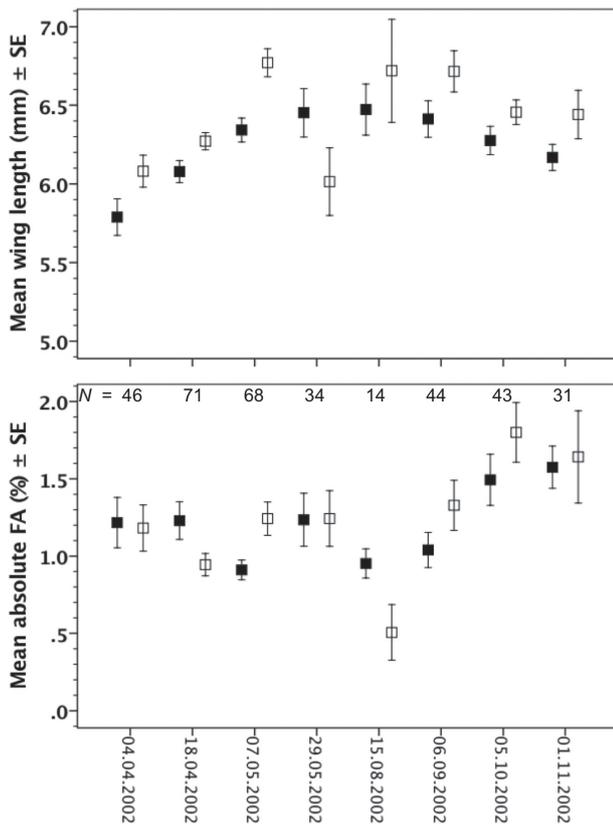
## Results

Fungus prevalence (1/0) varied over the season and between the sexes. Infections (as high as 50%) were most common during the cooler and more humid periods at the beginning (spring) and the end of the season (autumn), whereas they were rare during the hotter summer (nearly 0%; significant season effect:  $\chi^2 = 29.40$ ;  $P < 0.001$ ). The sexes were overall affected similarly (main sex effect:  $\chi^2 = 0.35$ ;  $P = 0.553$ ), although a significant sex by season interaction indicates some differential susceptibility across the season ( $\chi^2 = 34.04$ ;  $P < 0.001$ ; Fig. 1). Adding potentially explaining variables, the probability of dying by fungal infection (i.e. fungal prevalence) was unaffected by mean FA (main effect of covariate:  $\chi^2 = 1.99$ ;  $P = 0.159$ ) but increased with fly body size (main effect of covariate:  $\chi^2 = 12.56$ ;  $P < 0.001$ ; Table 1), an effect that however varied among seasonal samples (size by season interaction:  $\chi^2 = 12.55$ ;  $P < 0.001$ ) but not the sexes (size by sex interaction:  $\chi^2 = 0.27$ ;  $P = 0.602$ ).

Fecundity selection (based on clutch size) on female body size was significantly positive, as is typical in this species (Jann et al. 2000; Kraushaar and Blanckenhorn 2002). The intensity of fecundity selection, i.e. the slope relating relative clutch size to standardized body size (PC), varied significantly but unsystematically over the season (Table 1;  $F_{6,109} = 3.50$ ,  $P = 0.03$ ). These estimates refer only to uninfected flies because all females infected with the fungus died before laying eggs, and therefore do not refer to fecundity selection exerted by the fungus beyond the parasite's effect on adult mortality.

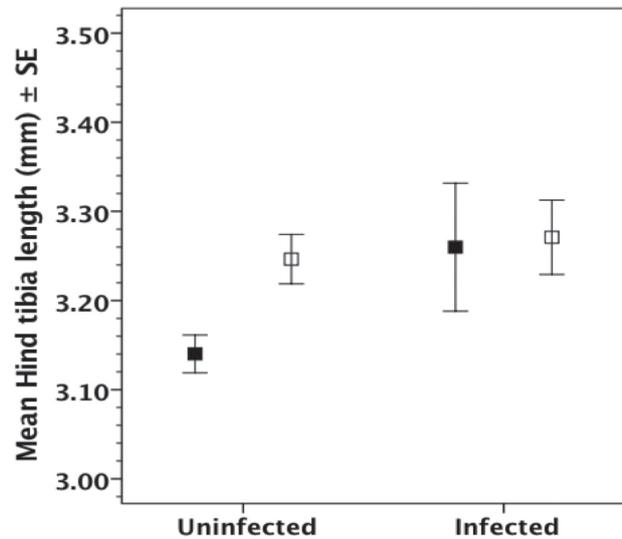
As usual in yellow dung flies, larger males had a mating advantage (Jann et al. 2000; Kraushaar and Blanckenhorn 2002; Blanckenhorn et al. 2003; main effect of body size (PC):  $\chi^2 = 14.23$ ;  $P < 0.001$ ), while mean FA of

all paired appendages did not affect male mating success ( $\chi^2 = 1.17$ ;  $P = 0.279$ ; Table 1; Fig. 2). Except for one seasonal sample on 29 May, the large male advantage was consistent throughout the season such that sexual selection intensity did not significantly vary across the season (body size by season interaction:  $\chi^2 = 0.11$ ;  $P = 0.920$ ; Table 1; Fig. 2). Interestingly, this typical pattern of positive sexual selection did not hold for those 28 of a total of 47 infected males (of a total of 370 males, of which 148 had acquired a mate) that were found mating in the field and later succumbed to the fungus (main effect of fungal infection:  $\chi^2 = 7.61$ ;  $P = 0.006$ ; Fig. 3).



**Figure 2.** Body size (top; here exemplified by wing length) and mean percentage of fluctuating asymmetry (FA; bottom) of all traits for unpaired (filled squares) and paired males (open squares) over the season.

Table 1 presents weighted mean directional selection coefficients,  $\beta$ , for the entire data set. Corresponding non-linear (quadratic) selection coefficients,  $\gamma$ , were mostly low and not significant and are therefore not presented. The only exception was female fecundity selection on body size, for which  $\gamma = 0.056 \pm 0.025$  was significantly positive overall, signifying accelerating selection (which has been reported before: Blanckenhorn 2007, 2009). Leg and wing lengths were expectedly highly correlated in both sexes (range of bivariate correlations:  $r = 0.887$  to  $0.972$ ), whereas FA of the legs and wings were largely uncorrelated (range:  $r = -0.024$  to  $+0.215$ ). Measurement of all paired traits was generally repeatable using our methods ( $R = 0.83$ – $0.97$ ), which was also true for asymmetry



**Figure 3.** Body size (here exemplified by hind tibia length) of unpaired (filled squares) and paired males (open squares) when they were infected by the fungus or not (all seasonal samples combined).

( $R = 0.53$ – $0.61$ ), so that FA could indeed be discerned from measurement error (all side by individual interactions  $P < 0.01$ ), fulfilling the criteria of proper FA assessment (Palmer and Strobeck 1986; Knierim et al. 2007).

## Discussion

At our Swiss study population, the entomophagous fungal parasite *Entomophthora scatophagae*, which has previously been described as a specific parasite of adult yellow dung flies at several sites in Europe and North America (Hammer 1941; Steinkraus and Kramer 1988; Maitland 1994; Steenberg et al. 2001), showed high and generally fatal infection rates of up to 50% during the cooler and more humid periods of the year 2002. Although the fungus is likely present most years, 2002 was a year of extraordinary high fungal prevalence, which before we had experienced only once before in the mid 1990s. I could document that this fungus exerts relatively strong and consistent negative viability selection on female and male adult body size in *S. stercoraria* (Table 1). Fungal infection further nullified the usual large male mating advantage in this fly (Borgia 1982; Jann et al. 2000; Blanckenhorn et al. 2003; Fig. 3), but did not affect female fecundity beyond its impact on mortality. This represents the first evidence demonstrating viability disadvantages of large yellow dung flies mediated by a parasite, which is generally rare in animals and particularly invertebrates (Blanckenhorn 2000, 2005; Kingsolver and Pfennig 2004; Gotanda et al. 2015). These results complement previous evidence of viability disadvantages of large flies at the juvenile stage, and lend further credence to the notion that the male-biased sexual size dimorphism of yellow dung flies is indeed at evolutionary equilibrium (Blanckenhorn 2007).

This study is merely phenomenological, so I could not assess underlying mechanisms. Nonetheless, I speculate

that the reduced parasite resistance of larger flies signifies a trade-off between body size and immunity (Rantala and Roff 2005; Schwarzenbach and Ward 2006; Cotter et al. 2008). Based on age grading by wing injuries, Burkhard et al. (2002) found that adult age (i.e. longevity) of yellow dung flies in the field tends to be positively related to body size at least during part of the season. Energy reserves also scale positively with body size (Reim et al. 2006a; Blanckenhorn et al. 2007) and positively influence mating success (Blanckenhorn et al. 2003). Adult longevity under most environmental circumstances, including complete starvation, can therefore generally be expected to increase with body size on physiological grounds (Reim et al. 2006b). One possible mechanism selecting against large body size is (positively) size-selective predation and/or parasitism (Blanckenhorn 2000). However, beyond expectations of a general positive correlation between predator and prey size (Brose et al. 2006; Vucic-Pestic et al. 2010), evidence for systematic size-selectivity of predators is generally weak at best, also for yellow dung flies (Blanckenhorn 2000; Busso and Blanckenhorn 2018; Blanckenhorn et al. 2021). Size-selective parasitism has been reported for some parasitoids because larger hosts result in larger parasite offspring (e.g. McGregor and Roitberg 2000), but otherwise few data exist (Zuk and Kolluru 1998; Blanckenhorn 2000). Rather than invoking increased infection rates of larger flies with the parasite, for whatever reasons, I rather suspect that the ability of larger flies to combat the parasite is compromised due to their generally greater absolute energy demands in stressful environments (trade-off hypothesis: Rantala and Roff 2005; Reim et al. 2006a, b; Schwarzenbach and Ward 2006, 2007; Cotter et al. 2008). Females were infected more by the parasite at least in spring (Fig. 1), possibly related to their generally greater reproductive burden (i.e. the cost of producing expensive eggs rather than cheap sperm; cf. Nunn et al. 2009, but see e.g. Rantala et al. 2007 for opposite results). Nevertheless, the standard sex differences in reproductive (energetic) costs should be somewhat offset by the male-biased sexual size dimorphism of yellow dung flies, which implies relatively greater costs of producing and maintaining the larger, condition-dependent male size (Blanckenhorn 2000, 2007), and might explain why size-dependent viability selection here turned out to be stronger in males (Table 1). Yellow dung fly females indeed produce higher heritable levels of phenoloxidase than males (Schwarzenbach et al. 2005), one of the central mediators of insect immunity (Schmid-Hempel 2005; Rolff and Reynolds 2009; González-Santoyo and Córdoba-Aguilar 2012), and higher phenoloxidase levels decrease adult longevity in this species, demonstrating a trade-off (Schwarzenbach and Ward 2006). However, higher phenoloxidase levels did not lead to greater resistance against mites or another fungus (Schwarzenbach and Ward 2007), and phenoloxidase is also unrelated to body size in *S. stercoraria* (Schwarzenbach et al. 2005). Overall, therefore, the evidence in favour of immunity

mediating the higher mortality of large-bodied dung flies documented here remains rather limited.

In contrast to body size, fluctuating asymmetry (FA) of legs and wings influenced none of the fitness components investigated here (contrary to Liggett et al. 1993, but confirming an earlier sexual selection study by Blanckenhorn et al. 2003). Based on evidence in other animals (Rantala et al. 2000, 2004), I had expected that low FA would be a signal of greater immunocompetence augmenting resistance against parasites, but this was not found. It is not unlikely that FA is a bad indicator of developmental stability in general, as various reviews have revealed no clear verdict based on the available evidence on this question, so the entire concept remains controversial (Møller and Swaddle 1997; Møller and Thornhill 1997; Palmer 2000; see various articles in Polak 2003; Van Dongen 2006; Knierim et al. 2007). In yellow dung flies, beyond Liggett et al. (1993) there is no evidence for a role of FA in sexual selection (Blanckenhorn et al. 2003; Blanckenhorn and Hosken 2003; this study). What remains is that FA reliably indicates at least hot temperature stress in this species (Hosken et al. 2000).

## Conclusions

I here took advantage of an unusually intense epidemic outbreak of the species-specific entomophagous fungus *Entomophthora scatophagae* in our experimental Swiss field population of yellow dung flies to assess natural selection exerted by this fatal parasite. Overall, the survival of flies of both sexes infected with the fungus was negatively related to fly size, thus exerting negative size selection, but not the fluctuating asymmetry of their wings and legs. Whereas reduced ability to combat parasites such as *Entomophthora* may be an immunity cost of large body size in dung flies explaining the selection patterns presented, I conclude that fluctuating asymmetry is no good indicator of immunocompetence in yellow dung flies (cf. Rantala et al. 2000, 2004, 2007; Yourth et al. 2002; Rantala and Roff 2005; Schwarzenbach and Ward 2006; Cotter et al. 2008).

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## Supplementary material 1

### Table S1

Author: Wolf U. Blanckenhorn

Data type: species data

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Link: <https://doi.org/10.3897/alpento.5.65653.suppl1>



# Unraveling a complex problem: *Dichrorampha velata* sp. nov., a new species from the Alps hitherto confounded with *D. alpestrana* ([Zeller], 1843) sp. rev. = *D. montanana* (Duponchel, 1843) syn. nov. (Lepidoptera, Tortricidae)

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<http://zoobank.org/068B9815-2442-473D-A7D7-0D50C63C1595>

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## Abstract

Analysis of wing pattern, genital morphology and results of DNA barcoding indicates that the name *Dichrorampha montanana sensu auct.* actually comprises two species. *D. alpestrana* ([Zeller], 1843) **sp. rev.** is considered as senior synonym of *D. montanana* (Duponchel, 1843) **syn. nov.**, and a lectotype is designated for the latter name to fix the identity. After thorough search for possible synonyms, *Dichrorampha velata* **sp. nov.** is described and differentiated morphologically and with DNA barcodes from *D. alpestrana* and adults and genitalia of both species are figured. *Dichrorampha velata* **sp. nov.** is restricted to the European Alps and adjacent regions whereas *D. alpestrana* is more widespread with likely arctic-alpine disjunction and records from the Alps and the northern part of Great Britain.

## Key Words

cryptic diversity, DNA barcoding, integrative taxonomy, nomenclature, revised synonymy

## Introduction

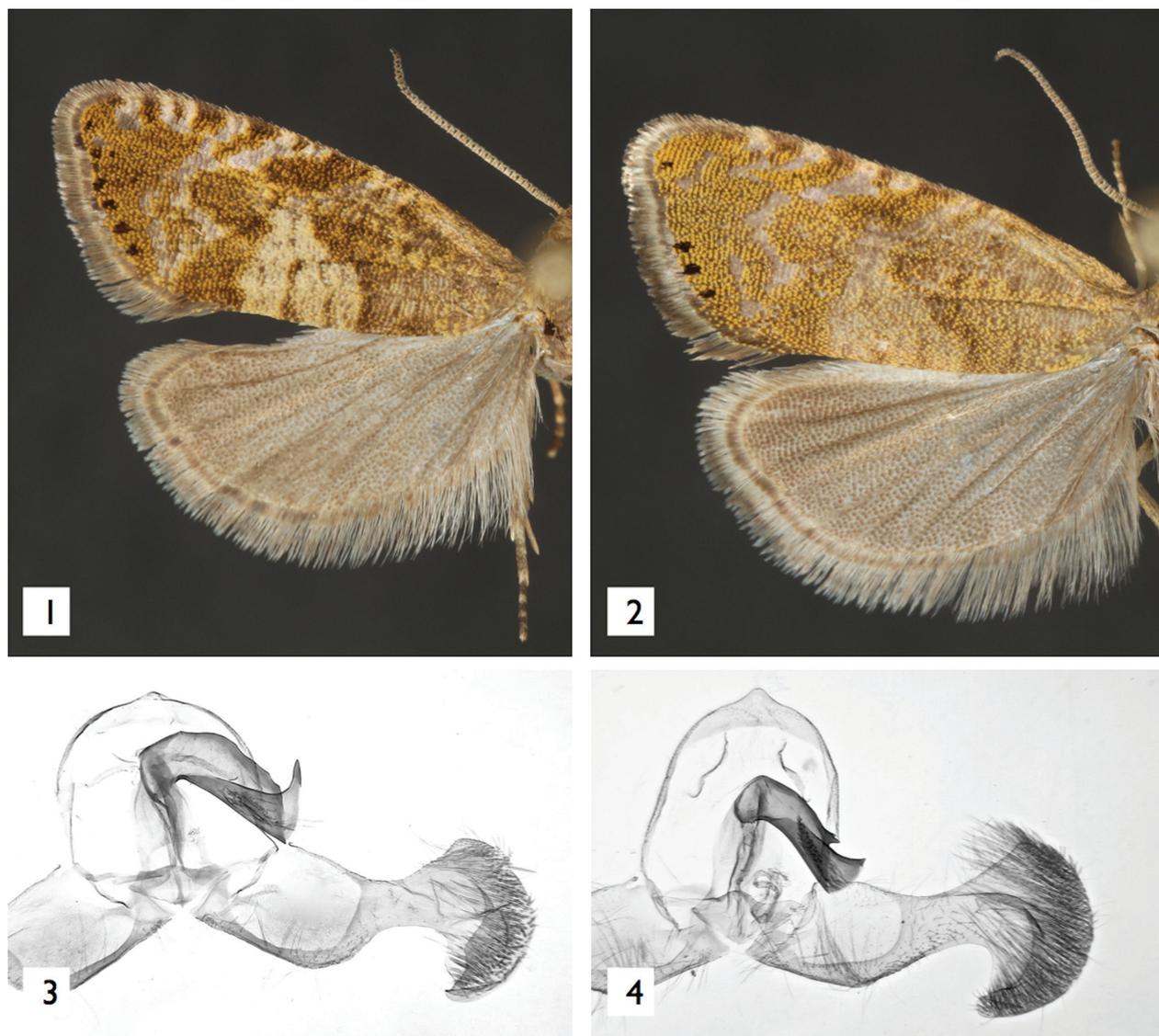
With currently 62 species records *Dichrorampha* Guenée, 1845 is the most diverse genus of European Tortricidae (Razowski 2003; Rennwald and Rodeland 2021). Though occasionally new taxa have been described during the last two decades, the genus can taxonomically be considered as well explored, however, with exceptions as will be shown herein for a widespread central/northern European species pair.

In 2006, the first author collected two superficially similar fresh male *Dichrorampha* specimens occurring syntopically at a site in the Engadine, Switzerland. They differed in their wing pattern in that one specimen displayed a distinct whitish triangular mark arising from the dorsal border of the forewing, while in the other, this mark was hardly apparent (Figs 1, 2). Their genital structures showed clear

differences. The specimen with the triangular mark on the forewing had a broad phallus, ending in a large tooth-like, curled structure and the inner border of the valva showed a triangular bulge (Fig. 3). The other specimen had a narrower, multi-peaked phallus and there was no triangular bulge on the inner border of the valva (Fig. 4).

Already more than a decade earlier the junior author found similar discrepancies in the context of material from Austria and Germany. However, there was no intensive processing of the problem at the time because these genital differences had already been described in detail and figured by Danilevski and Kuznetsov (1968) who attributed them to intraspecific variability of *D. montanana* (Duponchel, 1843).

The history of this taxon, however, is characterized by confusion and misunderstandings:



Figures 1–4. Two male *Dichrorampha* spp. and their respective genitalia. CH-La Punt, 1820 m, 26.6.2006 leg. Schmid.

Sometime before 1843, the Austrian entomologist Josef Emanuel Fischer von Röslerstamm captured an unknown tortricid at Gscheidt in the Rax mountain range, in the Austrian province of Styria. He sent it under the name “*Montanana* n.sp.” to the famous German entomologist Philipp Christoph Zeller who described the new species as “*Grapholita alpestrana*” ([Zeller] 1843) with the *in litteris* name “*montanana* FR” published in synonymy. Unfortunately his description was published anonymously and thus the new name was later considered to be invalid (e.g. Obraztsov 1953) which is incorrect according to current rules of ICZN (1999). Horn and Schenkling (1928) wrongly ascribed the description to Bischoff (1843) who, however, only published an independent subsequent note to an earlier article, whereas Zeller himself had already admitted his authorship of the newly described species (Zeller 1878). According to our research, the author of the general article is Fischer von Röslerstamm (1843) because in the introduction the anonymous writer of the travelogue refers to his son Oscar and Mr.

M[ann]. Indeed, the name of one of the sons of Fischer von Röslerstamm was Oscar and there is evidence that he went on numerous excursions with the Viennese entomologist Josef Mann. However, the descriptions in Latin published exclusively in separate footnotes do not come from the author of the article, who never described his new species in Latin, but stylistically fully corresponds to Zeller, who should therefore be considered the author.

Herrich-Schäffer (1849) provided another description based on Zeller’s diagnosis, whereupon two mistakes occurred: he identified his illustration 193 as “*montanana*”, and in the text, while using Zeller’s name “*alpestrana*”, he attributed it erroneously to Fischer von Röslerstamm [=FR]. Probably in order to correct his first mistake, he added to the description the explanatory “*montanana* FR. olim” (Herrich-Schäffer [1849]). Finally, the taxon became known as *Grapholita alpestrana* HS.

Thus, in short: “*montanana* FR” in litt. became *alpestrana* [anonymous, but in fact Zeller], in error, then *alpestrana* FR, *montanana* HS and finally *alpestrana*

HS. According to the International Code of Zoological Nomenclature's Recommendation 51D, this taxon should bear the name *Dichrorampha alpestrana* ([Zeller], 1843), because the anonymous description can unambiguously be traced to Zeller (ICZN 1999).

Unfortunately almost simultaneously with [Zeller] (1843) the French entomologist Philogène Auguste Joseph Duponchel described *Ephippiphora montanana* (Duponchel, 1843). He referred to the name "*Grapholita montanana*" in the catalogue of Mr. Parreyss of Vienna. In another context, Duponchel wrote, that Mr. Parreyss, natural history dealer in Vienna, and "Mr. Fischer de Roeslerstamm" provided him with a large number of the Microlepidoptera he described and figured in his work (Duponchel 1844). In the very same book, he also mentioned in the index of species, that his *montanana* originated from Germany which is most likely an error for Austria.

As of today, *Dichrorampha alpestrana* ([Zeller], 1843) is considered an invalid junior synonym of *Dichrorampha montanana* (Duponchel, 1843), both in Razowski (2003) and in Fauna Europaea ([www.faunaeur.org](http://www.faunaeur.org) – accessed on 02.iv.2021).

We will subsequently prove that this view does not follow the regulations of ICZN (1999).

## Materials and methods

In the course of this study, a total of 104 male and 12 female specimens of "*D. montanana sensu auct.*" originating mainly from different parts of the Alps and the Jura mountains were investigated:

Specimen repositories:

- Research collection Jürg Schmid, Ilanz, Switzerland;
- Research collection Tiroler Landesmuseen, Hall, Austria (TLMF);
- Research collection Rudolf Bryner, Biel/Bienne, Switzerland;
- Research collection Wolfgang Wittland, Wegberg-Dahlheim, Germany.

The following specimen characteristics were analyzed:

- **Wing pattern:** male and female wings were photographed with a MP-E 65 mm photo lens mounted on a Canon EOS 7D digital camera, illuminated by a Macro ring lite MR-14EX flash.
- **Genitalia morphology male and female:** In 64 of these specimens standard genital preparations were done (Robinson 1976) whereby the final genitalia were either permanently embedded, or alternatively submerged into water-soluble Berlese's fluid (Chroma Ges. D-Köngen) and enclosed between two transparent acetate foils. These were pinned to the needle carrying the moth specimen thus ensuring the spatial coherence of genital preparation with the respective insect.

The genital preparations were photographed with a Canon EOS 7D digital camera, using a Zeiss Primo Star microscope with a 4× and 10× plan-achromat lens.

- **DNA Barcodes:** DNA samples (dried legs) to obtain DNA barcode sequences of a 658 base-pair long segment of the mitochondrial COI gene (cytochrome c oxidase 1) were prepared according to the prescribed standards. Legs from 35 specimens of the suspected species pair were successfully processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) to obtain DNA barcodes and using the standard high-throughput protocol described in de Waard et al. (2008). We furthermore analysed 317 supplementary sequences from BOLD, covering 37 additional European species and two subspecies. Sequences were submitted to GenBank, and further details including complete voucher data and images can be accessed in the public dataset "*Dichrorampha* Europe [DS-DICHMONT]" in the Barcode of Life Data Systems (BOLD; Ratnasingham and Hebert 2007). Degrees of intra- and interspecific variation of DNA barcode fragments were calculated under the Kimura 2 parameter model of nucleotide substitution using analytical tools of BOLD systems v. 4.0. (<http://www.boldsystems.org>). A Neighbor-Joining tree of DNA barcode data was constructed using MEGA 6 (Tamura et al. 2013) under the Kimura 2 parameter model for nucleotide substitutions. A three-letter code (ISO 3166-1 alpha-3, [https://en.wikipedia.org/wiki/ISO\\_3166-1\\_alpha-3](https://en.wikipedia.org/wiki/ISO_3166-1_alpha-3)) was used to abbreviate country names.

## Results

### Wing pattern characteristics

Most of fresh specimens of both sexes could be grouped into two main categories: those with olive ground colour and irregular silvery lines on their forewings and those with more brownish ground colour and a more or less conspicuous bright triangular mark arising from dorsum and extending beyond mid-wing. A few specimens, however, presented a pattern/colour not easily assignable to either group.

### Male genital features

The serial dissection of alpine "*Dichrorampha montanana sensu auct.*" specimens disclosed that the genital phenotype of all male specimens could unambiguously be assigned to two well defined groups with no intermediate forms:

- Group I, associating a broad phallus ending in a very dominant, acute tooth with a distinct projection at the inner valval border, corresponding to Fig. 3.

- Group II with a rather broad, bi- or multi-teethed phallus with a straight inner valva border, corresponding to Fig. 4.

## Molecular analysis

DNA sequencing resulted in full barcode fragments for 35 specimens of "*D. montanana* s. *auct*"-complex. These grouped into two well delimited clusters, corresponding to the above mentioned groups I (18 specimens) and group II (17 specimens). Furthermore 248 full barcode sequences, 64 sequences > 500 bp and four shorter sequences < 500 bp from BOLD, covering 37 European species and two subspecies, were considered for analysis. Thirty-seven distinct DNA barcode clusters were observed, separating the vast majority of sequenced taxa, including the two suspected species in the *D. montanana* species group. However, DNA barcodes failed to separate

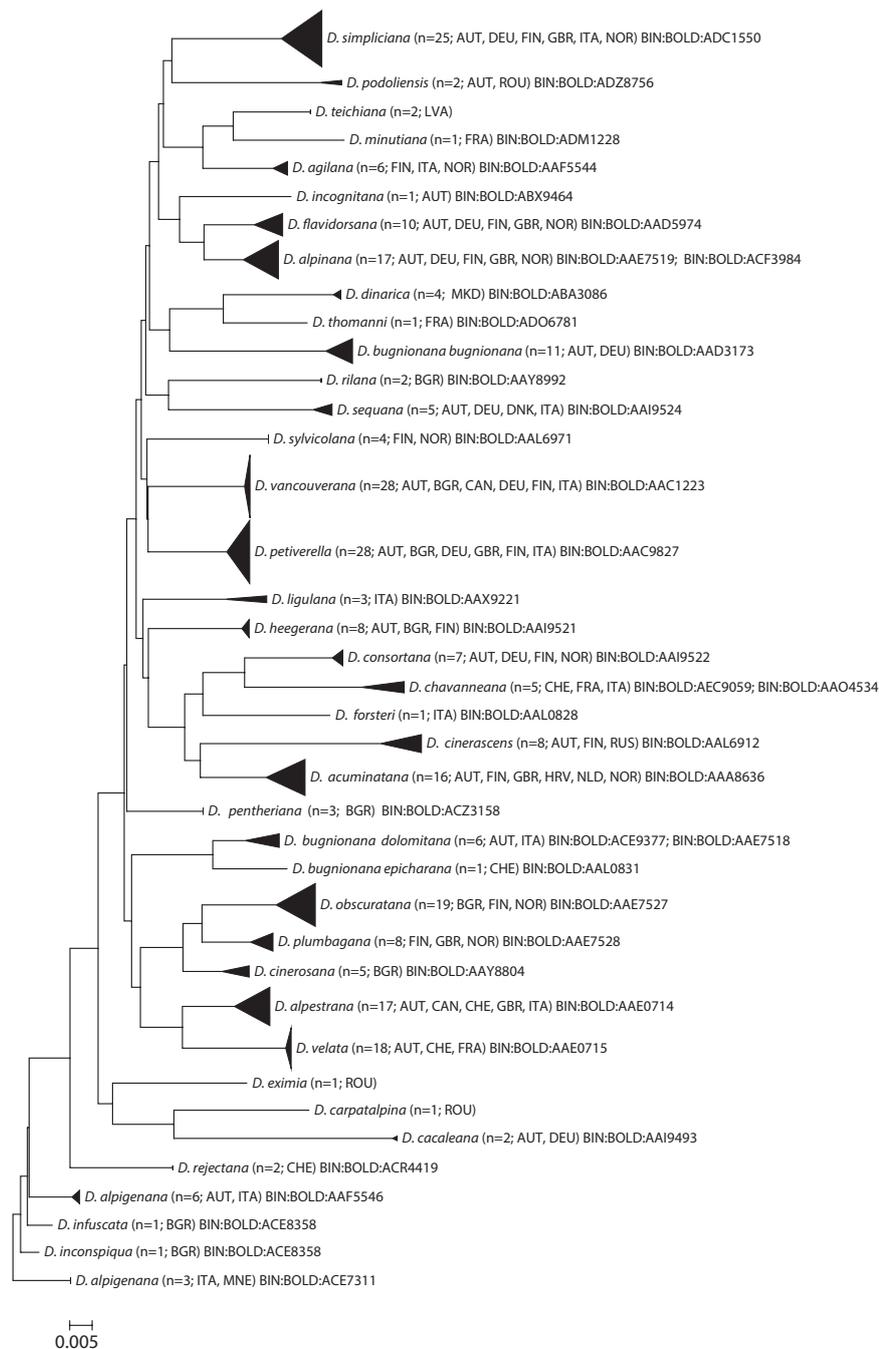
closely related species of the *D. plumbana* species group (*D. plumbana* (Scopoli, 1763), *D. sedatana* Busck, 1906, *D. aeratana* (Pierce & Metcalfe, 1915), *D. tarmanni* Huemer, 2009), as well as *D. infuscata* (Danilevsky, 1960) and *D. inconspiqua* (Danilevsky, 1948).

Sequences of the COI barcode region in European *Dichrorampha* reveal moderately low intraspecific but significant interspecific genetic distances. Mean distances within species are 0.54% with a minimum of 0% and maximum of 4.54% in *D. bugnionana* (Duponchel, 1843) subspecies which likely represent distinct species. Mean distances to nearest neighbours are much higher with 3.45%, ranging from minimum 0% in the above mentioned species with barcode sharing to maximum 7.94% (Fig. 5, Table 1).

Thus, based on male genital, wing pattern characteristics, and DNA barcode divergences the existence of two well defined species was postulated. However, the search for valid names of these two taxa was challenging.

**Table 1.** Intraspecific mean K2P (Kimura 2 Parameter) divergences, maximum pairwise distances, nearest species, nearest neighbor and distance to nearest neighbor (%).

Species	Mean Intra-Sp %	Max Intra-Sp %	Nearest species	Nearest Neighbour	Distance to NN %
<i>Dichrorampha acuminatana</i>	0.37	1.87	<i>Dichrorampha petiverella</i>	BTLP376-11	4.83
<i>Dichrorampha aeratana</i>	1.32	5.08	<i>Dichrorampha sedatana</i>	LON5763-17	0.46
<i>Dichrorampha agilana</i>	0.39	0.64	<i>Dichrorampha teichiana</i>	LEEU626-11	4.18
<i>Dichrorampha alpestrana</i>	0.72	2.5	<i>Dichrorampha velata</i>	PHLAD201-11	3.96
<i>Dichrorampha alpigenana</i>	1.54	3.1	<i>Dichrorampha inconspiqua</i>	BTLP451-11	1.4
<i>Dichrorampha alpinana</i>	0.92	1.99	<i>Dichrorampha flavidorsana</i>	FBLMT309-09	2.5
<i>Dichrorampha bugnionana</i>	4.54	9.34	<i>Dichrorampha teichiana</i>	LEEU626-11	4.16
<i>Dichrorampha cacaleana</i>	0.17	0.17	<i>Dichrorampha carpatalpina</i>	LEASV661-19	7.94
<i>Dichrorampha carpatalpina</i>	N/A	0	<i>Dichrorampha alpigenana</i>	PHLAF568-11	5.65
<i>Dichrorampha chavanneana</i>	0.78	1.87	<i>Dichrorampha consortana</i>	FBLMZ645-12	4.92
<i>Dichrorampha cinerascens</i>	1.23	2.44	<i>Dichrorampha acuminatana</i>	LEAST411-17	6.4
<i>Dichrorampha cinerosana</i>	0.86	1.24	<i>Dichrorampha plumbagana</i>	CGUKC685-09	2.76
<i>Dichrorampha consortana</i>	0.27	0.58	<i>Dichrorampha chavanneana</i>	PHLAD710-11	4.92
<i>Dichrorampha dinarica</i>	0.15	0.31	<i>Dichrorampha thomanni</i>	LEASU278-18	4.47
<i>Dichrorampha eximia</i>	N/A	0	<i>Dichrorampha petiverella</i>	LASTS800-15	4.23
<i>Dichrorampha flavidorsana</i>	0.58	1.44	<i>Dichrorampha teichiana</i>	LEEU626-11	2.05
<i>Dichrorampha forsteri</i>	N/A	0	<i>Dichrorampha pentheriana</i>	LEATJ1152-16	5.91
<i>Dichrorampha gueneana</i>	0.13	0.25	<i>Dichrorampha vancouverana</i>	LPAB581-08	0.15
<i>Dichrorampha heegerana</i>	0.23	0.46	<i>Dichrorampha teichiana</i>	LEEU626-11	3.1
<i>Dichrorampha incognitana</i>	N/A	0	<i>Dichrorampha teichiana</i>	LEEU626-11	3.47
<i>Dichrorampha inconspiqua</i>	N/A	0	<i>Dichrorampha infuscata</i>	BTLP373-11	0.93
<i>Dichrorampha infuscata</i>	N/A	0	<i>Dichrorampha inconspiqua</i>	BTLP451-11	0.93
<i>Dichrorampha ligulana</i>	1.17	1.76	<i>Dichrorampha petiverella</i>	NOELE683-20	4.42
<i>Dichrorampha melaniana</i>	N/A	0	<i>Dichrorampha sedatana</i>	PHLAC013-10	0
<i>Dichrorampha minutiana</i>	N/A	0	<i>Dichrorampha teichiana</i>	LEEU626-11	4.18
<i>Dichrorampha obscuratana</i>	0.83	1.72	<i>Dichrorampha plumbagana</i>	CGUKC685-09	3.6
<i>Dichrorampha pentheriana</i>	0	0	<i>Dichrorampha teichiana</i>	LEEU626-11	2.82
<i>Dichrorampha petiverella</i>	0.73	1.55	<i>Dichrorampha teichiana</i>	LEEU626-11	3.11
<i>Dichrorampha plumbagana</i>	0.32	1.04	<i>Dichrorampha cinerosana</i>	BTLP382-11	2.76
<i>Dichrorampha plumbana</i>	1.26	3.65	<i>Dichrorampha sedatana</i>	PHLAC013-10	0
<i>Dichrorampha podoliensis</i>	0.89	0.89	<i>Dichrorampha petiverella</i>	TDAAT820-19	4.8
<i>Dichrorampha rejectana</i>	0	0	<i>Dichrorampha inconspiqua</i>	BTLP451-11	3.64
<i>Dichrorampha rilana</i>	0	0	<i>Dichrorampha teichiana</i>	LEEU626-11	3.82
<i>Dichrorampha sedatana</i>	0.27	1.24	<i>Dichrorampha plumbana</i>	PHLAJ255-14	0
<i>Dichrorampha senectana</i>	N/A	0	<i>Dichrorampha sedatana</i>	PHLAC013-10	0.15
<i>Dichrorampha sequana</i>	0.44	0.92	<i>Dichrorampha teichiana</i>	LEEU626-11	5.31
<i>Dichrorampha simpliciana</i>	1.29	3.46	<i>Dichrorampha teichiana</i>	LEEU626-11	4.92
<i>Dichrorampha sylvicolana</i>	0	0	<i>Dichrorampha teichiana</i>	LEEU626-11	4.57
<i>Dichrorampha tarmanni</i>	0.79	2.18	<i>Dichrorampha sedatana</i>	PHLAC013-10	0
<i>Dichrorampha teichiana</i>	0	0	<i>Dichrorampha flavidorsana</i>	FBLMT309-09	2.05
<i>Dichrorampha thomanni</i>	N/A	0	<i>Dichrorampha dinarica</i>	PHLAE559-11	4.47
<i>Dichrorampha vancouverana</i>	0.11	0.33	<i>Dichrorampha gueneana</i>	BTLP389-11	0.15
<i>Dichrorampha velata</i>	0.05	0.31	<i>Dichrorampha alpestrana</i>	PHLAB566-10	3.96



**Figure 5.** Neighbor-Joining tree of species in European *Dichrorampha* (Kimura 2 parameter, built with MEGA 6 cf. Tamura et al. 2013), only sequences (>500 bp) considered. Note: the scale bar only applies to internal branches between species. Width of triangles represent sample size, depth the genetic variation within the cluster. Source: DNA Barcode data from BOLD (Barcode of Life Database, cf. Ratnasingham and Hebert 2007).

### Type material of nominal taxa in the *Dichrorampha montanana sensu auct.* complex

*Dichrorampha montanana* (Duponchel, 1843)  
*Ephippiphora montanana* Duponchel [1843]: 413,  
 [1845]: pl. 83, fig. 7.

In the “Muséum national d’histoire naturelle” in Paris, Mr. Patrice Leraut kindly checked the *D. montanana* specimens of the collection. He found that J.D. Bradley

(BMNH) had already dissected a syntype specimen of *D. montanana* Duponchel, a male, and that the genitalia slide still exists. Mr. Christian Gibeaux kindly forwarded us photographs of the genitalia preparation, the mounted specimen and the labels. The original description of the species does not give any indication to the number of examined specimens but according to de Joannis (1915) a second specimen should be preserved in coll. Duponchel. Following ICZN (1999), the above figured specimen is here designated as a lectotype in order to



Figures 6–8. *Dichrorampha montanana* (Duponchel), lectotype, labels and male genitalia.

fix the identity of the species and conserve stability of nomenclature (Figs 6–8).

The lectotype of *D. montanana* obviously has a large-toothed phallus combined with a valval inner border bulge. Thus, specimens of the abovementioned group I represent *D. montanana*.

As synonyms of *D. montanana* Duponchel, Razowski (2003) lists the following taxa:

*Grapholitha alpestrana* [Zeller], 1843; *Grapholitha alpestrana* Herrich-Schäffer, 1851; *Dichrorampha tanacetii* Stainton, 1857; *Dichrorampha herbosana* Barrett, 1872; *Hemimene blasiana* Kennel, 1919; *Hemimene modestana* Müller-Rutz, 1922 [false 1992]

1) *Grapholitha alpestrana* [Zeller], 1843

*Grapholitha alpestrana* Herrich-Schäffer, 1851

Mr. Kevin Tuck from the British Museum-Natural History kindly informed us, that in the collection of his institution, there is no material of *D. alpestrana* originating from the Herrich-Schäffer collection (Herrich-Schäffer [1851]). One specimen of *D. alpestrana* comes from the collection of Zeller; it was however collected by Heineemann and cannot be considered as syntype.

In the Berlin Museum, Dr. Wolfram Mey allowed us to screen the Palaearctic Tortricidae collection for Herrich-Schäffer/Zeller material, unfortunately without success.

The Senckenberg Museum at Frankfurt, however, owns two specimens of *Dichrorampha* [*alpestrana*] *montanana* which obviously are from the time of discovery of this species. One male without abdomen is labelled “*Gr.* [*apholita*] *Montanana* FR, Styria, Fischer v.R.” with an additional minute red square label with nr. 7. A second male is labelled “*Gr. Montanana* FR. Styria Mann

(FR vid.)” and therefore obviously has been identified by Fischer von Röslerstamm himself. Thus these specimens come closest to the original material Zeller must have based his description on but it cannot be proved that the material was studied by him. It is therefore not suitable for designation of a lectotype. Similarly two additional males from the Heyden collection in Frankfurt labelled as “*Gr. Alpestrana*” are not to be considered as syntypes as they have been collected by Mann at a different locality “Schneeberg” or just labelled insufficiently “Austr. Alp.”.

Dr. Wolfgang Nässig kindly allowed us to examine these specimens which, judging from wing pattern, all clearly represent *D. alpestrana*.

Finally Mr. Daniel Bartsch informed us that there is no European type material from Herrich-Schäffer in the Stuttgart Museum.

## 2) *Dichrorampha tanaceti* Stainton, 1857

The description of this species mentions “...*macula magna triangulari dorsali dilutiore.*” [with a big triangular diluted dorsal patch], thus describing the obvious differentiating wing pattern character of *D. montanana* [*alpestrana*]. Obratzov (1953) depicted the male genitalia of *D. tanaceti*, which are identical with *D. montanana*. Then, in 1958, the same author formally synonymized *D. tanaceti* with *D. montanana* [*alpestrana*].

3) *Dichrorampha monticolana* described in detail by Heinemann (1863) and clearly referring to *D. alpestrana* is considered as an unjustified emendation of *D. montanana* as Duponchel is mentioned as author of the species in the headline. Following article 33.2.3 of ICZN (1999) the name therefore is a junior objective synonym of *D. montanana*.

## 4) *Dichrorampha herbosana* Barrett, 1872

The description says: “dorsal blotch triangular, oblique, pointed at the apex” [...] “Readily distinguished from the allied species by its pointed wings and distinct, pointed dorsal blotch.”, thus, referring it to *D. montanana* [*alpestrana*]. *D. herbosana* was already synonymized by Obratzov (1953).

## 5) *Hemimene blasiana* Kennel, 1919

In the description of this species, Kennel mentions: “... ohne dass ein scharfer, heller Dorsalfleck gebildet wird...” [without there being formed a sharp, bright dorsal blotch], but the concomitant illustration depicts a male with such a blotch. Obratzov (1967), after having examined the lectotype, confirmed his earlier judgement (1958) according to which this taxon is synonymous with *D. montanana* [*alpestrana*]. Thanks to the courtesy of Dr. Wolfram Mey we have been able to study the lectotype and a female paralectotype, stored at the Museum Berlin.

The damaged lectotype labelled “Gastein” “Lectotype” “115.116 *Hemimene blasiana* n.sp. Type ♂ Kenn” “*Dichrorampha montanana* Dup. ♂ N. Obratzov det. 1961” as well as the female paralectotype with labels “*blasiana* Kenn Type ♀ Gastein” “Typus” “DNA Barcode TLMF Lep 29806” fully correspond with *D. alpestrana*.

## 6) *Hemimene modestana* Müller-Rutz, 1922

The description of this new species is very detailed and particularly mentions the special form of the end of phallus with its marked curled peak. Mr. Daniel Burckhardt of the Basel Museum allowed us to study the two males labelled as “types” in the Müller-Rutz collection. Their wing pattern corresponds well with *D. alpestrana*, so do the nice illustrations in Müller-Rutz (1934). Therefore, *H. modestana* is clearly a junior synonym of *D. alpestrana*.

## 7) *Dichrorampha alpestrana* (?) ab. *schatzmanni* Rebel, 1927

Rebel, in 1927 published a description and a photograph of his *Dichrorampha alpestrana* (?) ab. *schatzmanni* both of which fit perfectly the characteristics of the taxon of group I. According to article 45.6.2 of ICZN (1999) however, the term “ab.” denotes an infrasubspecific rank and is therefore not available.

## 8) *Dichrorampha alpestrana* f. *olivana* Müller-Rutz, 1934

Specimens of the type series were examined at the Basel Museum (Müller-Rutz collection). These specimens, originating from the Zermatt region, correspond well with the taxon of group I. However, the name was used infrasubspecifically for an alpine form and subsequently not adopted as the valid name of a species or subspecies. Following article 45.6.4 of ICZN (1999) the name is therefore not available.

## 9) *Dichrorampha pseudoalpestrana* Danilevsky (in Obratzov, 1953)

According to Obratzov, Danilevsky described this taxon in order to give a valid name to the unavailable name “*alpestrana*”. There is a figure of the male genitalia which proves that this taxon is neither *D. alpestrana* nor the taxon of group II.

Further additional synonyms of *D. montanana* [*alpestrana*] listed by Obratzov (1958), namely *D. subsequana* Lederer, 1859, *D. plumbagana* Wocke, 1871 (partim) belong to non-related species (Gilligan et al. 2018).

Application of the correct name:

*Dichrorampha montanana* or *D. alpestrana*?

According to our inquiries Zeller’s description of *D. alpestrana* is both valid and also published in advance of

Duponchel's work on *D. montanana*. From the imprinted date of the relevant issue of Stettiner entomologische Zeitung the description was published in May 1843. Duponchel's description was published in fascicle 26 of Godart and Duponchel (1842–[1844]) which according to de Joannis (1915) was firstly registered in “Dépôt légal” on the 18<sup>th</sup> of August 1843. Reversal of precedence as regulated in Article 23.9. of ICZN (1999) cannot be applied in this case since the senior synonym has been used as a valid name after 1899 (i.e. Rebel 1927) (see Article 23.9.1.1). Both names are based on the same original series collected by Fischer von Röslerstamm, distributed under the *in litteris* name “*montanana* FR”, and conspecificity from originals we have studied (see below) is undoubted. Accordingly we revoke *D. alpestrana* ([Zeller], 1843) sp. rev. from synonymy and consider *D. montanana* (Duponchel, 1843) syn. nov. as junior synonym.

### Synonymic list

*Dichrorampha alpestrana* ([Zeller], 1843) (*Grapholitha*) sp. rev.

= *D. montanana* (Duponchel, 1843) (*Ephippiphora*) syn. nov.

= *D. alpestrana* (Herrich-Schäffer, 1851) (*Grapholitha*)

= *D. tanacetii* Stainton, 1857 syn. rev.

= *D. monticolana* Heinemann, 1863, unjustified emendation

= *D. herbosana* Barrett, 1872 syn. rev.

= *D. blasiana* (Kennel, 1919) (*Hemimene*) syn. rev.

= *D. modestana* (Müller-Rutz, 1922) (*Hemimene*) syn. rev.

*Dichrorampha velata* sp. nov.

= *D. alpestrana* ab. *schatzmanni* Rebel, 1927 (infraspecific, unavailable)

= *D. alpestrana* f. *olivana* Müller-Rutz, 1934 (infraspecific, unavailable)

Conclusion: Despite the fact that several authors introduced names within the “*montanana/alpestrana*”-complex, no valid name for the taxon of group II could be ascertained. Therefore, this species is newly described.

### Taxonomic part

#### *Dichrorampha velata* sp. nov.

<http://zoobank.org/18331B68-D9DD-445F-95C3-0978D1FE6DF7>

Figs 2, 9, 11–16, 47

**Diagnosis.** *Dichrorampha velata* is in overall appearance very similar to *D. montanana* from which it differs in wing pattern mainly by its more olive ground colour (in fresh specimens), by its markedly weaker dorsal blotch and by its slightly larger wingspan.



Figure 9. *Dichrorampha velata* sp. nov., holotype, adult.

In male genitalia, the most obvious and constant differences are found in the shape of the phallus and the inner lobal line of the cucullus which both allow the unambiguous separation of the two taxa. In female genitalia, no clear differences could be ascertained.

**Derivatio nominis.** “velatus” Latin, meaning “veiled” with respect to its confused history.

**Material examined** (specimens identified from genitalia preparations and/or DNA barcodes). **Holotype.** ♂, wingspan: 15.2 mm. CH-La Punt GR, God Arscheida [46.5864°N, 9.91928°E], 1820 m; 26.VI.2006; GP 108; BOLD: BC TLMF Lep 04060. Deposited in TLMF. **Paratypes.** SWITZERLAND: 1♂: Felsberg GR, Sand [46.84541°N, 9.47091°E], 590 m, 24.6.2005, Schmid, BOLD 4061; 1♂: Avers, Innerferrera GR, [46.51657°N, 9.45399°E], 1750 m, 29.6.2009, Schmid BOLD 4057; 1♂: Bergün GR, Pentsch [46.63913°N, 9.73708°E], 1500 m, 1.7.2009, Schmid, DNA Barcode ID TLMF Lep 04056; 2♂: Laax GR, Nagens [46.85122°N, 9.24287°E], 1820 m, 28.7.2005, Schmid, DNA Barcode ID TLMF Lep 0 4062; 2♂: La Punt GR, God Arscheida [46.5864°N, 9.91928°E], 1820 m, 26.6.2006, Schmid, DNA Barcode IDs TLMF Lep 04060, TLMF Lep 04063; 1♂: Avers-Cresta GR [46.47579°N, 9.50389°E], 1880 m, 15.7.2009, Schmid; 1♂: Tarasp-Fontana GR, Val Zuort [46.77299°N, 10.25755°E], 1440 m, 10.7.2008 Schmid; 1♂: La Punt GR, God Arscheida [46.5864°N, 9.91928°E], 1980 m, 30.6.2007, Schmid; 3♂: Tujetsch GR, Selva [46.66171°N, 8.2043°E], 1600 m, 20.6.2005, Schmid; 1♂, 1♀: Pigniu GR, Lag [46.82367°N, 9.11229°E], 1430 m, 21.6.2003, Schmid; 1♂: Tujetsch GR, Oberalp-Canals [46.65123°N, 8.68557°E], 1900 m, 1.8.2005, Schmid; 1♀: Sedrun, Bugnei [46.69012°N, 8.78537°E], 1700 m, 31.7.2004, Schmid; 1♂: Pigniu GR, Alp [46.82784°N, 9.10864°E], 1460 m, 10.7.2001, Schmid; 1♂: Medel GR, Acla [46.63106°N, 8.83805°E], 1520 m, 12.7.2001, Schmid; 1♂: Cormoret BE, Métairie de Morat [47.14394°N, 7.06376°E], 1500 m, 10.6.2000, Bryner; 1♀: Cormoret BE, Métairie de Morat [47.14394°N, 7.06376°E], 1500 m, 10.6.2000, Bryner; 1♂, 1♀: Villeret, Chasseral, Krete west [47.12969°N, 7.04969°E], 1550 m, 23.7.1994, Bryner. 1♂: Cormoret BE, Métairie de Morat

[47.14394°N, 7.06376°E], 1500 m, 10.7.2003, Bryner; 1♂: Nods BE, Chasseral, Les Roches [47.13657°N, 7.07567°E], 1520 m, 15.7.2004, Bryner; 1♂: Nods BE, Chasseral, Piste [47.12568°N, 7.06243°E], 1285 m, 1.7.2013, Bryner; 1♂: Nods BE, Chasseral, sous les Roches [47.13398°N, 7.07345°E], 1380–1480 m, 13.6.2001, Bryner; 1♂: Villiers NE, Métairie de l’Ile [47.10633°N, 7.01728°E], 1350–1470 m, 14.6.2002, Bryner; 1♂: Ayers VS, Zinal, Pti Mountet [46.10759°N, 7.63174°E], 1800 m, 8.7.2015, Bryner; 1♂: Château-d’Oex, Bévieu-Le Crinson [46.51371°N, 7.16527°E], 1260–1540 m, 22.6.2013, Bryner; 1♂: Zinal VS [46.13081°N, 7.62554°E], 1600–1850 m, 6.7.2020, Wittland; 1♂: Avers-Cröt GR [46.47681°N, 9.48857°E], 1750 m, 5.8.2011, Wittland; 1♂: Zinaltal VS, Le Vichiesso [46.09454°N, 7.63751°E], 1950–2140 m, 1.7.2014, Wittland; 3♂: Zinaltal VS, Le Vichiesso [46.11087°N, 7.63369°E], 1700–1850 m, 1.7.2014, Wittland; 1♂: Turtmantal VS, Augstbordregion [46.2°N, 7.7666°E], 2400 m, 12.7.2010, Wittland; 1♂: Leuk VS, Guttet-Tschärmilong [46.47681°N, 9.48857°E] 1800 m, 8.8.2016, Wittland; 1♂: Leuk VS, Erschmatt-Brentschen [46.32883°N, 7.69125°E], 1550 m, 28.6.2017, Wittland; 1♂: Villeret BE, Chasseral [47.13194°N, 7.05477°E], 1430 m, 25.6.2020, Wittland.

GERMANY: 2♂: Immenstadt, Mittag [47.53833°N, 10.21861°E], 1450 m, 8.7.1983 Süssner/TLMF; 3♂: Schwäbische Alb, Urach, Nägeles Fels [48.50639°N, 9.38861°E], 700 m, 19.6.1970, Süssner/TLMF; 4♂: ditto, but 19.6.1968, Süssner/TLMF; 1♂: Schwäbische Alb, Urach 4 km SSW [48.48278°N, 9.37833°E], 630 m, 24.6.1975, Süssner/TLMF; 1♀: Schwäbische Alb, Urach [48.48278°N, 9.37833°E], 8.8.1954, Groschke/TLMF; 1♂: 2ditto, but 5.7.1955, Groschke/TLMF; 3♂: Schwäbische Alb, Neuffen-Hohenneuffen, Randweg [48.55833°N, 9.39167°E], 700 m, 19.6.1968, Süssner/TLMF; 1♀: ditto, but 30.6.1967, Süssner/TLMF; 1♀: Schwäbische Alb, Hohenneuffen [48.55833°N, 9.39167°E], 700 m, 8.7.1956, Süssner/TLMF; 1♀: ditto, but 30.6.1967 Süssner/TLMF.

AUSTRIA: Tirol, Umhausen [47.14027°N, 10.9290°E], 20.6.48, Burmann/TLMF; 2♂: Tirol, Umhausen N, unt. Farst [47.15694°N, 10.92278°E], 1100 m, 26.6.2010, Huemer/TLMF, DNA Barcode IDs TLMF Lep 03368, TLMF Lep 03607; 1♂: ditto, but 2.8.2014, Huemer/TLMF, DNA Barcode ID TLMF Lep 15225; 1♂: Tirol, Sölden [46.978°N, 11.002°E], 1600 m, 25.7.1956, Süssner/TLMF; 1♂: Salzburg, Grossglockner [47.0289°N, 6.40417°E], 1900 m, 1.7.1976, Zürnbauer/TLMF.

ITALY: 1♂: Gr. St. Bernhard [45.883°N, 7.191°E], 2350 m, 1.7.1967, Zürnbauer/TLMF; 1♂: Südtirol, Vinschgau, Graun, Rojental [46.80722°N, 10.47889°E], 1970 m, 7.7.2013, Huemer/TLMF, DNA Barcode ID TLMF Lep 12339; 1♂: ditto, but 1860–1880 m, 1.7.2014, Huemer/TLMF, DNA Barcode ID TLMF Lep 15529.

FRANCE: 1♂: Rhône-Alpes, Le Corbier [45.23722°N, 6.26029°E], 1650 m, 17.7.2008, Nel/TLMF, DNA Barcode ID TLMF Lep 03370; 1♂: Auvergne-Rhône-Alpes, La Ville des glaciers [45.73555°N, 6.75555°E], 2200 m, 12.7.2007, Nel/TLMF, DNA Barcode ID TLMF Lep

03369; 2♂: Provence-Alpes-Côte d’Azur, Col du Lautaret [45.0289°N, 6.40417°E], 2058 m, 20.7.2006, Nel/TLMF, DNA Barcode IDs TLMF Lep 03376, TLMF Lep 03377.

**Description.** Wingspan 12.8–16.5 mm (n = 25) mean: 14.6 mm. Forewing length: 6–8 mm. Head light grey, mixed with ochreous scales. Labial palpi dark grey, conspicuously ochreous at base. Proboscis pale yellow, antennae ochreous. Thorax and tegulae yellowish grey mixed with ochreous scales. Legs and abdomen grey with ochreous scales. Forewing ground colour olive brown or beige brown. Costal fold about one fourth of costal length. Costal strigulae darker brown alternating with creamy-white marks. Along termen variable number (3–5) of dark dots. Dorsal blotch faintly brighter than ground color, usually inconspicuous, pyramidal, with faint irregular darker strigulae. Silvery lines irregular, usually two more pronounced lines running parallel to termen. Ciliary area composed of a line of short dark scales in front of a line of longer dark-tipped creamy-white scales. Hindwing grey, paler at base, with a dark-white-dark banded ciliary line.

Male genitalia (Figs 10, 23–31, 38–40): Saccus ventrally straight, neck of valva rather broad, cucullus crescent-shaped, dorsal lobe short, ventral corner rather pointed. Inner lobal line broadly rounded, without projections. Phallus broad, half-pipe-like, both walls slightly twisted, each ending distally in a prominent thorn, sometimes also with two or more smaller thorns.



**Figure 10.** *Dichrorampha velata* sp. nov., holotype, male genitalia.

**Female** (Fig. 47): wingspan 10.9–13 mm (n = 4) mean: 12.0 mm. Forewing length: 5.5–6 mm.

Forewing ground color dark brown, suffused with ochreous scales. Markings like in male but darker and more contrasting. Dorsal blotch variably conspicuous.

Female genitalia (Figs 48–52): Colliculum heavily sclerotized, broad, proximally asymmetrically bulbous. Ductus bursae very short, small sclerotic area before corpus bursae. Two signa: one bigger slightly curved thorn and one small, straight thorn.

**Molecular data.** BIN: BOLD:AAE0715. The intraspecific average distance of the barcode region is very



**Figures 11–16.** *Dichrorampha velata* sp. nov., variation in wing pattern. **11.** CH-Disentis, 1500 m, 9.7.2006; **12.** CH-Avers-Cresta, 1880 m, 15.7.2009; **13.** CH-La Punt, 1820 m, 26.6.2006; **14.** CH-Tujetsch, 1600 m, 20.6.2005; **15.** CH-Avers-Cresta, 1880 m, 15.7.2009; **16.** CH-La Punt, 1980 m, 30.6.2007, all coll. J. Schmid.

low with only 0.05%, the maximum distance 0.31% (p-dist) ( $n = 18$ ). The minimum distance to the nearest neighbor, *D. alpestrana*, is 3.96%.

**Distribution (Fig. 57).** *Dichrorampha velata* sp. nov. is currently known from Germany, Austria, Italy, Switzerland and France, mainly from the western Alps, extending to Salzburg (Austria) in the East. In Switzerland, this species inhabits also the Jura mountains, and further extra-alpine records are also documented for southern Germany (Swabian Alps).

Contrarywise *D. alpestrana* occurs only in the southern part of the Swiss Alps, i.e. in a region south of the Rhine-Rhône line. It is widely distributed in Austria but the only species of the group in the eastern part of the country (type locality of *D. montanana* and *D. alpestrana*). Further proved records come from the Italian Alps, Northern Macedonia and from the United Kingdom, indicating a highly disjunct arctic-alpine distribution pattern.

In some localities in Switzerland and Italy both species have been observed in sympatry.

**Material examined.** *Dichrorampha alpestrana* (specimens identified from genitalia preparations and/or DNA barcodes). SWITZERLAND: 12♂ 4♀: La Punt GR, God Arscheida [46.5864°N, 9.91928°E], 1820 m, 26.6.2006, Schmid, 1♂ DNA Barcode ID TLMF Lep 01366; 1♂: La Punt GR, God Arscheida [46.5864°N, 9.91928°E], 1820 m, 19.6.2006, Schmid; 3♂: Val Müstair GR, Sta Maria [46.60764°N, 10.41349°E], 1760 m, 30.6.2008, Schmid; 1♂ Avers, GR, Innerferera, Starlera [46.5167°N, 9.43308°E], 1750 m, 30.6.2008, Schmid, DNA Barcode ID TLMF Lep 04058; 3♂: Berninapass Süd GR [46.41390°N, 10.03627°E], 2300 m, 16.7.2008, Schmid; 1♂ DNA Barcode ID TLMF Lep 04059; 1♂: Valposchiavo GR, Bernina Ospizio [46.41056°N, 10.02278°E], 2350 m, 13.07.2009, Schmid; 1♂: Pontresina GR, Lagalb, 2100 m, 10.8.2010, Schmid; 1♂: Ardez GR [46.77352°N, 10.20102°E], Thomann TLMF; 2♂: Simplonpass VS, Bistinealp [46.25803°N, 8.03124°E], 2000–2200 m, 15.7.2010, Wittland; 1♂: S-chanf GR, Alp Chaschauna, 2250–



**Figures 17–22.** *Dichrorampha alpestrana*, variation in wing pattern; all: CH-La Punt, 1820 m, 19.6.2006–26.6.2006 all coll. J. Schmid.

2800 m, 25.7.2012, Wittland. Austria: 1♂: Salzburg, Katschberg [47.00605°N, 13.60972°E], 1750–1850 m, 2.8.1991, Huemer & Karsholt/TLMF; 1♂: Osttirol, Virgen-Obermauern [47.00645°N, 12.43286°E], 1410 m, 8.7.1993, Tarmann/TLMF; 1♂: Osttirol, Rieserfernergruppe, Patschertal [46.92477°N, 12.18629°E], 2080 m, 15.8.1989, TLMF; 1♂: Osttirol, Matrei [46.99966°N, 12.54313°E], 1200 m, 2.6.1963, Burmann/TLMF; 1♂: Nordtirol, Vennatal [47°N, 11.55°E], 2000 m, 2.8.1969, Kapeller/TLMF; 1♂: Nordtirol, Stanzach [47.39527°N, 10.56722°E], 920 m, 5.7.1989, Huemer/TLMF; 1♂: Osttirol, Dorfertal [47.04297°N, 12.33361°E], 1880–2100 m, 28.7.1988, Tarmann/TLMF; 1♂: Osttirol, Kals, Tauernhaus [47.0707°N, 12.6233°E], 1700 m, 5.7.1960, Süssner/TLMF; 1♂: Osttirol, St. Jakob in Defereggen [46.91722°N, 12.33083°E], 1380 m, 12.7.2002, Deutsch/TLMF, DNA Barcode ID TLMF Lep 03366; 1♂: Osttirol, Ködnitztal, Greiwiesen [47.01944°N, 12.6819°E], 2100–2300 m, 21.7.2002, Deutsch/TLMF, DNA Barcode ID TLMF Lep 03367; 1♂: Steiermark, Turracher Höhe NW, [46.92805°N, 13.86805°E], 1750–1850 m,

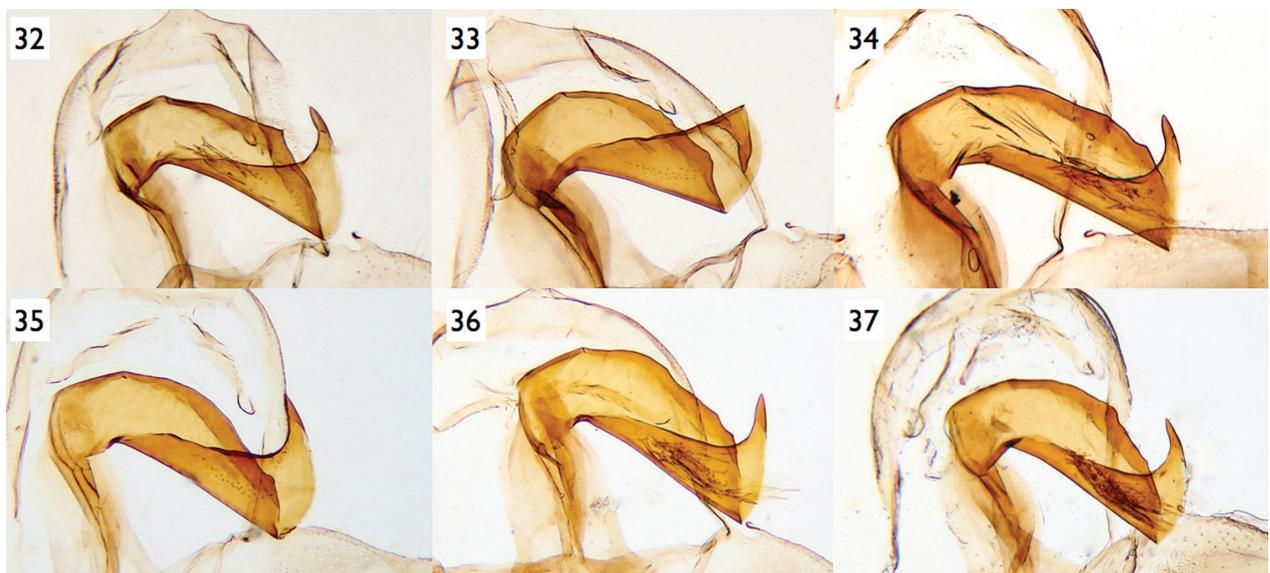
4.7.2009, Huemer/TLMF, DNA Barcode ID TLMF Lep 00818; 1♂: Kärnten, Sausalpe, Umg. Wolfberger Hütte [46.83333°N, 14.65°E], 1500–1800 m, 19.6.2000, Wimmer/TLMF; 1♂: Niederösterreich, Seeau S Hollenstein/Ybbs [47.75°N, 14.78°E], 600 m, 1.6.1986, Lichtenberger /TLMF. Italy: 1♂: Südtirol, Vinschgau, Graun, Rojental [46.80722°N, 10.47889°E], 1970 m, 7.7.2013, Huemer/TLMF, DNA Barcode ID TLMF Lep 12340; 1♂: ditto, but 1860–1880 m, 1.7.2014, Huemer/TLMF, DNA Barcode ID TLMF Lep 15528; 1♂: Südtirol, Ridnauntal [46.938°N, 11.256°E], 1500–1580 m, 8.6.2016, Wittland. Northern Macedonia: 2♂: NP Mavrovo, Korab, Korabska jezero, Kobilino pole [41.77833°N, 20.58194°E], 2080–2180 m, 28.7.-1.8.2011, Huemer & Tarmann/TLMF, DNA Barcode IDs TLMF Lep 05060, TLMF Lep 05061.

Furthermore, published genitalia preparations prove the occurrence of *D. alpestrana* in:

AUSTRIA: Niederösterreich, Sonnwendstein [47.63030°N, 15.86097°E], 1500 m, 15.7.2005, Buchner/Lepiforum; Steiermark, Ponigl bei Weiz



**Figures 23–31.** *Dichrorampha velata* sp. nov., male genitalia, variation in phallus; 23. CH-Avers GR; 24. CH-Tujetsch GR; 25. CH-La Punt GR; 26. CH-La Punt GR; 27. CH-Pigniu GR; 28. CH-Laax GR; 29. CH-Pigniu GR; 30. CH-Avers Cresta GR; 31. CH-Pigniu GR.



**Figures 32–37.** *Dichrorampha alpestrana*, male genitalia, variation in phallus; all: CH-La Punt GR

[47.27077°N, 15.63122°E], ca. 800 m, 6.6.2020, Pichler/Lepiforum; Steiermark, Fischbacher Alpen, St. Kathrein am Offenegg [47.3°N, 15.56666°E], 1400 m, 24.7.2019, Pichler/Lepiforum; Kärnten, Heiligenblut/Göbnitztal, Innere Ebenalm, , Strutzberg [47.02653°N, 12.78645°E], 1800 m, 27.7.2019, BOLD (ABOL-Biboblitz 2019 19–1740/Lepiforum; Steiermark, Graz,

Schöckl [47.19858°N, 15.46567°E], 1400 m, 2.7.2020, Pichler/Lepiforum. United Kingdom: Shropshire, Chapel Lawn, 10.6.2006, Clement/mothdissection.co.uk; RIS TrapTregaron, Ceredigion vc-46, 7.2013, Tillotson/mothdissection.co.uk; Bettws GG, North Wales, 6.2019, Graham/mothdissection.co.uk. A male adult from the Polish Tatra mts. figured by Razowski



**Figures 38–40.** *Dichrorampha velata* sp. nov., male genitalia, variation in inner valval border; 38. CH-Laax GR; 39. CH-Pigniu GR; 40. CH-Avers GR.



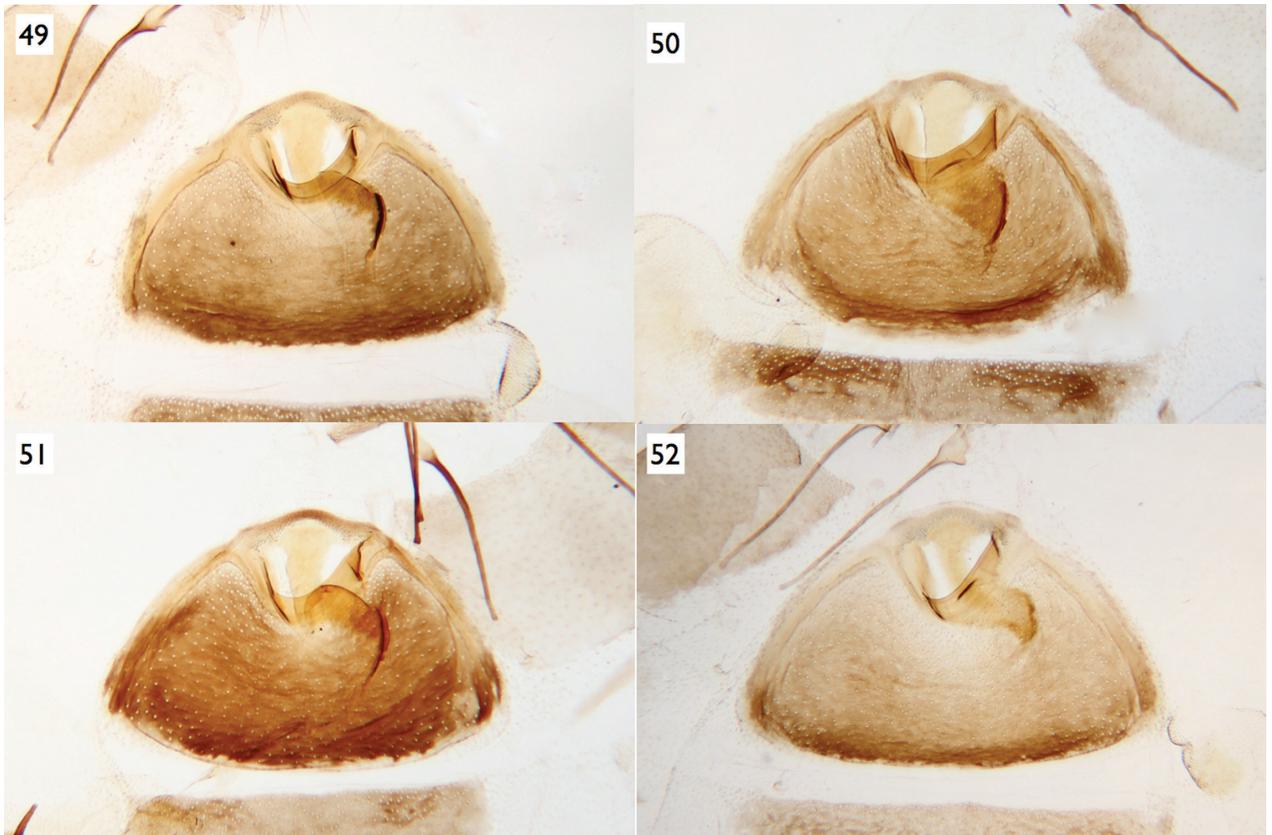
**Figures 41–46.** *Dichrorampha alpestrana*, male genitalia, variation in inner valval border; CH-La Punt GR.



Figure 47. *Dichrorampha velata* sp. nov., female paratype, CH-Pigniu GR.



Figure 48. *Dichrorampha velata* sp. nov. paratype, female genitalia,, CH-Cormoret BE, leg. Bryner.

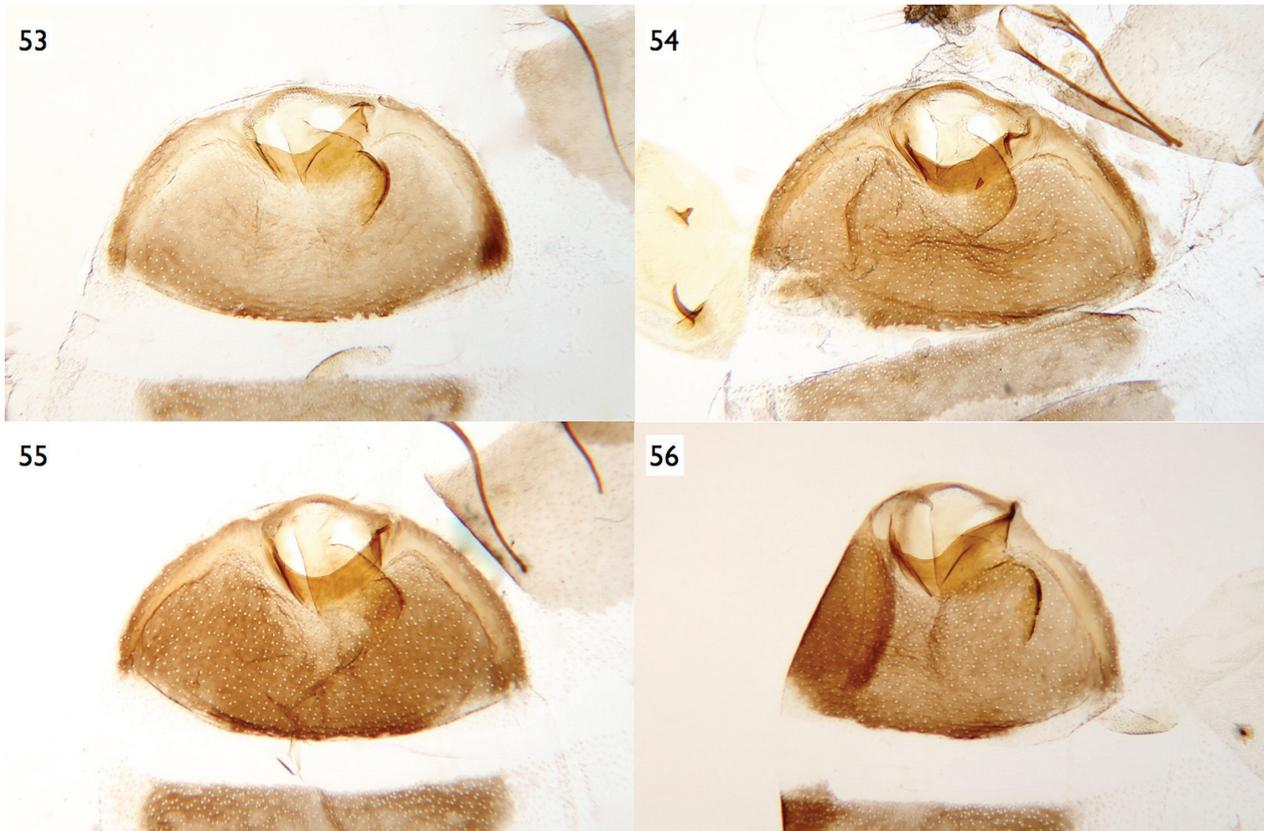


Figures 49–52. CH-Sedrun *Dichrorampha velata* sp. nov., female genitalia, variation in sterigma and ostium; 49. CH-Cormoret BE; 50. CH-Pigniu GR; 51. Sedrun GR; 52. CH-Villeret BE.

(2003) seems correctly identified, whereas male genitalia of a specimen originating from the W Ukraine likely also belong to *D. alpestrana* though particularly the inner border of the valva is not clearly visible in the relevant figure.

**Biology.** *Dichrorampha velata* sp. nov. occupies a wide variety of biotopes from dry lowland pastures to alpine grassland above the treeline. It would seem, however, that the species prefers montane to subalpine borders of fer-

tile meadows at woodland edges. The moths have been observed flying during daytime in the vicinity of *Leucanthemum* sp. and *Achillea* sp., in the roots of the latter, caterpillars of *Dichrorampha vancouverana* McDunnough, 1935 and *Dichrorampha ligulana* (Herrich-Schäffer, 1851) were found toptotypical. However, attempts at finding caterpillars of *D. velata/alpestrana* were unsuccessful so far, though *D. alpestrana* is recorded from the rootstocks of *Achillea ptarmica* (Kennel 1908–1921) as



Figures 53–56. *Dichrorampha alpestrana*, female genitalia, variation in sterigma and ostium; all: CH-La Punt GR.

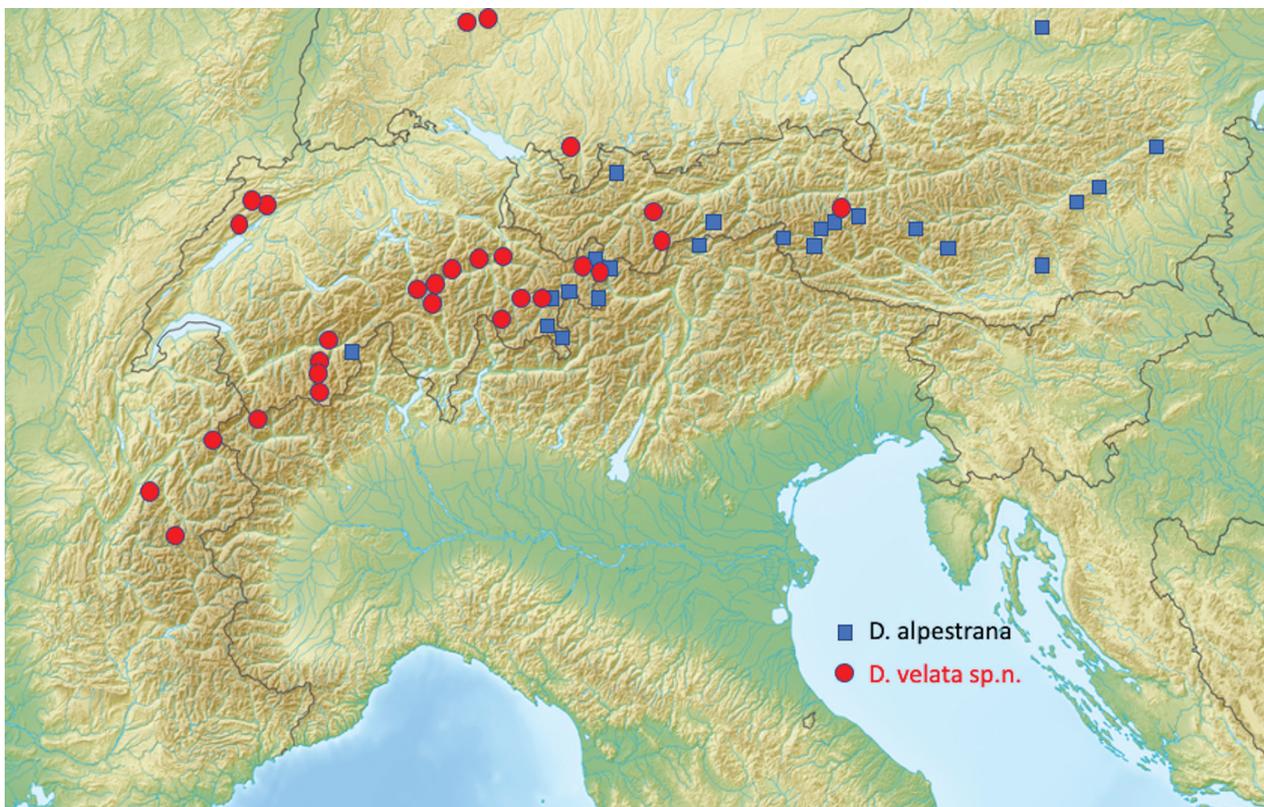


Figure 57. Proved records of *Dichrorampha velata* sp. nov. (red dots) and *D. alpestrana* (blue squares) in European Alps and nearby areas.

well as *Achillea millefolium* and *Chrysanthemum vulgare* (Bradley et al. 1979). Phenology: Specimens of *D. velata* sp. nov. have been observed from June 10<sup>th</sup> to August 8<sup>th</sup> at an altitudinal range from 590 m to 2400 m.

## Discussion

Nearly 30 years ago it became evident that “*Dichrorampha montanana sensu auct.*” morphologically is a complex of probably two species, a hypothesis later supported by genetic data. However, the subsequent search for type material became extremely tedious due to confounded taxonomy, scattered type material and cumbersome institutional bureaucracy.

The initial claim by Danilevski and Kuznetsov (1968) that the different shapes of phallus represent variation within the same taxon i.e. *D. montanana* can be refuted based on the strict coupling of phallus form with inner valval line, on DNA barcode results and on the absence of intermediate forms. It should however be emphasized that the abovementioned authors explicitly cautioned that further research was necessary to support their assumption. Also, in fairness, several authors like Rebel (1927), Toll (1954), Müller-Rutz (1934) were aware of there being a second species or at least a remarkable variation of *D. alpestrana* but all failed to disentangle the complex taxonomy and nomenclature. Even Zeller (1878) described phenotypical differences of Swiss specimens, but also he did not formally name this population.

While wing phenotype is a good indicator of taxon identity in most fresh specimens, in single cases and especially when specimens are worn, this trait may be doubtful. Thus, genitalia preparations and/or DNA barcode results are needed for unambiguous identification.

In male specimens, shape and number of phallus endthorns are very good differentiating characteristics. Unfortunately, in female genitalia, no clear distinguishing features could be detected so far; clearly more material will be necessary for future research.

The present geographical distribution, as far as it is known, suggests one or several south-eastern glacial refugia of *D. alpestrana*, while *D. velata* sp. nov. likely is of north-western peri-alpine glacial provenance (Fig. 56) with both species expanding in postglacial periods. Today, in some areas both species meet, and as seen in the topotypical area, may fly together at the same site on the same day. Even there, no intermediate forms could be observed.

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# Rediscovery of *Stactobia eatoniella* McLachlan, 1880 (Trichoptera, Hydroptilidae) in Switzerland after more than seventy years

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## Abstract

A specimen of *Stactobia eatoniella*, a hygropetric species of micro-caddisfly considered extinct in Switzerland, was discovered in the Morge in Valais in March 2020 during routine monitoring. This last instar larva in perfect condition is the first to be observed in Switzerland since 1944. Further research in the study area is needed to confirm the presence of a possible well-established population. This encouraging discovery should not hide the fact that two thirds of the micro-caddisfly species are on the Red List of threatened species of Switzerland, and that hygropetric habitats are both under-studied and highly endangered in Switzerland and worldwide.

## Key Words

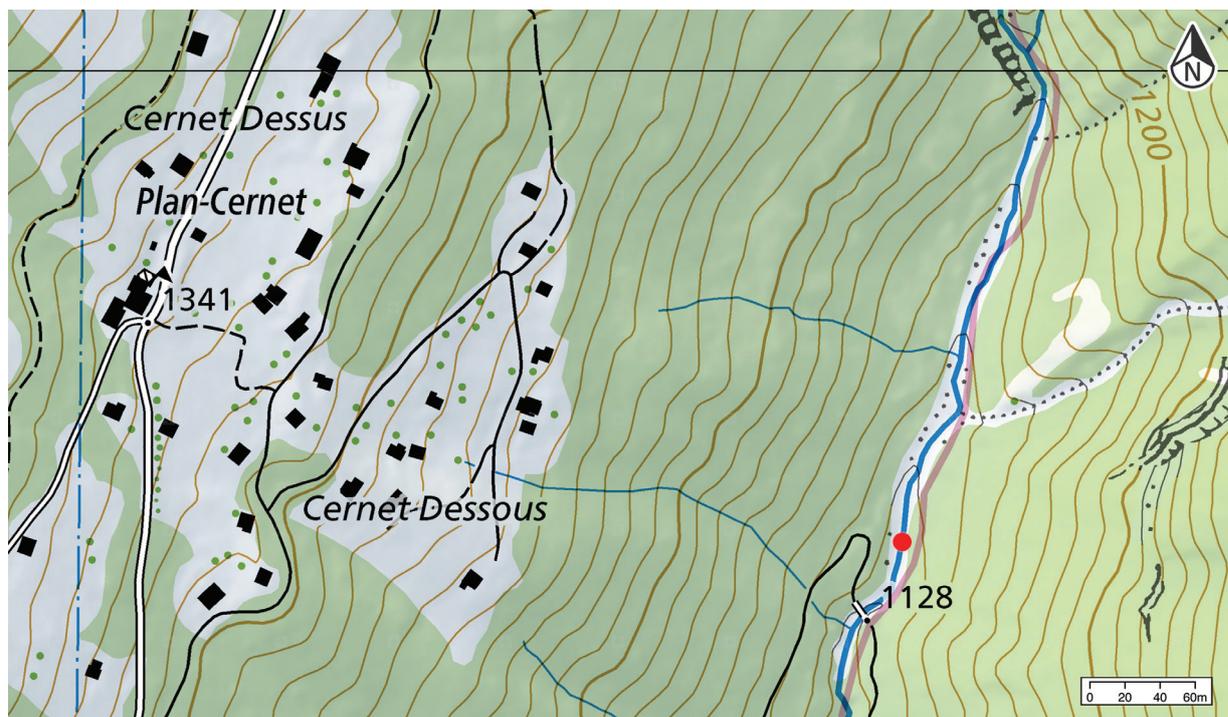
caddisfly, benthic macroinvertebrates, crenic habitats, petrimadiculous, stream, survey

## Introduction

The Swiss fauna includes 302 species of caddisflies (Lubini et al. 2012), 33 of which belong to the family Hydroptilidae (info fauna 2021). This family, whose members are commonly known as micro-caddisflies, is the most diverse in the world with more than 2000 valid species (Morse 2011) and is widely distributed globally (Waringer and Graf 2011), although diversity is highest in warm tropical regions (de Moor and Ivanov 2008). At the Swiss level, too, it accounts for a significant part of the diversity of caddisflies, being the second richest family in genera and species after Limnephilidae (Lubini-Ferlin and Vicentini 2005). Hydroptilidae are very small (1.5 to 6 mm; Marshall 1978), with a unique larval development in caddisflies, called “hypermetamorphosis”: the first four stages, tiny and without case, are very different morphologically from the last (fifth) instar, characterized by an enlarged abdomen and the presence of a silken case (Tachet et al. 2006; Waringer and Graf 2011). It is during this last stage that the larvae accumulate in their abdomen

most of the food reserves necessary for the future adult stage (Marshall 1978).

The genus *Stactobia* McLachlan, 1880 currently consists of 168 species, 41 of which are in the Western Palearctic (Morse 2020). Three are reported from Switzerland: *Stactobia eatoniella* McLachlan, 1880, *Stactobia furcata* Moselyi, 1930 and *Stactobia moselyi* Kimmins, 1949. *Stactobia* larvae live exclusively in hygropetric (petrimadiculous) environments (Graf et al. 2004; Graf 2014), i.e. in rocky areas with a constant and uninterrupted flow of a thin film of water, such as margins of stream courses, spring seepage areas or spray zones around waterfalls or rapids (Coineau and Jacquemart 1961; Malicky 2014). In hygropetric habitats of Europe, they are among the most common and abundant caddisflies (Vaillant 1951, 1984). As grazers, they feed on the film of algae and lichens that covers the substrate (Coineau and Jacquemart 1961). Their case does not have marked lateral flattening like most other genera of Hydroptilidae (Tachet et al. 2006). Adults remain in the immediate vicinity of hygropetric habitats, directly on the water film or on the surrounding



**Figure 1.** Location of the sampling site MOR 10.2 in the Morge (red symbol). Map generated in map.geo.admin.ch, scale 1: 2'500 (swisstopo, public.geo.admin.ch) and adapted in Photoshop CS5 (Adobe Systems, San Jose, CA).

dry areas (Coineau and Jacquemart 1961), no more than a meter away (Malicky 2014). Flying very little, they run quickly (Schmid 1959), hop (Waringer and Graf 2011) or make short circular flights over the substrate during the hottest hours of the day (Lodovici and Valle 2013).

Before the rediscovery of *S. eatoniella* reported here, eight observations between 1888 and 1944 were officially recorded in Switzerland (info fauna 2021): one in Zürich, one in gorges de l'Orbe, and six in Canton du Valais (in Val d'Illiez, Val d'Hérens, Crans and Binntal). The last official observation dates back to 27.07.1944 around Les Haudères in Val d'Hérens. The species was considered as extinct in Switzerland (category RE; Lubini et al. 2012) and is included in the Swiss List of National Priority Species and Habitats (high degree of priority; OFEV 2019a). Besides Switzerland, the species is recorded in France (Coppa and Tachet 2020), Italy (Lodovici and Valle 2013), Spain (González and Menendez 2011), Austria (Graf et al. 2017), Germany (Robert 2004) and Slovenia (Urbanič 2004). The species is also reported from Slovakia (Stloukal 2001) and Hungary (Vadadi-Fulop et al. 2007), but these observations are not mentioned in recent synthesis works (see Neu et al. 2018). The development cycle of *S. eatoniella* is univoltine (one generation per year; Waringer and Graf 2011). Adults are black with white markings (Schmid 1959) and are observed from June to August. About seventy red-orange eggs are deposited in empty pupal cases. The first larval instars appear in mid-June, and the last instar larvae can be found in August. Pupation takes place from May to June of the following year (Danecker 1961). Observations of the other two *Stactobia* species reported from Switzerland are as rare as for *S. eatoniella*: *S. furcata*, reported only from Canton Ticino, was not assessed in the Red List due to lack

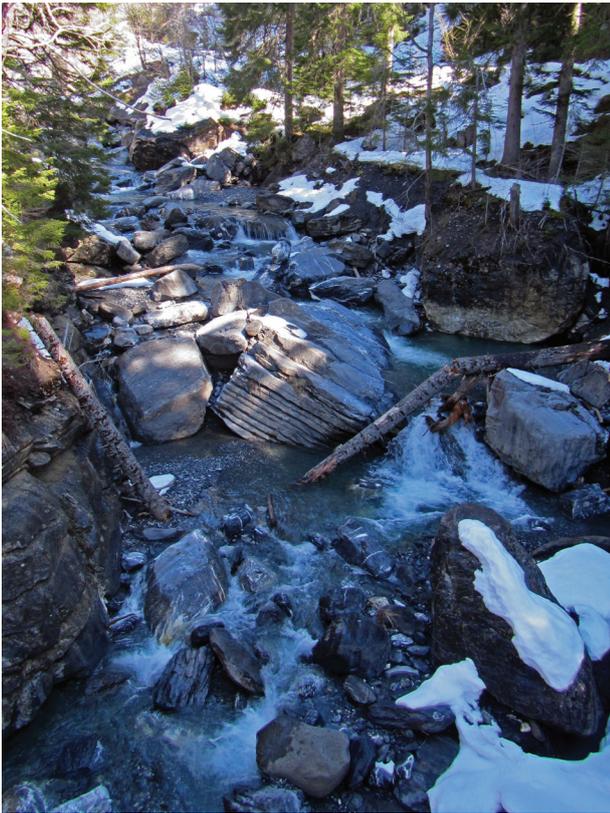
of sufficient data (category data deficient); *S. moselyi* is considered endangered (category EN), with a medium degree of priority (Lubini et al. 2012; OFEV 2019a).

## Materials and methods

As part of the surface water quality monitoring of the Canton du Valais, the "Service de l'environnement" (SEN) commissioned the consultancy office "biol conseils" to conduct samplings of benthic macroinvertebrates in the Morge catchment using the Swiss biotic index (IBCH method; Stucki 2010; OFEV 2019b). These samplings were coupled with other analyses (physico-chemistry, flow measurement, diatom studies). Five sites were sampled in spring 2020 at altitudes between 480 (at the mouth of the Morge in the Rhone River) and 1480 masl. For each site, eight samples were taken from eight different substrates. These samples, consisting of benthic macroinvertebrates and various mineral and organic debris (composite samples), were combined into one sample per site and fixed with 100% ethanol. In the laboratory, the samples were sieved and benthic macrofauna was sorted out and identified to family level under a stereo microscope following the IBCH method.

## Results

One last instar larva of *S. eatoniella* was found at the site located below the place called Cernet Dessous (Morge, site code MOR 10.2, Cernet, site coordinates 46°17'30.924"N, 7°19'46.046"E, 1125 masl, 18.03.2020; Figs 1, 2 and 4). The data was transmitted to info fauna,

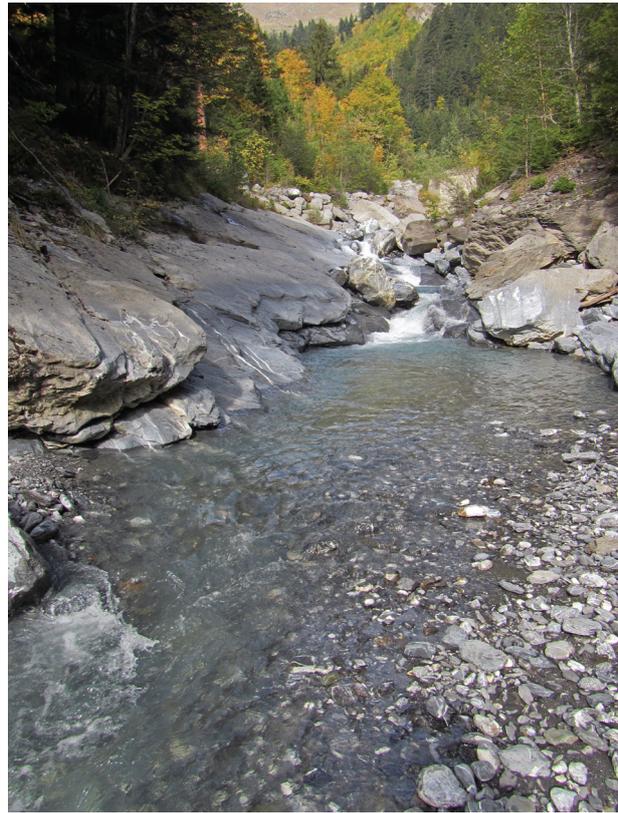


**Figure 2.** View (downstream) of the sampling site on 18.03.2020.

and the specimen was deposited at the Museum of Zoology in Lausanne (GBIFCH0082987) according to the official archiving procedure (available at [www.cscf.ch/cscf/home/projekte/makrozoobenthos/sammlung-und-archivierung.html](http://www.cscf.ch/cscf/home/projekte/makrozoobenthos/sammlung-und-archivierung.html)).

## Discussion

The sampling site is situated in a deeply incised section of the Morge, accessible by a logging road. It is regularly subject to active water erosion which destabilizes the stream banks. The stream bed is made up of very large boulders, or even locally stone slabs, as well as sand and gravel on the stream banks (Figs 2 and 3). The bed incision forms steep banks, into which water seeps. The slope of the bed is around 12% on this section. All samples were taken from the wetted bottom (water depth between 15 and 25 cm), with flow velocities ranging from 75 cm/s to less than 5 cm/s (almost stagnant environment). Two mobile blocks, two organic litters, pebbles, gravel, sand and silt, and the top of one block were sampled. These environments do not correspond to the description of the microhabitat in which *S. eatoniella* usually lives. Moreover, all other investigations at the Cernet site of which we are aware, including a second survey on 13.10.2020 (Fig. 3), did not reveal any additional specimen. These observations suggest that the discovered specimen might have been dislocated from its original habitat (e.g. lateral seeps, films of water on the slabs or boulders wetted by



**Figure 3.** View (upstream) of the sampling site on 13.10.2020.

spray from small waterfalls), and drifted to the river bed. It would be necessary to investigate more specifically the lateral wetlands and seepages to more precisely locate a possible well-established population. However, caution should be exercised in this type of research, to ensure that the investigations do not harm a population that would undoubtedly be fragile if it consists of a very small number of individuals.

More than half (51%) of the 302 assessed species of caddisflies are on the Red List of threatened species of Switzerland (Lubini et al. 2012), of which 21% have a high or very high national priority status (OFEV 2017). Within the family Hydroptilidae, this percentage is even higher (67% of the species on the Red List; 36% with high or very high national priority status). The main explanation for this alarming finding is an incomplete knowledge of the distribution of Hydroptilidae species, which contributes to a bias in the evaluation criteria. In fact, knowledge of their ecology is often lacking (Komzák and Kroča 2018), and the small size of these species and the difficulty in identifying larvae to species level results in neglecting them in general, as no adults are collected during monitoring projects or other routine studies (Urbanič 2004; Komzák and Kroča 2018). This is particularly true for *Stactobia* species, whose tiny size (ca. 2 mm for larvae) leaves them unnoticed by non-specialists (Coineau and Jacquemart 1961; Graf 2014). Moreover, the nature of hygropetric environments, which generally escape standardized sampling within the framework of routine monitoring, implies a distribution of species into small,



**Figure 4.** Discovered specimen (last instar larva) of *Stactobia eatoniella*. The larva and its case are shown in lateral (top), dorsal (bottom left), and ventral (bottom right) view. Figure adapted in Photoshop CS5 from photographs taken with a Canon 65 mm MP-E lens mounted on a Canon EOS 6D camera integrated in an LK lab imaging system (Dun, Inc., Virginia).

isolated populations (Schmid 1959). A second explanation invokes the extreme threats on freshwater ecosystems, both globally (e.g. Abell 2002; Dudgeon 2006; Reid et al. 2019) and in Switzerland (e.g. Kunz et al.

2016; Doppler et al. 2017). Crenic (spring-fed) ecosystems are emblematic examples of this reality. These habitats, which are in sharp decline in Switzerland (Zollhöfer 1997) mainly due to massive spring capture and drainage

(Küry 2009), are rich in specialized species and are home to numerous species of caddisflies (22% of European species; Hering et al. 2009). More than 30% of the red-listed Hydroptilidae species in Switzerland are closely linked to springs, including *S. eatoniella*, which colonizes spring brooks in particular (Lubini et al. 2012; Malicky 2014). These two considerations clearly illustrate, on the one hand, the lack of attention paid to Hydroptilidae in general, and to hydropetric habitats in particular, and, on the other hand, the importance of protecting our freshwater aquatic environments. At the Swiss level, the inventory of the ecological value of springs, which has been carried out or is in progress in several cantons (Küry et al. 2019), is an important step in this direction. Eventually, this inventory should make it possible to fill some of the gaps in our faunistic knowledge, while highlighting the crenic habitats to be protected as a priority, including the many hydropetric environments that depend on them.

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# Energetic underpinnings of yellow dung fly mating success in the field

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## Abstract

Foraging provides the basis for animal reproduction, but requires energy and time to be sustained, entailing a trade-off. Whereas females should maximize their time foraging for resources, males should minimize their foraging time by optimizing time budgets to maximize their access to mating partners.

Mark-resight field studies are difficult and hence uncommon for small insects. Yellow dung flies (*Scathophaga stercoraria* L.) abound on pastures in cold-temperate regions across the northern hemisphere. Adult flies lick nectar from flowers for energy, but require small insect prey to produce eggs and sperm. Males wait for females around fresh cow dung, but at one point also need to replenish their energy and/or sperm reserves in the surrounding vegetation. Their foraging time budgets should depend on their body size, nutritional energy reserves, availability of sperm, competitor and female density.

Marked male dung flies whose nutritional status was experimentally manipulated – water only (null control); water + sugar (energy replenishment); or water, sugar + *Drosophila* prey (energy and sperm replenishment) – were repeatedly observed on an experimental pasture for an entire day. Both nutrient types were expected to increase the mating success of especially large males. The total number of resighted males seen copulating was lowest for water-treated flies. Mating success was positively related to body size. The distance travelled between dung pats was greater for males fed sugar or prey and also increased with body size, while pat residence times decreased with size. No differences were found between the sugar- and prey-fed groups. Crucially however, there was no evidence in the field for a time budget or mating advantage of small males when nutrients were limited.

## Key Words

body size, energy reserves, field observations, food manipulation, foraging, mating success, *Scathophaga stercoraria*, reproduction

## Introduction

Foraging provides the basis for animal life histories (Stephens and Krebs 1986), as all necessary energy first needs to be collected before it can subsequently be allocated to the various life history or fitness components such as growth, survival, and reproduction (Roff 1992; Stearns 1992). Moreover, foraging itself requires energy and time to be sustained. In this sense foraging is an unusual, merely intermediating life history component. Nevertheless, foraging and mating are mutually exclusive activities in terms of time or energy (Blanckenhorn et al. 1995; Zera and Harshman 2001), and males and females are not expected to resolve this trade-off in similar ways. Sexual

selection theory predicts that females should maximize their time foraging because their offspring production depends directly on the quality and quantity of resources gathered (Darwin 1971; Trivers 1972). Males, in contrast, should instead minimize their time spent foraging as long as they can energetically sustain their activities, because their fitness is a direct function of their access to female mating partners (Bateman 1948). Within species, smaller individuals (of both sexes) require less food in absolute terms to maintain their activity (Ghiselin 1974; Reiss 1989; Blanckenhorn et al. 1995, 2007; Reim et al. 2006a, b). Small males can therefore increase their mating effort at the expense of foraging effort (called the small-male time budget advantage: cf. Blanckenhorn et

al. 1995; Blanckenhorn and Viele 1999). This may partly compensate their other usual competitive disadvantages, as large males are usually more successful in acquiring mates (Andersson 1994; Clutton-Brock 1988) and also tend to be stronger and more efficient at subduing prey or extracting nutrients (Blanckenhorn and Viele 1999; Blanckenhorn 2000, 2005). Therefore, male and female time and energy budgets are expected to differ substantially for any species (Stephens and Krebs 1986).

To understand the mating system of any particular species, time and energy allocation of both sexes to various activities must be investigated (Shuker and Simmons 2014). This first and foremost concerns the expected trade-off between foraging and reproduction (defined above). While assessment of field behaviour is relatively straightforward for vertebrates (Clutton-Brock 1988; Andersson 1994), individualized observations are difficult if not impossible for small insects (e.g. Fincke 1982; Blanckenhorn and Perner 1996). Yellow dung flies (*Scathophaga stercoraria* L.; Diptera: Scathophagidae) approach the size of honey bees (ca. 7–13 mm long) and are common on livestock (especially cattle) pastures in cold-temperate regions of the northern hemisphere (Blanckenhorn et al. 2010; Simmons et al. 2020). Adult flies lick nectar from flowers for energy but additionally require small insect prey to produce eggs and sperm (anautogeny: Foster 1967; Gibbons 1980; Blanckenhorn et al. 2007, 2010; Kaufmann et al. 2013). Therefore, females spend most of their time foraging for prey and nectar in the forest or the vegetation surrounding a pasture, and only come to the dung when ready to lay eggs (Parker 1970, 1978). Males, in contrast, mainly are found waiting for females on pastures around freshly deposited (cow) dung, although territorial defence of this resource necessitated by females as oviposition substrate is often precluded by the sheer number of competitors present (Borgia 1981, 1982; Jann et al. 2000). In this mating system of resource defence polygyny with at times severe scramble as well as contest competition (Parker 1978; Shuker and Simmons 2014), males attempt to copulate with incoming females without any courtship, and subsequently guard and defend their females against other males during oviposition (Parker 1978; Simmons et al. 2020). Struggles for possession of a female may harm all individuals involved, particularly the smaller females and males. After oviposition into the dung, in which the coprophagous (dung-eating) larvae develop and feed, the female leaves the pat to forage and replenish her eggs, whereas males tend to wait or switch pats to secure more females. Males only rarely forage on or around the dung pat even though they could (Gibbons 1980). However, at one point also males need to replenish energy and/or sperm, and thus leave to forage in the vegetation. This mating system requires males to make repeated decisions about whether to stay or leave a particular dung pat in search of females vs. temporarily abandoning reproduction altogether to feed elsewhere (Parker 1978; Simmons et al. 2020). These decisions should depend on their body

size, nutritional energy reserves, availability of sperm, as well as the competitor (male) and female density.

I here report the results of replicated field observations of individual yellow dung fly males using the classic mark-resight approach, with male nutritional status additionally being experimentally manipulated. Numerous males of various ages and sizes were randomly collected on a given (random) day in the season (cf. Jann et al. 2000), weighed, marked and subsequently supplied in the laboratory for 24–48 h with three different nutrient regimes, before being released again on their pasture to be observed for an entire day. The nutritional treatments were: 1) water only; 2) water + sugar (in lieu of nectar); and 3) water, sugar + *Drosophila* prey. Although the current nutritional status and age of the captured field males was unknown, I had the following expectations/predictions. Relative to the water only treatment (= null control), I expected the water + sugar treatment to replenish energy (for flight and fight), while the water + sugar + prey treatment additionally would replenish male sperm stores (for mating; Blanckenhorn and Henseler 2005). The extra nutrients were expected to disproportionately help large males because of their greater absolute energy and sperm demand (Ward and Simmons 1991; Reim et al. 2006a, b, 2009; Blanckenhorn et al. 2007; Kaufmann et al. 2013). Ultimately, I expected both nutrient supplements, but especially the treatment including prey, to increase the mating success of all, but especially the large males, as they generally enjoy competitive mating advantages (Jann et al. 2000; Blanckenhorn et al. 2003). Because small males require less energy to begin with to sustain their activity, I expected the general size advantage of large males in acquiring mates to diminish, or even reverse, under energy-limited conditions (water treatment).

## Materials and methods

### Field procedures

We conducted a total of six field markings (days), three during the spring and three during the fall fly season (Jann et al. 2000), spread over two years, always working on our experimental farm in Fehralt Dorf near Zürich, Switzerland (47°23'N, 8°44'E). Each field marking started with randomly catching ca. 100 male yellow dung flies of various sizes and ages currently active on the pasture. These flies were subsequently grouped into 3.5 litre plastic containers ( $2.2 \times 1.2 \times 1.2 \text{ dm}^3$ ) supplied with water only. Back in the laboratory, all flies were first weighed with a Mettler balance, and subsequently marked with numbered, coloured opalith discs on their thorax (described below). Males were then randomly allocated to one of three of the above containers in groups of 30 numbered individuals. Containers were supplied with one of three nutrient treatments: water, water + sugar, or water + sugar + *Drosophila* prey. The containers with the nour-

ished flies were kept overnight in a climate chamber in the laboratory at ca. 20 °C for at least 24 h (but up to 48 h depending on outside weather conditions). In the morning of the experimental day, containers were transported back to our pasture in Fehrltorf for the marked flies to be released and observed for the entire day.

On each observation day, from early morning to late evening, up to 5 people (students of our annual ecology course) regularly screened the entire pasture for individually identifiable marked male flies, particularly all freshly appearing dung pats, which were marked with coloured, numbered flags. Returning to the same dung pat in haphazard, more or less regular intervals, observers noted fly identity (coloured number) and observation time as well as the pairing status of any marked fly seen. From these raw data, I later extracted the following variables ultimately analysed for all marked individuals resighted at least once on the pasture: 1) pairing status (paired or not) as an estimate of mating success; 2) the estimated distance from the previous to the next dung pat occupied, in case an individual switched pats (in m), as an indicator of flight endurance; 3) the number of times a given individual was observed during a given day (anywhere it was seen); 4) the total number of different pats visited by an individual (i.e. pat switches) as an indicator of searching activity, with distances between the pats estimated and averaged (cf. 2 above); 5) the daytime a fly was first and last seen on the pasture as an indicator of total activity time during the experimental day.

### Preliminary marking experiment

Flies were individually marked with numbered (1–99) opalith discs (6 available colours) that were dorsally glued with shellac onto the flies' thorax. Disks and shellac glue are commercially available for marking honey bees from *Bienen-Meier* (Künten, Switzerland; Burkhard 1999). We only marked males because for the smaller females these disks are too large or heavy, and also because disks are not visible for females in copula.

Prior to our field experiment, two tests of our marking technique were conducted in April and May 1998, during which 276 and 447 (respectively) marked but otherwise untreated males of various sizes were released on two different pastures near Fehrltorf during the course of Burkhard's (1999) thesis project. The results of these preliminary experiments are here briefly reported to validate our results.

Three days after marking, ca. 15% of all originally marked flies were resighted on the pasture; two days later this number dropped to 3%, and after 10 days no marked individuals remained to be seen. Neighbouring pastures were also searched. Thus, not least because of many other cow pastures in the vicinity, marked flies disappeared quite fast from the focal pasture. As usual in such assessments, emigration and death could not be distinguished.

### Statistical analyses

The variables defined above were computed and all data aggregated per individual male as the independent statistical unit. All variables were subjected to separate analyses of variance with food treatment as fixed factor (3 levels), initial body weight as continuous covariate (first also including the interaction, which was removed if not significant at  $P > 0.15$ ), and sampling date as random effect. The number of flies resighted (of all originally marked) were analysed with binomial errors, the total number of copulations per individual were analysed with Poisson errors, and all other variables were  $\log_{10}$ -transformed as necessary to meet statistical assumptions to be analysed with normal errors.

### Results

Of roughly 540 males originally marked and released (6 dates  $\times$  3 treatments  $\times$  30 flies/treatment), 231 were resighted (ca. 43%). Of these, 46 were resighted only once (on one dung pat), and 114 occupied only one dung pat for longer time, such that the total sample of resighted males having switched pats at least once was  $N = 117$  (Table 1). Resighting rate was relatively high compared to Burkhard's (1999) preliminary experiments reported above because observations started within one hour after fly release on the pasture in the morning.

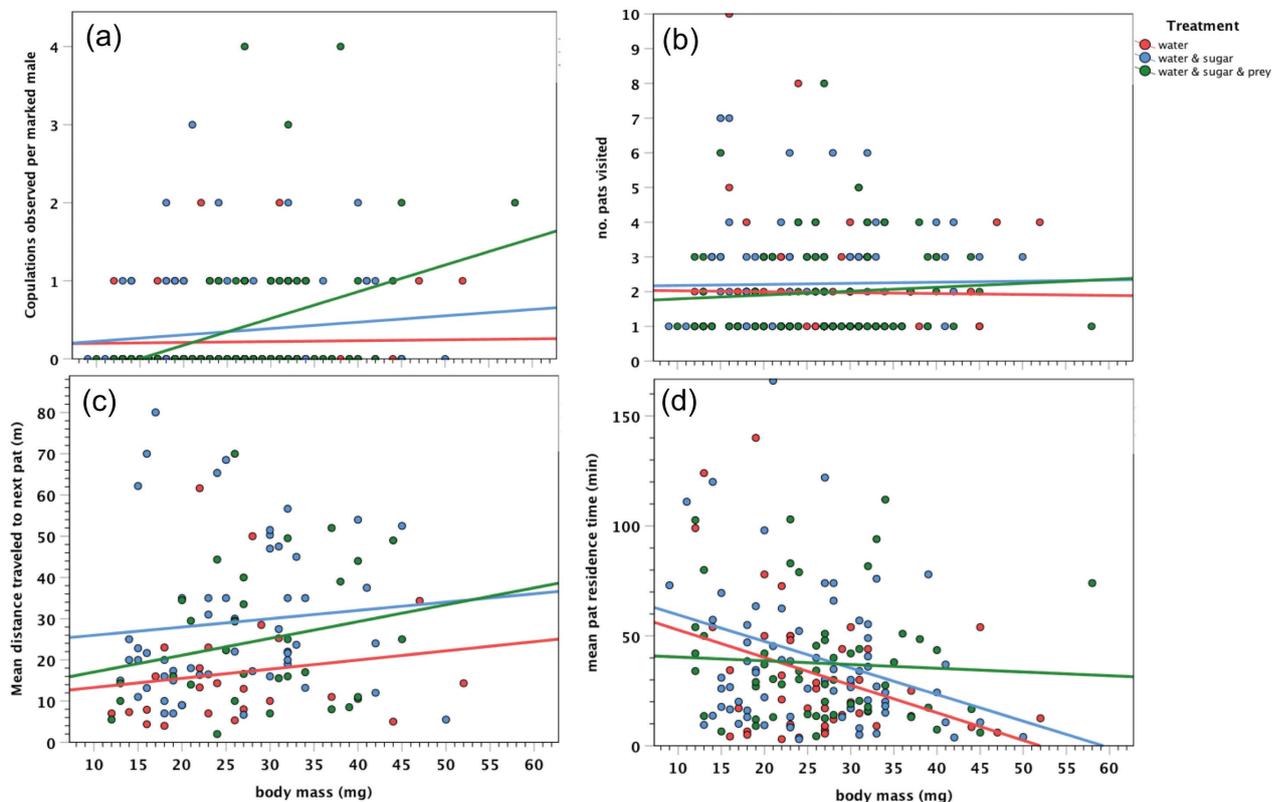
The body mass of the flies did not vary significantly among our three treatments, nor did the total number of daily sightings or the total observation time, as of course should not be the case given random assignment to feeding treatments (Table 1). All variables varied strongly among the six experimental days (random effect; Table 1), mainly due to seasonal weather conditions.

The proportion of males resighted tended to be lower for the water treatment (Table 1), as these males were expected to be in utmost energy demand. The proportion of water-treated flies seen copulating was also lower (Table 1: 0.22 vs. 0.35 vs. 0.40), although this effect was not quite significant due to the low number of observed copulations in our entire sample. We saw a total of 89 copulations: two males were found copulating 4 times, two males 3 times, 8 males 2 times, and 59 males once (Fig. 1a). Independent of nutritional treatment, copulation success was overall positively related to male body size (Table 1; Fig. 1a). The distance travelled to the next pat increased with body size (Fig. 1c), and there was a trend of larger males visiting more pats (Fig. 1b; Table 1), both indicating greater energy reserves of larger individuals. In contrast, pat residence times decreased with body size, again suggesting greater activity of larger males (except for the males fed with sugar and prey; Fig. 1d). Nutritional treatment only influenced the distance travelled to the next pat, which was greater for sugar- and prey-fed males than

**Table 1.** Mean  $\pm$  SE and statistical significance of all behavioural variables assessed for three nutritional treatments ( $N$  refers to total males seen, and males seen on more than one pat). Data for the six observation dates are absolute counts.

	water		water, sugar		water, sugar, prey		$\chi^2 / F^*$			
	(N = 60, 26)		(N = 93, 54)		(N = 78, 37)		treat	size	date	txs
	mean	SE	mean	SE	mean	SE				
<b>No. of flies (of 30) resighted</b>	10	$\pm 1.81$	15.5	$\pm 2.86$	13	$\pm 2.21$	<b>3.18</b>	-	-	-
18 May 1999	11		24		8					
5 June 1999	14		14		14					
15 June 1999	8		14		13					
18 October 2004	17		24		21					
27 October 2004	6		8		6					
4 November 2004	4		9		11					
<b>Pr. copulated</b>	0.22	$\pm 0.06$	0.35	$\pm 0.06$	0.40	$\pm 0.09$	1.98	<b>20.0</b>	<b>25.1</b>	-
<b>Initial body mass (mg)</b>	25.43	$\pm 1.16$	25.87	$\pm 0.87$	26.49	$\pm 1.06$	0.45	-	<b>18.8</b>	-
<b>Total time active (min)</b>	129.1	$\pm 18.1$	182.3	$\pm 17.6$	146.9	$\pm 17.0$	1.17	0.09	<b>2.21</b>	-
<b>Times observed</b>	4.28	$\pm 0.47$	6.55	$\pm 0.60$	5.40	$\pm 0.61$	<b>2.88</b>	0.27	<b>5.62</b>	-
<b>No. of pats visited</b>	2.00	$\pm 0.22$	2.23	$\pm 0.15$	2.00	$\pm 0.15$	1.68	<b>2.75</b>	<b>3.23</b>	-
<b>Distance to next pat (m)</b>	16.41	$\pm 2.78$	28.19	$\pm 2.43$	23.90	$\pm 2.68$	<b>5.24</b>	<b>6.34</b>	<b>1.93</b>	-
<b>Min. pat residence time (min)</b>	33.23	$\pm 5.96$	38.70	$\pm 4.36$	36.17	$\pm 3.45$	1.14	<b>7.59</b>	1.66	2.18

\* bold:  $P < 0.05$ ; bold italic:  $P < 0.1$



**Figure 1.** (a) Total number of copulations observed, (b) no. of pats visited, (c) distance to next pat visited, and (d) pat residence times of males as a function of their body mass and food treatment.

for water-fed males (Table 1; Fig. 1c). The body mass by treatment interaction was never significant ( $P > 0.1$ ; Table 1), contrary to expectations.

## Discussion

Reproductive success of an organism is a function of intrinsic (e.g. body size) as well as extrinsic, environmental factors (e.g. mate or food availability, weather conditions,

etc.). Although foraging success is often far removed from fitness (Stephens and Krebs 1986), it ultimately provides all energy to be invested in reproduction (e.g. Blanckenhorn 1991; Lemon 1991). I here manipulated the feeding status of yellow dung fly males caught and marked on a pasture, expecting that this would influence their subsequent time budgets, mate search behaviour and ultimate mating success. While such mark-resight studies combined with food manipulations are common in vertebrates (e.g. Clutton-Brock 1988; Andersson 1994), they

are tricky and thus rarely performed with small insects. In general, larger and flightless insects are more suited for such studies (e.g. dragonflies, butterflies or water striders: Fincke 1982; Elgar and Pierce 1988; Blanckenhorn and Perner 1996).

Adult yellow dung flies feed on nectar for energy but additionally prey on other insects, and the nutrients derived from these different foraging modes serve different purposes. Sugars are required for fuelling flight, and proteins from prey are used to produce the eggs or sperm needed for reproduction, although sugars can likely be derived also from prey (Foster 1967; Gibbons 1980; Blanckenhorn et al. 2007, 2010; Kaufmann et al. 2013). I therefore employed three feeding treatments: water only, water plus sugar, and water plus sugar plus *Drosophila* prey.

Although not quite statistically significant, the total number of resighted individuals and the proportion of males seen copulating following release on their native pasture after food treatment was lowest for the flies only given water. This indicates that these flies were energetically limited and needed to first feed before becoming reproductively active again (Table 1). Although the total number of copulations observed (89) was low, copulation success was positively related to male body size, as is typical in this species (Fig. 1; Jann et al. 2000; Kraushaar and Blanckenhorn 2002; Blanckenhorn et al. 2003). As expected in response to their extra energy supply, the distance travelled by males when switching dung pats was greater for males fed sugar or prey, and also increased with body size (Table 1; Fig. 1). Further, pat residence times decreased with body size (except for males fed with sugar and prey, possibly relating to their greater copulation success), again signifying energetic advantages for large males. Crucially however, there were few differences between the sugar- and prey-fed groups, contrary to expectations, especially not for their copulation rates (Table 1). The adult age of our test males caught on the pasture remained unestimated here, which would have required assessment of wing injuries (so-called age-grading, usually requiring wing removal for digitizing; Burkhard et al. 2002). In addition to body size, fly age likely influences the behavioural variables assessed here, although no correlation between body size and age can be safely assumed in our data set (Blanckenhorn et al. 2001; Burkhard et al. 2002).

While yellow dung flies cannot convert sugars into proteins (contrary to some other insects; Foster 1967; Tauber et al. 1986; Blanckenhorn et al. 2007), it seems that they can derive sugars for flight also from prey, as flies can be kept in the laboratory with prey only (i.e. without sugar; personal observation). Thus our two food treatments overlapped, potentially explaining lack of differences. As both male and female flies can store sperm for extended periods of time in their testes and spermathecae (respectively), apparently many of the sugar-fed males still had sufficient sperm for mating when caught to begin with. Sperm are initially produced upon adult male emergence given prey is available, a physiological process requiring

3–7 days (Blanckenhorn and Henseler 2005). Sperm production may thereafter continue throughout their adult life, so the males must forage prey once their sperm reserves are depleted (which suffice for ca. 4–5 copulations: Ward and Simmons 1991).

Some of our behavioural traits showed expected time budget differences between feeding groups (Table 1). The initial body mass of flies, and the total time they were observed were not meant to differ among feeding groups because flies were randomly allocated. By contrast, more available energy for flight and fight would predict more pat switches, lower patch residence times, and/or farther distances covered by males fed with sugar and/or prey, which was indeed found and should have contributed to the observed higher mating success of these well-fed males (Fig. 1). Well-fed males would also likely engage in more fights with other males when trying to take over females, and especially large males are able to fly away with their female in case of such attacks (Parker 1978; Blanckenhorn et al. 2008; Simmons et al. 2020). Importantly, however, I did not find any evidence in the field for the small-male time budget advantage (Blanckenhorn et al. 1995; Blanckenhorn and Viele 1999; Blanckenhorn et al. 2008), which would have been indicated by greater mating chances of smaller males in the energy-limited, water-only group, but there were no significant body mass by treatment interactions whatsoever.

Our six observation days were distributed evenly across typical spring and fall fly seasons (Parker 1970; Gibbons 1987; Jann et al. 2000; Blanckenhorn et al. 2001). Even within seasons fly densities and body sizes change markedly, as there are at least four overlapping generations per year in Switzerland (Jann et al. 2000). Together with unpredictable weather conditions, seasonality best explains the rather variable resighting rates found here for this heat-sensitive fly during our six experimental days (Table 1). This rather erratic random effect likely contributed to the lack of significance and low effective sample sizes for our key variables.

In conclusion, our study shows that even for small insects, mark-recapture studies can be effective for gaining behavioural insights into reproductive success in the field. Ironically, Switzerland is not the best place for such studies because of the high density of cow pastures, rendering the tracking of small marked flies in confined geographic space difficult.

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## Supplementary material 1

### Data File in Excel for Supplemental publication

Author: Wolf U. Blanckenhorn

Data type: Excel text file

Explanation note: Sheet1 contains the complete data file for the analyses performed in this paper. Variable names are self-explanatory. Sheet 2 contains some extra but incomplete (hence excluded) data from one day in 2005 because the weather did not allow completion.

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Link: <https://doi.org/10.3897/alpento.5.68153.suppl1>



# *Mitrapsylla rupestris* sp. nov., a psyllid (Hemiptera, Psylloidea) associated with *Poiretia bahiana* (Fabaceae) endemic to the Espinhaço mountain range (Brazil, Bahia)

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<http://zoobank.org/F018B488-5FE5-4948-A28F-56E958920321>

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## Abstract

*Mitrapsylla rupestris* sp. nov., associated with *Poiretia bahiana* C. Mueller (Fabaceae, Faboideae, Dalbergiaceae), is described, diagnosed and illustrated. The new species is morphologically similar to *M. aeshynomenis*, *M. aurantia*, *M. cubana* and *M. didyma* from which it differs in details of the terminalia and the host plant. *Poiretia* constitutes a previously unknown psyllid host. As its host, *Mitrapsylla rupestris* sp. nov. is probably endemic to rock habitats of the Espinhaço Range in eastern Brazil. These rock habitats display a high species diversity but are seriously threatened by human activities. More research on these habitats is urgently needed to design efficient conservation strategies.

## Key Words

Sternorrhyncha, Psyllidae, Ciriacreminae, systematics, phytophagy, distribution

## Introduction

The Serra do Espinhaço, a mountain range in eastern Brazil (states of Bahia and Minas Gerais), is famous for its high floristic diversity and endemism. Both, species richness and narrow endemism, are mostly concentrated in the “campos rupestres” (= rock fields, rupestrian fields) (Rapini et al. 2008). The disjunct distribution of the rock fields along the Espinhaço Range with extreme environmental conditions and the heterogeneity of habitats are responsible for this huge plant diversity (Ribeiro et al. 2014). The Espinhaço Range harbours around 10% of the angiosperm species known from Brazil even though it covers less than 1.5% of the Brazilian territory (Ribeiro et al. 2014), and up to a third of its plant species are endemic (Giulietti et al. 1987; Carneiro et al. 2009). Examples of taxa that are concentrated in rock fields have been reported from the Apocynaceae, Eriocaulaceae, Melastomataceae and Orchidaceae (Ribeiro et al. 2014).

Much less is known about host specific, phytophagous insects from the Espinhaço Range. The study of Carneiro et al. (2009), showing that in this mountain range, rock fields bear the highest species richness of gall-inducing insects, suggests that the entomofauna of the Espinhaço Range may be similarly diverse and rich in endemics as the flora.

Psylloidea or jumping plant lice are highly host specific phloem-feeders. The world fauna comprises just over 4000 described species but the fauna of the tropics is generally poorly known, and many more species can be expected. From Brazil 160 species have been reported (Burckhardt and Queiroz 2021) but there may be as many as 1000 species (Burckhardt and Queiroz 2012). A recent survey of the psyllid fauna of the Serra do Espinhaço produced many undescribed species, among them also five species from “campos rupestres”. Here we describe one of them, *Mitrapsylla rupestris* sp. nov., associated with *Poiretia bahiana* C. Mueller (Fabaceae, Faboideae,

Dalbergieae), a species that is endemic to rocky habitats in the Espinhaço Range (Müller 1986). *Mitropsylla* constitutes a neotropical genus of around 50 described species whose Brazilian members were recently revised (Rendón-Mera et al. 2020).

## Material and methods

Material is deposited in the Naturhistorisches Museum, Basel, Switzerland (NHMB) and the Coleção Entomológica Padre Jesus Santiago Moure, Centro Politécnico, Universidade Federal do Paraná, Curitiba, PR, Brazil (UFPR). The morphological terminology follows mostly Halbert and Burckhardt (2020) and Rendón-Mera et al. (2020). Measurements were taken as follows: adult body length from specimens preserved in 70% ethanol, measuring the distance between fore margin of head and tip of forewings when folded over body; the other measurements were taken from slide-mounted specimens. The measurements and ratios are given as range. For the identification of specimens, we used the key of Rendón-Mera et al. (2020) and the psyllid collection of the NHMB. The nomenclature and classification of Psylloidea follows Burckhardt and Queiroz (2021), that of the plants accords with the World Flora Online (2021).

## Results

### Taxonomy

#### *Mitropsylla* Crawford

**Notes.** With currently 51 described species, the neotropical *Mitropsylla* constitutes the largest genus of Ciriaceinae (Psyllidae). It occurs from the southern United States in the north to northern Argentina in the south with 40 species reported from Brazil. The genus was reviewed by Rendón-Mera et al. (2020) who provided descriptions of the genus and the Brazilian species, an identification key to males of the Brazilian species and a list of host plants. These belong to the subfamilies Caesalpinioideae, Detarioideae and Faboideae (Fabaceae). The genus is morphologically homogeneous and differences between species are often small.

#### *Mitropsylla rupestris* sp. nov.

<http://zoobank.org/2214CFA7-2BDB-4BD8-835B-A39FB85D548D>  
Figs 4–21, 23

**Type locality.** Brazil, Bahía, Palmeiras, Morro do Pai Inácio, 12.4572°S, 41.4727°W, 1110 m.

**Type material.** *Holotype*. Male. BRAZIL: Bahía, Palmeiras, Morro do Pai Inácio, 12.4572°S, 41.4727°W, 1110 m, 23.iv.2021, D. Burckhardt & D.L. Queiroz #424(1) // *Poiretia bahiana* Fabaceae, rock vegetation //

*Mitropsylla rupestris* sp. nov., holotype, det. D. Burckhardt, 2021 // UFPR, dry.

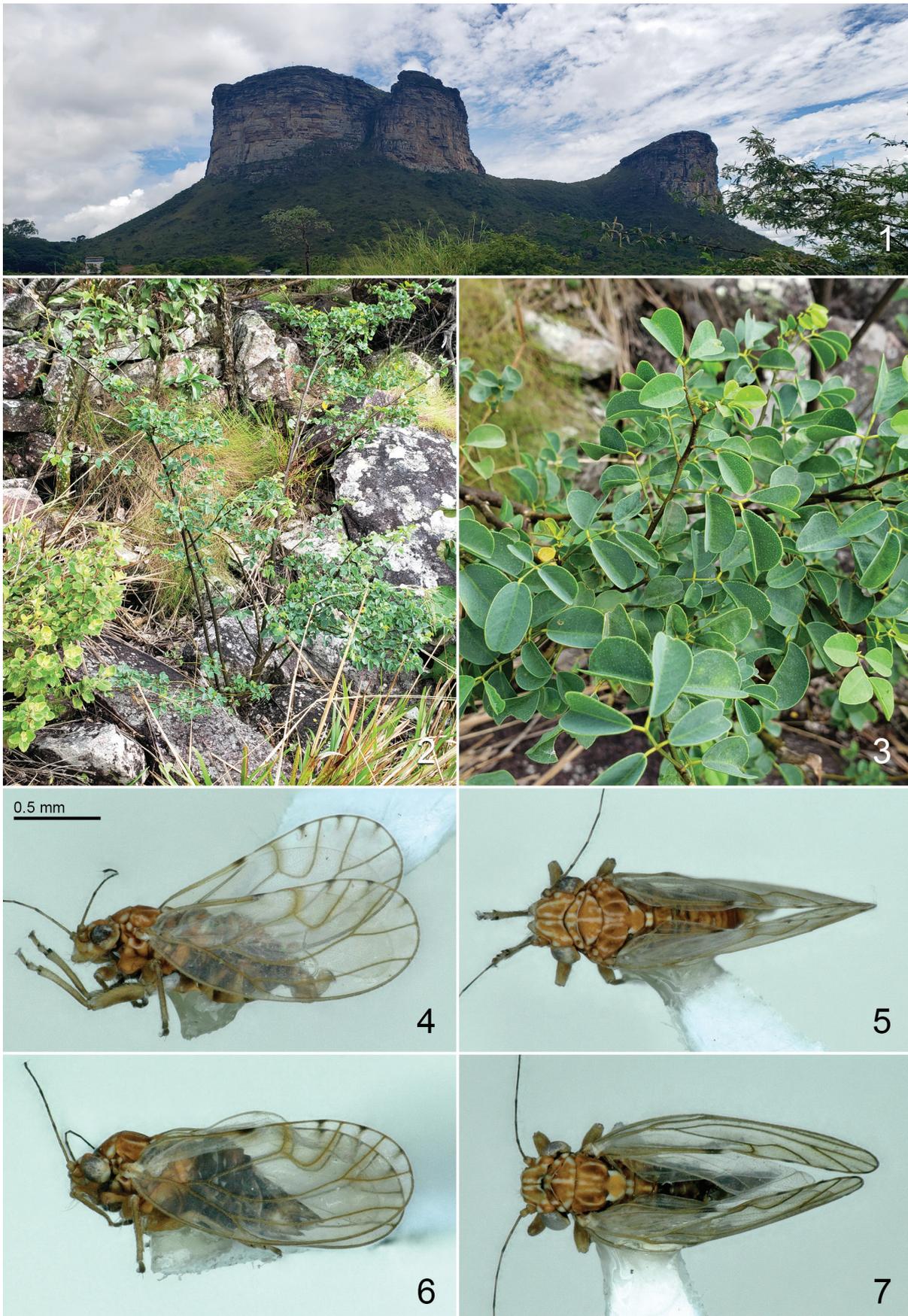
**Paratypes.** BRAZIL, 5 males, 6 females, Bahía, same data as holotype (NHMB, UFPR, dry, slide, ethanol 70%, NMB-PSYLL0007048–NMB-PSYLL0007055).

**Material not included in type series.** BRAZIL, 4 first, 2 second instar immatures, Bahía, same data as holotype (NHMB, ethanol 70%, NMB-PSYLL0007056).

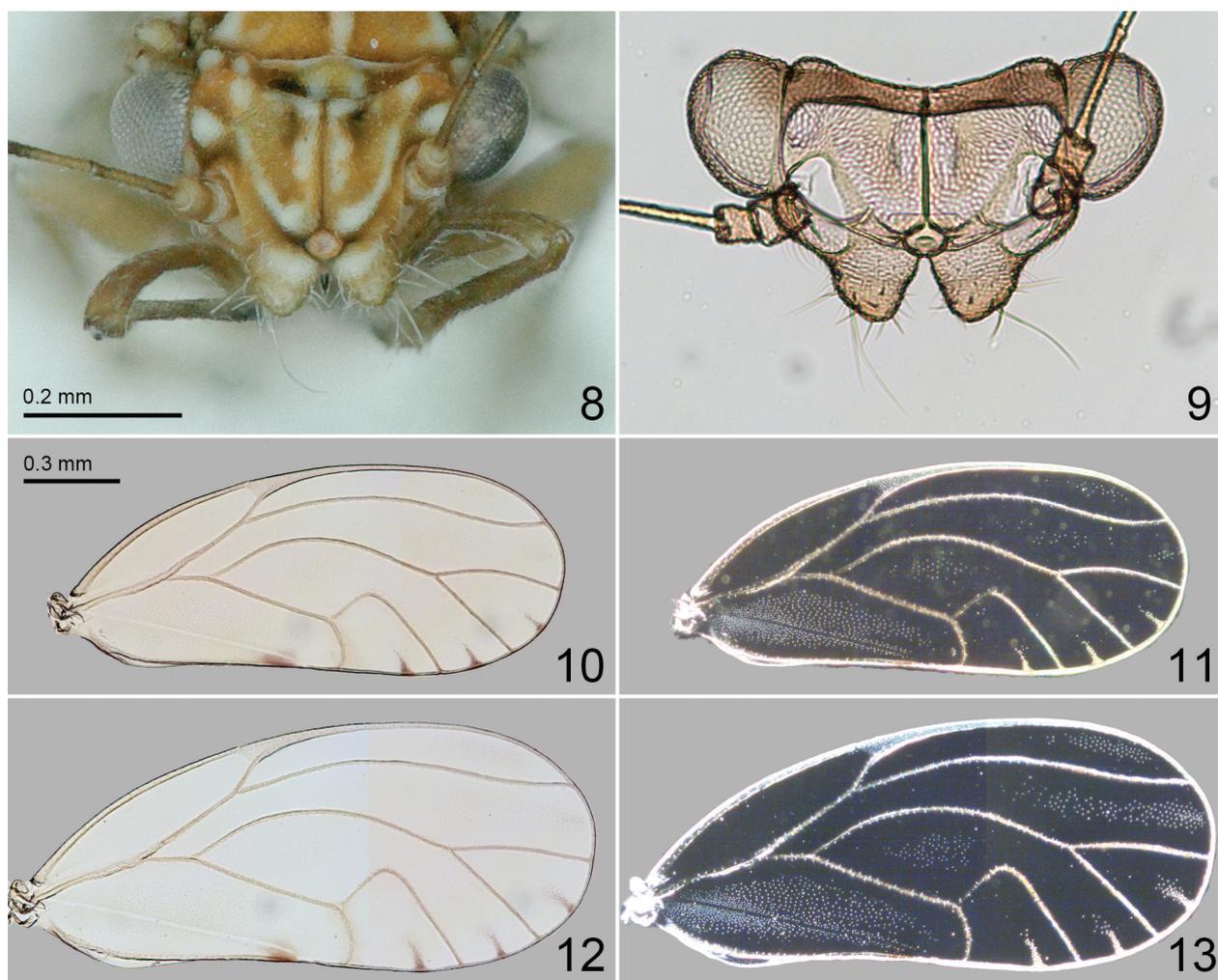
**Diagnosis.** Adult head and thorax with pattern consisting of fine whitish lines and dots. Genal processes irregularly conical, subacute apically, 0.5–0.7 times as long as vertex along midline. Forewing with surface spinules usually present in all cells but much reduced, present in cell  $c+sc$  at the apex, in  $r_1$  along apical margin, in  $r_2$  in apical half of cell, in  $m_1$  in apical third or half, in  $m_2$  in basal half and near apex of cell, in  $cu_1$  almost completely reduced, in cell  $cu_2$  covering most of the cell but leaving broad spinule-free stripes along the veins; radular spinules present in cells  $m_1$ ,  $m_2$ ,  $cu_1$  and sometimes in  $r_2$ . Paramere, in profile, narrow, clavate; sclerotised ridge apically, more or less in the middle, in dorsal view bearing two small teeth. Distal segment of aedeagus complex, with unipartite dorsal lobe. Female proctiger, in profile, with dorsal outline weakly indented adjacent to circumanal ring, in apical half almost straight or weakly convex; apex narrowly rounded.

**Description.** Adult (Figs 4–7). Colouration. Orange to brown. Head and thorax with pattern consisting of fine whitish lines and dots (Figs 5, 7, 8). Ocelli orange, eyes grey. Antennal segments 3–7 yellow at base, dark brown at apex, dark portion becoming longer from proximal to distal segment; segments 7–10 dark brown. Head, clypeus and thorax yellow in ventral view. Thoracic pleura irregularly brown with dark margins of sclerites (Figs 4, 6). Legs yellow or brown, tarsi greyish brown. Forewing (Figs 10, 12) transparent, colourless or slightly yellowish with small dark brown dots on radular spinules in cells  $m_1$ ,  $m_2$  and  $cu_1$  as well as at apex of clavus; veins light brown with brown tips. Hindwing whitish, transparent. Abdominal sclerites brown with two longitudinal submedian rows of whitish dots on tergites; intersegmental membranes yellow or orange. Apex of paramere and female terminalia black. Young specimens lighter with less expanded dark colour, getting gradually darker with age.

**Structure.** Conforming to the generic description of Rendón-Mera et al. (2020). Body length ♂ 2.0–2.2 mm, ♀ 2.2–2.4 mm (6 ♂, 6 ♀). Head inclined in a 30° angle from longitudinal body axis (Figs 4, 6). Vertex with scaly microsculpture (Fig. 9). Genal processes irregularly conical, subacute apically, 0.5–0.7 times as long as vertex along midline (Figs 8, 9). Antenna 2.1–2.3 times as long as head width. Rostrum short, apical and part of the subapical segments visible in profile, 0.4 times as long as head width. Metatibia 0.7–0.8 times as long as head width. Forewing (Figs 10–13) 2.8–3.1 times as long as head width, 2.2–2.4 times as long as wide; fore margin relatively evenly curved, wing widest near the middle; broadly, evenly rounded apically, wing apex lies in cell



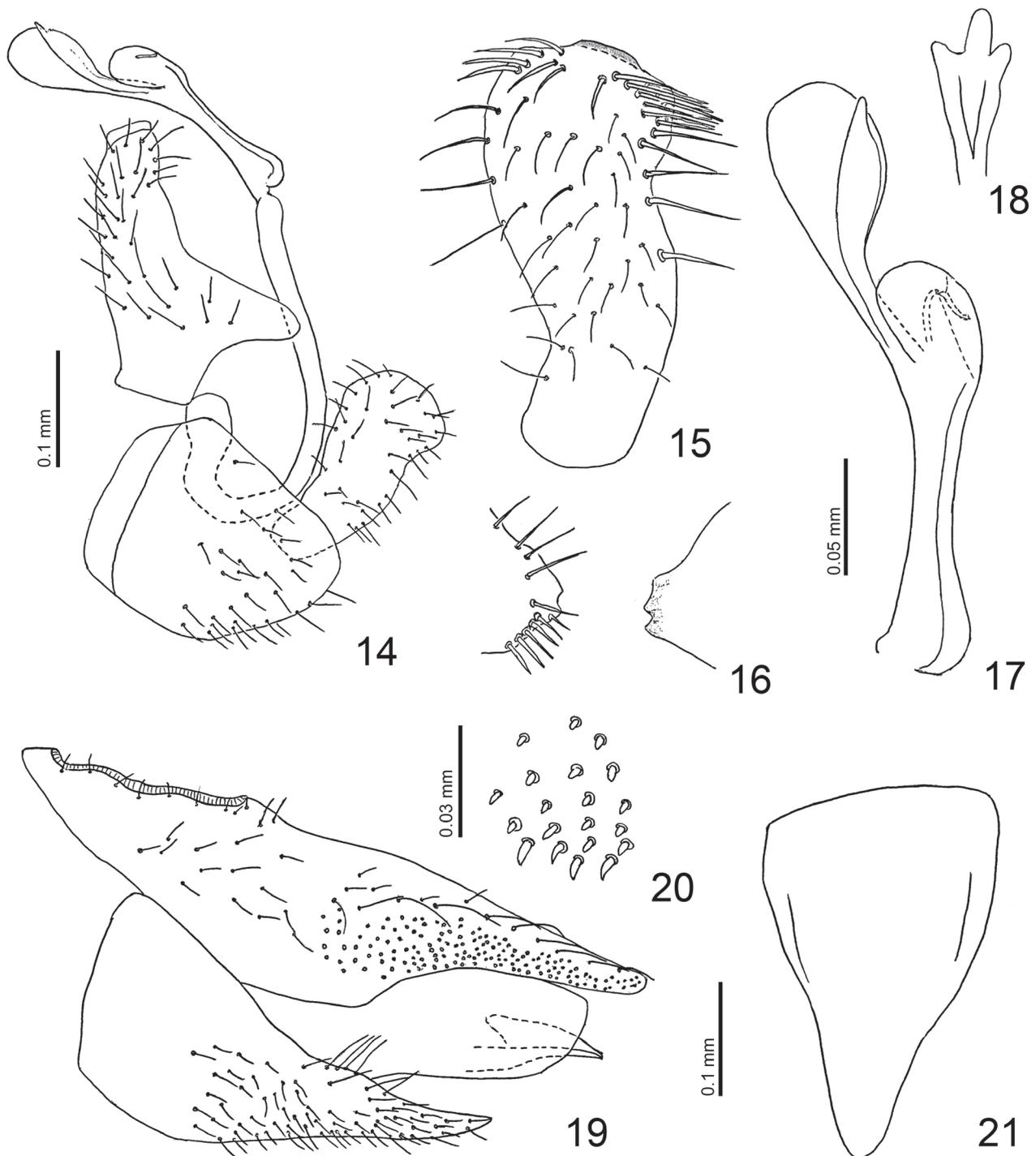
**Figures 1–7.** Habitat, host and habitus of *Mitropsylla rupestris* sp. nov. **1.** Morro do Pai Inácio (Bahía, Palmeiras), type locality of *M. rupestris* sp. nov.; **2, 3.** *Poretia bahiana*, the host of *M. rupestris* sp. nov., growing in rock habitats (**2**) with detail of glandular leaflets (**3**); **4–7.** habitus, adults **4, 6.** in profile; **5, 7.** in dorsal view; **4, 5.** male; **6, 7.** female. Scale bar: 0.5 mm.



**Figures 8–13.** *Mitrapsylla rupestris* sp. nov. **8, 9.** Head, in dorsal view, showing colour pattern (**8**) and microsculpture (**9**); **10–13.** forewing; **10, 12.** bright field, showing venation and colour; **11, 13.** dark field, showing surface spinules; **10, 11.** male; **12, 13.** female. Scale bars: 0.2 mm (**8, 9**); 0.3 mm (**10–13**).

$r_2$ ; pterostigma relatively short, at base slightly narrower than adjacent part of cell  $r_1$ ; cell  $cu_1$  0.8–0.9 times higher than wide. Surface spinules usually present in all cells but much reduced, present in cell  $c+sc$  at the apex, in  $r_1$  along apical margin, in  $r_2$  in apical half of cell, in  $m_1$  in apical third or half, in  $m_2$  in basal half and near apex of cell, in  $cu_1$  almost completely reduced, in cell  $cu_2$  covering most of the cell but leaving broad spinule-free stripes along the veins; in females (Fig. 13) areas with surface spinules more expanded than in males (Fig. 11) where they are much reduced; radular spinules present in cells  $m_1$ ,  $m_2$  and  $cu_1$ , sometimes with also a few indistinct spinules in  $r_2$ . Terminalia as in Figs 13–20. Male proctiger (Fig. 14) 0.3–0.4 times as long as head width, with narrow, relatively straight posterior lobes in basal third. Paramere (Figs 14, 15), in profile, clavate, irregularly expanding towards apex; anterior margin weakly, irregularly concave proximally to kink in distal quarter; apex broadly irregularly rounded; posterior margin weakly, irregularly convex in proximal two thirds and distal third, slightly indented at distal third; outer face with long fine setae, sparser in anterior half, denser in posterior half

(Fig. 14); inner face with long bristles along fore margin in apical half, sparse proximally, dense apically, with a group of long stout, densely spaced bristles near apex anteriorly and posteriorly, and with a few sparse long bristles along hind margin; remainder covered in long setae; sclerotised apical ridge, more or less in the middle (Figs 15, 16). Distal segment of aedeagus (Fig. 17) complex, with unipartite dorsal lobe; dorsal lobe, in profile, ovoid; ventral process hardly upturned, its apical expansion ovoid to subglobular, larger than dorsal lobe, lateral tubercles long, situated near apex, dorsally (Figs 17, 18); sclerotised end tube of ductus ejaculatorius short, weakly sinuous. Female proctiger (Fig. 19) 1.0 times as long as head width, dorsal outline weakly indented adjacent to circumanal ring, weakly concave otherwise almost straight or weakly convex; apex narrowly rounded; with moderately long setae around circumanal ring and in proximal half laterally, distal half with a submedian longitudinal row of long setae on each side and densely spaced peg setae (Fig. 20) laterally; circumanal ring 0.3–0.4 times as long as proctiger, consisting of two unequal rows of pores. Female subgenital plate 0.5 times as long



**Figures 14–21.** *Mitrapsylla rupestris* sp. nov., terminalia. **14.** Male terminalia, in profile; **15.** inner face of paramere; **16.** dorsal view of parameres, setae on right paramere omitted (anterior = up); **17.** distal portion of aedeagus; **18.** ventral lobe of distal portion of aedeagus with lateral tubercles, in ventral view; **19.** female terminalia, in profile; **20.** peg setae on female proctiger; **21.** female subgenital plate, in ventral view. Scale bars: 0.1 mm (**14**, **19**, **21**); 0.05 mm (**15–18**); 0.03 mm (**20**).

as proctiger, pointed apically; densely beset with moderately long setae in distal two thirds except for a seta-free “window” in apical third laterally; in ventral view (Fig. 21) weakly narrowing in proximal half, strongly narrowing in distal half; apex subacute.

Measurements (in mm; 2 ♂, 2 ♀). Head width ♂ 0.56–0.58, ♀ 0.60; antenna length ♂ 1.24–1.26, ♀ 1.30–1.32; forewing length ♂ 1.60–1.64, ♀ 1.68; male proctiger

length 0.20–0.22; paramere length 0.20; length of distal segment of aedeagus 0.26–0.28; female proctiger length 0.60–0.62.

Fifth instar immature unknown, only first and second instars available.

**Etymology.** From Latin *rupe* = rock, referring to its occurrence in rock habitats; *rupestris* is an adjective in the nominative case, feminine.



**Figures 22, 23.** *Poiretia bahiana*. **22.** Plant with folded leaflet (arrow) housing immatures; **23.** immatures of *Mitrapsylla rupestris* sp. nov. (arrows).

**Distribution.** Brazil (Bahía) where it is probably endemic to the Serra do Espinhaço.

**Host plant, biology and habitat.** *Poiretia bahiana* C. Mueller (Fabaceae, Fabioideae, Dalbergieae) (Figs 2, 3). The immatures (Fig. 23, arrows) develop in the fold of the still partially doubled leaflets (Fig. 22, arrow). The host grows in rock habitats (Figs 1, 2).

**Comments.** *Mitrapsylla rupestris* sp. nov. resembles *M. aeshynomenis* Rendón-Mera, Burckhardt, Cavichioli & Queiroz, 2020, *M. aurantia* Rendón-Mera, Burckhardt, Cavichioli & Queiroz, 2020, *M. cubana* Crawford, 1914, and *M. didyma* Rendón-Mera, Burckhardt, Cavichioli & Queiroz, 2020, in the apically weakly expanded paramere, in profile, bearing the sclerotised apical ridge medially and in the unipartite dorsal lobe on the distal portion of the aedeagus. *Mitrapsylla rupestris* sp. nov. differs from the four species in the lateral tubercles on the ventral aedeagal process which are situated near the apex (rather than near the middle), and in the female proctiger which is dorsally straight or weakly convex in apical half (rather than weakly sinuous) and narrowly rounded apically (rather than obliquely truncate). In *M. aeshynomenis* and *M. aurantia*, the antennae and the genal processes are slightly shorter: antenna length/ head width ratio < 2.1 versus > 2.1 in *M. rupestris* sp. nov.; length ratio of genal processes/ vertex < 0.5 versus > 0.5 in *M. rupestris* sp. nov. From the former, *M. rupestris* sp. nov. differs also in the slightly more acute genal process-

es and from the latter in the more spaced surface spinules of the forewing. In the key of Rendón-Mera et al. (2020), *M. rupestris* sp. nov. runs to couplet 31 together with *M. cubana* and *M. didyma* from which it differs the shape of the sclerotised ridge of the paramere in dorsal view. In the last two species, the ridge bears one big posterior tooth, while in *M. rupestris* sp. nov. it forms two small teeth. From the former it differs in the apically slightly more expanded paramere and from the latter in the slightly shorter postero-apical lobe of the paramere. It differs also in the host association: *M. aeshynomenis* develops on *Aeshynomene*, which belongs to the same tribe as *Poiretia* (Dalbergieae), *M. cubana* and *M. didyma* are associated with *Desmodium*, which is a member of the more distantly related Desmodieae within the same subfamily (Faboideae). The host of *M. aurantia* is unknown.

## Discussion and conclusions

Hosts are known for 34 of the 51 previously known *Mitrapsylla* species (Rendón-Mera et al. 2020). They belong to 12 genera of Fabaceae of the three subfamilies Caesalpinioideae (Cassiae: *Cassia* and *Senna*), Detarioideae (Detarieae: *Copaifera*) and Fabioideae (Dalbergieae: *Aeshynomene*, *Andira*, *Machaerium* and *Pterogyne*; Desmodieae: *Desmodium*; Dipterygeae: *Pterodon*; Exostyleae: *Holocalyx*; Phaseoleae: *Periandra*; and

Sophoreae: *Sophora*). *Poiretia bahiana* (tribe Dalbergieae), the host of *M. rupestris* sp. nov., constitutes a previously unknown psyllid host. All *Mitrapssylla* species for which hosts are known are either monophagous on a single host species or oligophagous on several species of the same host genus. In terms of host taxon and range, *M. rupestris* sp. nov. fits the general pattern of *Mitrapssylla*.

True endemism in psyllids is probably rare and apparently restricted distributions may merely reflect incomplete faunistic knowledge. Among the 40 *Mitrapssylla* species previously reported from Brazil, 26 have a relatively wide geographic distribution and are also known from outside of Brazil or have been recorded from two or more states in Brazil (Rendón-Mera et al. 2020). Of the remaining 14 species, 10 are known from only a single municipality. Whether these species are endemic or just reflect insufficient sampling cannot be judged without more fieldwork. For three of the 10 species the hosts are known: *M. aeshynomenis* (on *Aeshynomene paniculata*), *M. hamata* Rendón-Mera, Burckhardt, Cavichioli & Queiroz, 2020 (on *Machaerium amplum*) and *M. pterogynis* Rendón-Mera, Burckhardt, Cavichioli & Queiroz, 2020 (on *Pterogyne nitens*). All three hosts are widely distributed suggesting that the associated psyllids also may be. *Mitrapssylla rupestris* sp. nov., in contrast, is probably narrowly endemic as it is monophagous on *Poiretia bahiana*, an endemic of rock habitats of the Serra do Espinhaço (Müller 1986).

The flora of the “campos rupestres” of the Espinhaço Range is extremely species rich with a high degree of endemism (Ribeiro et al. 2014). The psyllids seem to reflect this pattern. Apart from *Mitrapssylla rupestris* sp. nov., we found in these rock fields also two *Isogonoceraia* spp. (Psyllidae, Ciriacreminae) on *Chamaecrista* (Fabaceae), one *Heteropsylla* sp. (Psyllidae, Ciriacreminae) on *Calliandra* (Fabaceae) and one *Trioza* sp. (Trioziidae) on *Eugenia* (Myrtaceae). The four species are undescribed, probably host specific and endemic to “campos rupestres” of the Serra do Espinhaço. Despite their floristic and faunistic interest, there is a lack of studies of the mountainous regions of Brazil, which harbour some of the most threatened plant ecosystems (Bünger et al. 2014). Studies on the flora and fauna are urgently required for designing efficient measures for the sustainable conservation of this unique biome.

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# An updated checklist of the Cantharidae and Lycidae of Switzerland (Coleoptera, Elateroidea)

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## Abstract

An updated checklist of the Swiss species belonging to the families Cantharidae and Lycidae, is presented and briefly discussed. This checklist includes 106 species and is based on over 26'000 occurrences obtained from the identification of specimens held in museum and private collections, as well as from records taken from the literature. *Cantharis liburnica* Depoli, 1912, *C. paradoxa* Hicker, 1960, *Malthinus rubricollis* Baudi di Selve, 1859 and *Malthodes umbrosus* Kiesenwetter, 1871 are recorded from Switzerland for the first time. Two species previously recorded from Switzerland (*Malthodes montanus* Kiesenwetter, 1863, *M. boicus* Kiesenwetter, 1863) are excluded from this list, as those records were based on misidentified material.

## Key Words

Insecta, soldier beetles, species list, new country records, faunistics, distribution

## Introduction

With more than 5600 described species worldwide (Delkeskamp 1977, Kazantsev and Brancucci 2007), Cantharidae are the tenth most diverse family of Coleoptera. They are soft-bodied, predatory beetles, ranging in size from about 1.0 to roughly 30 mm in some tropical species. Lycidae are a related group comprising roughly 4000 described species worldwide (Bocák and Bocáková 2016), though the vast majority of them are found in the tropics. Their life history and size range is similar to that of Cantharidae. Together, those families form a part of Elateroidea, one of the major clades of the suborder Polyphaga, which has undergone major changes in its family-level classification in recent decades, mostly due to advances in molecular phylogeny (e.g. Bocák et al. 2016). “Soft-bodiedness” (i.e. a weakly sclerotised exoskeleton) has been shown to be a derived character that evolved multiple times independently within Elateroidea. As such, the former grouping “Malacodermata” and “Cantharoidea”, which included Cantharidae and Lycidae, have now become obsolete (Kusy et al. 2018, 2020).

Within the fauna of Switzerland, Cantharidae are a moderately diverse and certainly very abundant and commonly recorded family, while Lycidae is represented only by a small handful of mostly uncommon species. The most recent faunistic treatment of these families was provided by Allenspach and Wittmer (1979), which included detailed distribution maps for some of the rarer species, but only rough distributional information for the more common ones. Walter Wittmer (Basel 1915 – Prague 1998), a world expert on Cantharidae, described approximately 3600 species and subspecies (Brancucci 2005), including several new taxa from Switzerland, one of which was published after his faunistic treatment (Wittmer 1981).

Allenspach and Wittmer (1979) also included the two small families Omalidae and Drilidae, neither of which is currently recognised as valid after recent phylogenetic studies showed them to be derived members of Elateridae (Kundrata and Bocák 2011, Kusy et al. 2018). For the Swiss fauna, Omalidae is only represented by *Omalisus fontisbellaquaei* (Geoffroy in Fourcroy, 1785) while Drilini (now part of Elateridae: Agrypninae) includes the two

species *Drilus flavescens* (Geoffroy in Fourcroy, 1785) and *D. concolor* Ahrens, 1812. These three species are widespread and well-documented within Switzerland, so no faunistic update is needed for them. The Swiss fauna of Lampyridae, another closely related elateroid family, was recently treated by Gurcel et al. (2020), while the morphologically similar (but unrelated) families Melyridae and Rhadalidae (of superfamily Cleroidea) were updated by Chittaro and Sanchez (2019b). Although our understanding of the beetle fauna of Switzerland has greatly improved since the publication of Allenspach and Wittmer (1979), many groups are still in urgent need of attention. For example, several species found in Switzerland and published since 1979 must be added to the list (e.g. Scherler 1981, Walter and Weber 1999, Kopetz and Duelli 2006), while other species that were recorded from Switzerland based on unreliably labelled material should be excluded. Furthermore, updates are urgently required for the many nomenclatural changes to the Swiss fauna, as well as for the distribution of certain species in Switzerland. Using Allenspach and Wittmer (1979) as a foundation, our objective is to update the Swiss checklist for Cantharidae and Lycidae, to add new data and to flag problems when needed.

## Material and methods

The goal of this study was to evaluate all existing information in order to present a complete list of the Swiss fauna. We therefore performed an exhaustive examination of the relevant material present in major Swiss museum collections, as was recently done for other beetle groups (see for example Chittaro and Sanchez 2019a, 2019b, Sanchez et al. 2020). The collections in the following museums were studied (the contact person is reported in parentheses after each institution):

- AGRO** Agroscope-Changins, Nyon (Stève Breitenmoser);  
**BNM** Bündner Natur-Museum, Chur (Stephan Liersch);  
**ETH** Eidgenössische-Technische Hochschule, Zürich (Michael Greeff);  
**KMLI** Archäologie und Museum Baselland, Liestal (Marc Limat);  
**MHNF** Musée d'histoire naturelle de Fribourg (Peter Wandeler, Sophie Giriens);  
**MHNG** Muséum d'histoire naturelle de Genève (Giulio Cuccodoro);  
**MHNN** Musée d'histoire naturelle de Neuchâtel (Jessica Litman);  
**MHNS** Musée de la nature du Valais, Sion (Sonja Gerber);  
**MSNL** Museo cantonale di storia naturale, Lugano (Lucia Pollini Paltrinieri);  
**MZL** Musée cantonal de zoologie, Lausanne (Anne Freitag);  
**MZA** Museum zu Allerheiligen, Schaffhausen (Urs Weibel);  
**NMAA** Naturama, Aarau (Janine Mazenauer);  
**NMB** Naturhistorisches Museum Basel (Matthias Borer);

- NMBE** Naturhistorisches Museum Bern (Hannes Baur);  
**NMLU** Natur-Museum, Luzern (Marco Bernasconi, Peter Herger);  
**NMSG** Naturmuseum St. Gallen (Karin Urfer);  
**NMTG** Naturmuseum Thurgau, Frauenfeld (Barbara Richner);  
**NMSO** Naturmuseum, Solothurn (Marc Neumann).

We also cite data gathered from two museums outside Switzerland:

- BMNH** Natural History Museum, London, United Kingdom;  
**SMNS** Staatlichen Museum für Naturkunde Stuttgart, Germany.

Moreover, we included data from the private collections of the authors, as well as those of the following individuals: Stève Breitenmoser (Givrins VD), Vivien Cosandey (Essertines-sur-Rolle VD), Berndt Eismann (Kreuzlingen TG), Bastien Guibert (Gy GE), Roman Graf (Horw LU), Barbara Huber (Thuisis GR), Christian Monnerat (Neuchâtel NE), Wolfgang Pankow (Dogern, Germany) and Arnaud Vallat (Bienne BE).

All available data from the literature relevant for Switzerland were also considered. The references from these publications are included in the bibliography. Literature not explicitly cited is supplied as Suppl. material (see Suppl. material 1: File S1).

Nomenclature and systematics followed are those of the “Catalogue of Palaearctic Coleoptera” (Kasantsev and Brancucci 2007, Bocáková and Bocák 2007), with the following exceptions:

- The valid name for *Ancistronycha violacea* (Paykull, 1798) should be *A. tigurina* (Dietrich, 1857), following Silfverberg (2010).
- *Malthodes icaricus* Wittmer, 1940 is now a separate species and no longer a subspecies of *M. penninus* (Liberti 2015).
- *Malthodes lucernensis*, described by Wittmer (1981) from Switzerland, was recently synonymised with *M. maurus* by Liberti (2016): the examination of a large amount of material suggests indeed that *M. lucernensis* is simply an “extreme” morphological form of *M. maurus*, usually found sympatrically.
- *Malthodes transeuropaeus* Wittmer, 1970 was synonymised with *M. europaeus* by Liberti (2015).
- The subspecies *Malthodes trifurcatus atramentarius* Kiesenwetter, 1852 is here treated as synonymous with *M. trifurcatus*, following Liberti (2017). Those two morphological forms (with the last abdominal segments more or less developed in the male) are often found together in the same localities or the same general area.
- *Crudosilis ruficollis* (Fabricius, 1775) is in fact the type species of *Silis* Charpentier, 1825. As such, the name was changed back to *Silis ruficollis*, according to Kazantsev (2011).

- *Silis nitidula* (Fabricius, 1792) is now a member of the genus *Autosilis*, following Kazantsev (2011).

The specimens were identified using the following publications: Geisthardt (1979, 1992), Dahlgren (1968, 1979), Wittmer (1979), Liberti (2011, 2015, 2016, 2017, 2018), Švihla (2006), Constantin (2014c), Bretzendorfer (2010, 2017) and Kazantsev (2005).

When not otherwise specified, general information on species' distributions are taken from the "Catalogue of Palaearctic Coleoptera" (Kasantsev and Brancucci 2007, Bocáková and Bocák 2007).

We have also used the relevant literature concerning the countries and regions adjacent to Switzerland, such as Fanti (2014) for Italy and the regional treatment of Kahlen and Hellrigl (1996) for South Tyrol / Alto Adige, Constantin (2014a, b, c) for France and regionally Calot (2018) for Alsace, Köhler and Klausnitzer (1998) and Köhler (2000, 2011) for Germany, as well as the regional treatment of Bretzendorfer (2017) for south-western Germany, and Brandstetter and Kapp (1998) for Vorarlberg (Austria) and Liechtenstein.

The list of the main synonyms of each taxon is provided in "Catalogue of Palaearctic Coleoptera" (Löbl and Smetana 2007) and is therefore not reported here. The subfamily and tribal classifications adopted here follow Bouchard et al. (2011), which is based upon the morphological phylogenetic study by Brancucci (1980).

Once an exhaustive list of species was compiled, we followed the procedure proposed by Monnerat et al. (2015) in order to assess which of these species should be considered indigenous to Switzerland. We only retained species whose relative data were deemed sufficient (unambiguous labeling, reliable collections, etc.) for inclusion on the national checklist.

Those species whose presence in Switzerland is substantiated by less than twenty valid observations are subject to an additional comment. In these cases, species names in the table are followed by a letter and a number in bold ("C1" for example) and all the examined specimens and published observations are mentioned in order to document and justify the presence of these species on the checklist. When not otherwise specified, all examined material was identified or reviewed by the authors.

There are various genera and species groups in Cantharidae for which the only known reliable characters are the male terminalia. For those species, only dissected males are counted as "verified" records, while records based exclusively upon female specimens were omitted as unverifiable.

The specimens and literature-based records presented here are listed in chronological order of discovery (or publication date) and then in alphabetical order by locality, depending on available information. All occurrences are cited according to the following scheme: number of specimens, locality (pre-2000 data) or municipality and abbreviated canton (post-2000 data), date, collector, determinant (in the case that the determinant was not one of the authors), collection and official acronym of the institution where the insect is deposited.

Information about localities and dates are reported as found on the labels. Interpretations of alphabetical abbreviations are placed within square brackets ("[" ]"). In old collections, the collector (leg.) is not always explicitly labelled. In such cases, we favored the « coll. » tag. In some cases, the original collection holder was not labelled but we were nonetheless able to identify the source of the collection based on type labels and/or handwriting.

The Charles Maerky collection, held by the Natural History Museum of Geneva, has long been considered problematic (Monnerat et al. 2015). In addition to specimens coming from his personal collection ("coll. Maerky C."), it also contains insects from other sources (labelled, for instance, as "ex coll. Melly A.") but lacking any original labels. In such cases, we maintained the "coll. Maerky C." mention for his whole collection to ensure the association of these samples with the Maerky C. collection.

For the literature-based data, detailed under "Published data", we retained the locality as it appeared in the original citation. We consider the "source" of the records to be the author of the publication, for example: "Ormontsthal by Venetz I. (Stierlin and Gautard 1867)". If the same records have been published more than once, then only the oldest publication is retained, given that localities in later publications are often altered and sometimes truncated. Under the heading "Published data" we avoided repeating the data reported in Allenspach and Wittmer (1979) when the relevant specimens they cite have been examined and their old determinations verified; these data already appear under "Examined material". On the other hand, we report in full the Allenspach and Wittmer (1979) data for which the corresponding material was not located or in the case where the original identification was deemed to be erroneous. Among the data cited in this paper under "Examined material" or "Published data", we inserted a superscript number code before those entries we considered insufficiently documented to be retained, using the following code to describe error type (following Monnerat et al. 2015). Thus if one of the following eight criteria is fulfilled, a record is considered as doubtful:

1. data source cannot be verified;
2. incorrect identification;
3. specimen from problematic collection;
4. specimen of unknown origin but attributed to a Swiss locality;
5. double labeling, original locality misinterpreted or incorrectly copied;
6. confusion between localities: original finding, breeding or hatching place and collection storage site;
7. non-Swiss localities or potentially Swiss localities that share their names with foreign place names (and thus of dubious Swiss origin);
8. chorological or ecological inconsistencies.

Abbreviations used: coll. = collection, det. = determinant, ex. = specimen, leg. = collector. Abbreviated Swiss cantons (only cantons cited in the text): AG = Aargau,

BE = Bern, BL = Basel-Landschaft, FR = Fribourg, GE = Geneva, GR = Grisons, LU = Lucerne, NE = Neuchâtel, SH = Schaffhausen, SZ = Schwyz, TI = Ticino, TG = Thurgau, VD = Vaud, VS = Valais, ZH = Zurich.

## Results

### Swiss fauna Cantharidae and Lycidae list

We consider that the 106 species (107 taxa) listed in bold and without square brackets “[ ]” either currently do or formerly did form populations in Switzerland, even if only scant information is available for many of them.

On the other hand, the seven species listed in square brackets “[ ]” should not be considered as belonging to the Swiss fauna, until new data show otherwise. In this category, we placed species whose individuals come from problematic collections, such as Charles Maerky’s or Max Täschler’s (Monnerat et al. 2015), those that were erroneously mentioned for Switzerland due to incorrect identifications and those cited in old publications, like Stierlin and Gautard (1867), without reference to specific individuals and consequently considered as doubtful. Other species may eventually be found in the Swiss territory but currently available data are not sufficient to confirm their establishment in Switzerland.

A special problem is presented by the four species of *Hapaloderus* (now *Malthodes*) described by Motschulsky (1853) from Switzerland: *Hapaloderus alpinus* (described from “Suisse orientale [sic!]” (eastern Switzerland) and “Koschutna in Carniolia” (Košutna planina) in today’s Slovenia), *H. angusticollis* (described from “Alpes de la Suisse (Appenzell)”), *H. croceicollis* (described from “Switzerland”, as well as “Saxe, dans l’Odewalder Grund près de St. Wählen”, probably Uttewalder Grund near Stadt Wehlen in Saxony, Germany) and *H. ventralis* (described from “Berne” (Switzerland) and “Styrie” in Austria). The descriptions of these species are insufficient and are not accompanied by illustrations, thus making it impossible to recognise the species and match them with currently accepted *Malthodes* names (Liberti 2015). Whether or not the type material is still in good enough condition to be examined cannot be said at the moment, but it seems questionable for at least part of them (see Kazantsev and Nikitsky 2008), also considering the fact that most *Malthodes* are only identifiable from the male terminalia, so females are often unrecognisable. Those species have been excluded from the Swiss checklist by Allenspach and Wittmer (1979) for the reason of being “incertae sedis”. Kazantsev and Brancucci (2007), however, listed them as valid. Without access to Motschulsky’s type material we are currently not able to address the taxonomic status of those four names. But as no author has ever been able to interpret them and match them with an actual valid *Malthodes* species,

we decided to omit them from the present checklist, pending further taxonomic studies.

To facilitate the species’ search in this document, taxa appear in alphabetical order for families, subfamilies, tribes, genera, subgenera, species and subspecies.

All collected information represent 26’208 occurrences within the concerned families. Updated distribution maps of these species are available on the info fauna – CSCF cartographic server (<http://lepus.unine.ch/cartof/>). All the valid data are also available in <http://www.GBIF.org> (<https://doi.org/10.15468/dl.ngkguj>).

## CANTHARIDAE

### Cantharinae Imhoff, 1856

#### Cantharini Imhoff, 1856

*Ancistronycha abdominalis* (Fabricius, 1798)

*Ancistronycha erichsonii erichsonii* (Bach, 1852)

[*Ancistronycha occipitalis* (Rosenhauer, 1847)] C1

*Ancistronycha tigurina* (Dietrich, 1857)

*Cantharis (Cantharis) annularis* Ménétrés, 1836

*Cantharis (Cantharis) cryptica* Ashe, 1947

*Cantharis (Cantharis) decipiens* Baudi di Selve, 1872

*Cantharis (Cantharis) figurata* Mannerheim, 1843

*Cantharis (Cantharis) flavilabris* Fallén, 1807

*Cantharis (Cantharis) fusca* Linnaeus, 1758

*Cantharis (Cantharis) livida* Linnaeus, 1758

*Cantharis (Cantharis) liburnica* Depoli, 1912 C2

*Cantharis (Cantharis) montana* Stierlin, 1889

*Cantharis (Cantharis) nigra* (DeGeer, 1774)

*Cantharis (Cantharis) nigricans* (O. F. Müller, 1776)

*Cantharis (Cantharis) obscura* Linnaeus, 1758

*Cantharis (Cantharis) pallida* Goeze, 1777

*Cantharis (Cantharis) paludosa* Fallén, 1807

*Cantharis (Cantharis) paradoxa* Hicker, 1960 C3

*Cantharis (Cantharis) pellucida* Fabricius, 1792

*Cantharis (Cantharis) pulicaria* Fabricius, 1781

*Cantharis (Cantharis) quadripunctata* (O. F. Müller, 1776) C4

*Cantharis (Cantharis) rufa* Linnaeus, 1758

*Cantharis (Cantharis) rustica* Fallén, 1807

*Cantharis (Cantharis) terminata* Faldermann, 1835

*Cantharis (Cantharis) tristis* Fabricius, 1798

*Cantharis (Cyrtomoptila) fibulata* Märkel, 1852

*Cantharis (Cyrtomoptila) gemina* Dahlgren, 1974

*Cantharis (Cyrtomoptila) lateralis* Linnaeus, 1758

*Cantharis (Cyrtomoptila) pagana* Rosenhauer, 1847 C5

*Cratosilis denticollis* (Schummel, 1844)

*Cratosilis distinguenda* (Baudi di Selve, 1859)

*Cratosilis laeta* (Fabricius, 1792)

*Metacantharis clypeata* Illiger, 1798

*Metacantharis discoidea* (Ahrens, 1812)

*Podistra (Absidia) rufotestacea* (Letzner, 1845)

*Podistra (Absidia) schoenherri* (Dejean, 1836)

*Podistra (Pseudoabsidia) prolixa* (Märkel, 1852)

*Rhagonycha (Rhagonycha) atra* (Linnaeus, 1767)

*Rhagonycha (Rhagonycha) elongata* (Fallén, 1807) C6  
 [*Rhagonycha (Rhagonycha) femoralis* (Brullé, 1832)] C7  
*Rhagonycha (Rhagonycha) fugax fugax* Mannerheim,  
 1843

*Rhagonycha (Rhagonycha) fulva* (Scopoli, 1763)  
*Rhagonycha (Rhagonycha) fuscitibia* Rey, 1891  
*Rhagonycha (Rhagonycha) gallica* Pic, 1923  
*Rhagonycha (Rhagonycha) lignosa* (O. F. Müller, 1764)  
*Rhagonycha (Rhagonycha) lutea* (O. F. Müller, 1764)  
*Rhagonycha (Rhagonycha) maculicollis* Märkel, 1852  
*Rhagonycha (Rhagonycha) nigriceps* (Waltl, 1838)  
*Rhagonycha (Rhagonycha) nigripes* (W. Redtenbacher, 1842)  
*Rhagonycha (Rhagonycha) nigriventris* Motschulsky,  
 1860  
*Rhagonycha (Rhagonycha) pedemontana* Baudi di  
 Selve 1872 C8  
*Rhagonycha (Rhagonycha) testacea* (Linnaeus, 1758)  
*Rhagonycha (Rhagonycha) translucida* (Krynicky, 1832)

Podabrini Gistel, 1856

*Podabrus alpinus* (Paykull, 1798)

## Malthininae Kiesenwetter, 1852

Malthinini Kiesenwetter, 1852

*Malthinus (Malthinus) balteatus* Suffrian, 1851  
*Malthinus (Malthinus) biguttatus* (Linnaeus, 1758)  
*Malthinus (Malthinus) bilineatus* Kiesenwetter, 1852 C9  
*Malthinus (Malthinus) facialis* C. G. Thomson, 1864  
*Malthinus (Malthinus) fasciatus* (A. G. Olivier, 1790)  
*Malthinus (Malthinus) flaveolus* (Herbst, 1786)  
*Malthinus (Malthinus) frontalis* (Marshall, 1802)  
*Malthinus (Malthinus) glabellus* Kiesenwetter, 1852  
*Malthinus (Malthinus) rubricollis* Baudi di Selve,  
 1859 C10  
*Malthinus (Malthinus) seriepunctatus* Kiesenwetter,  
 1852  
*Malthinus (Malthinus) sordidus sordidus* Kiesenwetter,  
 1871 C11

Malthodini Böving & Craighead, 1931

*Malthodes (Malthodes) aemulus* Kiesenwetter, 1861 C12  
*Malthodes (Malthodes) alpicola* Kiesenwetter, 1852  
*Malthodes (Malthodes) bertolinii* Fiori, 1905 C13  
 [*Malthodes (Malthodes) bifurcatus* Kiesenwetter,  
 1852] C14  
 [*Malthodes (Malthodes) boicus* Kiesenwetter, 1863] C15  
*Malthodes (Malthodes) brevicollis* (Paykull, 1798)  
*Malthodes (Malthodes) caudatus* J. Weise, 1892 C16  
*Malthodes (Malthodes) crassicornis* (Maeklin, 1846) C17  
*Malthodes (Malthodes) cyphonurus* Kiesenwetter, 1861  
*Malthodes (Malthodes) debilis debilis* Kiesenwetter,  
 1852 C18  
 [*Malthodes (Malthodes) dimidiaticollis dimidiaticollis*  
 (Rosenhauer 1847)] C19

*Malthodes (Malthodes) dispar* (Germar, 1824)  
*Malthodes (Malthodes) europaeus* Wittmer, 1970  
*Malthodes (Malthodes) facetus* Kiesenwetter, 1863 C20  
*Malthodes (Malthodes) fibulatus* Kiesenwetter, 1852 C21  
*Malthodes (Malthodes) flavoguttatus* Kiesenwetter, 1852  
*Malthodes (Malthodes) fuscus* (Waltl, 1838)  
*Malthodes (Malthodes) guttifer* Kiesenwetter, 1852  
*Malthodes (Malthodes) hexacanthus* Kiesenwetter, 1852  
*Malthodes (Malthodes) holdhausi* Kaszab, 1955 C22  
*Malthodes (Malthodes) icaricus* Wittmer, 1940 C23  
*Malthodes (Malthodes) kahleni* Wittmer, 1982 C24  
*Malthodes (Malthodes) lobatus* Kiesenwetter, 1852  
*Malthodes (Malthodes) marginatus* (Latreille, 1806)  
*Malthodes (Malthodes) maurus* (Laporte, 1840)  
*Malthodes (Malthodes) minimus* (Linnaeus, 1758)  
*Malthodes (Malthodes) misellus* Kiesenwetter, 1852  
 [*Malthodes (Malthodes) montanus* Kiesenwetter,  
 1863] C25  
*Malthodes (Malthodes) mysticus mysticus* Kiesenwetter,  
 1852  
*Malthodes (Malthodes) penninus penninus* Baudi di  
 Selve, 1872  
*Malthodes (Malthodes) penninus raeticus* Wittmer,  
 1970 C26  
*Malthodes (Malthodes) pumilus* (Brébisson, 1835)  
*Malthodes (Malthodes) setifer* Baudi di Selve, 1871  
*Malthodes (Malthodes) sculus* Kiesenwetter, 1852 C27  
*Malthodes (Malthodes) spathifer* Kiesenwetter, 1852  
*Malthodes (Malthodes) spretus* Kiesenwetter, 1852  
*Malthodes (Malthodes) stolzi* Hicker, 1915] C28  
*Malthodes (Malthodes) trifurcatus* Kiesenwetter, 1852  
*Malthodes (Malthodes) umbrosus* Kiesenwetter, 1871  
 C29  
*Malthodes (Malthodes) vincens* Gredler, 1870 C30

## Silinae Mulsant, 1862

Silini Mulsant, 1862

[*Autosilis nitidula* (Fabricius, 1792)] C31  
*Silis ruficollis* (Fabricius, 1775)

## LYCIDAE

### Lycinae Laporte, 1836

Calochromini Lacordaire, 1857

*Lygisteris sanguineus sanguineus* (Linnaeus, 1758)

Erotini LeConte, 1881

*Dictyoptera aurora* (Herbst, 1784)  
*Erotides (Glabroplatycis) cosnardi* (Chevrolat, 1831)  
*Lopheros (Lopheros) rubens* (Gyllenhal, 1817)  
*Platycis (Platycis) minutus* (Fabricius, 1787)  
*Pyropteris nigroruber* (DeGeer, 1774)

## Commented species

### C1) [*Ancistronycha occipitalis* (Rosenhauer, 1847)]

**Published data.** <sup>1</sup>Panix and <sup>1</sup>Savien by Frey-Gessner E. (Cafisch 1894).

**Comment.** While the above literature citation is not verifiable, all of the male specimens examined from various Swiss collections standing as *A. abdominalis* “*a. occipitalis*” or “*var. occipitalis*” turned out to be either *A. abdominalis* or *A. tigurina* after dissection. We were unable to find a single *A. occipitalis* among them. This species is therefore not confirmed for Switzerland, despite being present in Central and eastern Europe and also from the South-West of Germany (Bretzendorfer 2017). It is therefore possible that *A. occipitalis* may be found in northern Switzerland in the future.

### C2) *Cantharis (Cantharis) liburnica* Depoli, 1912

**Examined material.** <sup>3</sup>1 ex., Alpes, Mendrisio, coll. Maerky C., MHNG; 1 ex., Mendrisio, 25.IV., leg. Anonymous, MHNG.

**Comment.** Widely distributed in southern and western Europe, this species is newly recorded here for the Swiss fauna based on the above mentioned specimen from Mendrisio (25.IV.), despite the lack of a precise date and collector. Its occurrence in the extreme south of Ticino can be seen as a continuation of its range in northern Italy (Moscardini 1963, Fanti 2014). The first specimen cited here belongs to the « problematic » collection of C. Maerky (see Monnerat et al. 2015) and is therefore not retained as a valid record.

### C3) *Cantharis (Cantharis) paradoxa* Hicker, 1960

**Examined material.** 1 ex., Bâle, V., leg. Toumayeff G., MHNG; 2 ex., Soloth. Jura, Hofst. K., 22.V.1949, leg. & coll. Wolf J.-P., ETH; 1 ex., U. Stierenwald BL, V.1954, leg. Toumayeff G., MHNG; <sup>1</sup>1 ex., Stein a. Rhein, 20.V.1982, leg. Köstlin R., det. Bouwer R., SMNS.

**Comment.** This species is widespread in Europe from the Netherlands to Greece. It is rather similar to *C. obscura* based on external characters but the male genitalia are clearly different. For Switzerland, we have only found a small number of males that can be definitely assigned to this species, all from the north of the country, as a continuation of its range in southern Germany (Bretzendorfer 2017). *Cantharis obscura*, on the other hand, was found to be widespread throughout Switzerland. *Cantharis paradoxa* was also recently discovered in Alsace, at low altitude (Callot 2011). It must, however, still be confirmed for Italy (Fanti 2014).

### C4) *Cantharis (Cantharis) quadripunctata* (O. F. Müller, 1776)

**Examined material.** 1 ex., Valsot GR, 23.VI.2017, leg & coll. Chittaro Y.

**Published data.** Numerous citations in the older literature, partly repeated and added to by Allenspach and Wittmer (1979). None of those records are reliable, as none of them are based on dissected male specimens and may refer to either *C. quadripunctata* or *C. montana* (see below). We are therefore not repeating those citations here.

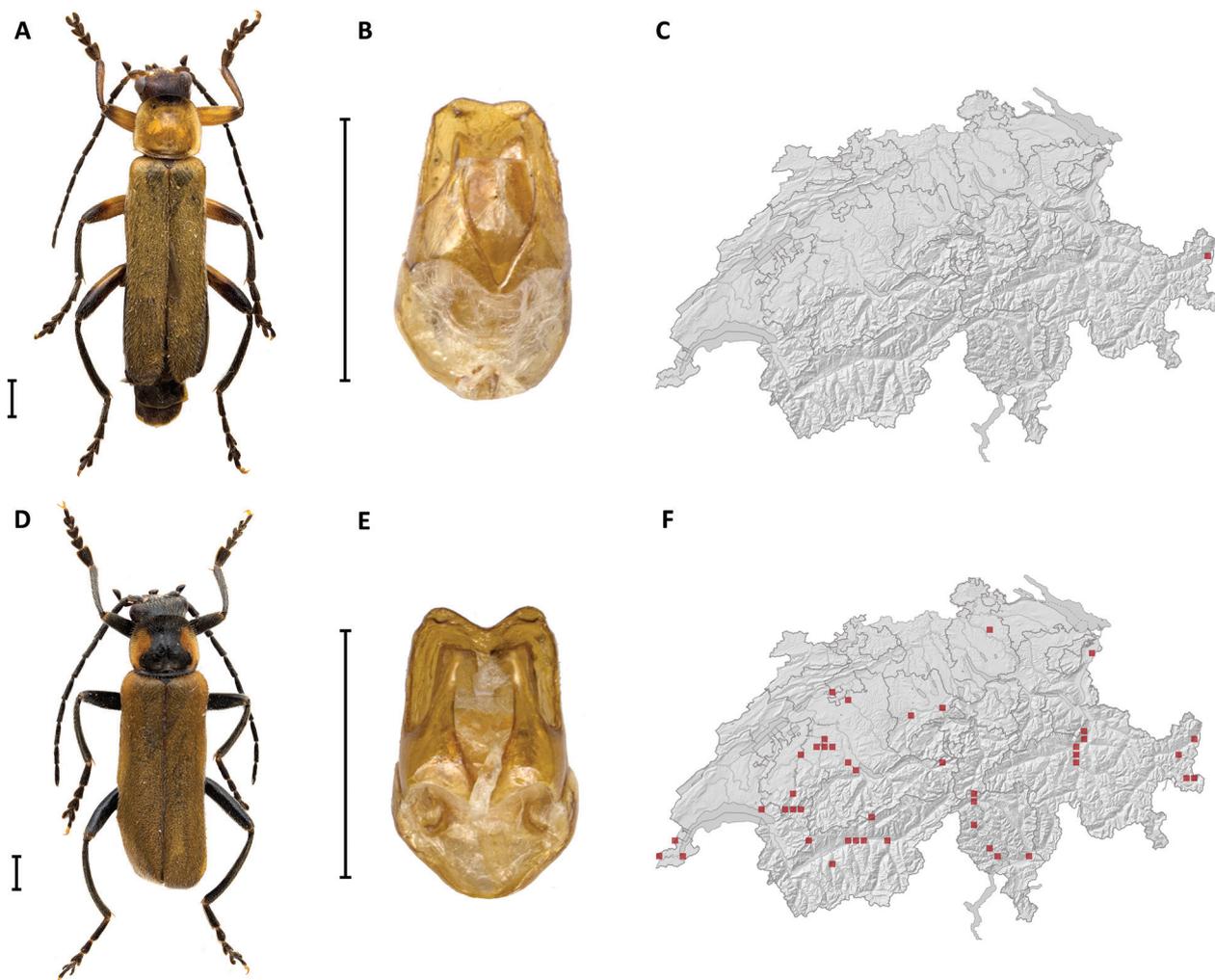
**Comment.** A systematic study of all the males of the *C. quadripunctata*/*C. montana* species complex present in Swiss collections revealed that all of them belong to *C. montana*, based on the shape of their laterophyses (Fig. 1B, E). To our knowledge, only a single specimen (Fig. 1A, B) recently caught in far eastern Grisons confirms the occurrence of *C. quadripunctata* in Switzerland (Fig. 1C), while *C. montana* is not very common, but widespread in various regions of the country (Fig. 1F). *Cantharis quadripunctata* has extremely variable colouration, making it easy to confuse with other species in the field. Bretzendorfer (2017) considered it a rare and endangered species in Baden-Württemberg, but listed several localities in the south of that region close to the Swiss border. Fanti (2014) recorded it from northern Italy. It is therefore likely that *C. quadripunctata* can also be expected in other regions of Switzerland, both in the north and the south of the country.

### C5) *Cantharis (Cyrtomoptila) pagana* Rosenhauer, 1847

**Examined material.** 1 ex. Kt. S. Gallen, Wildhaus, VI.1936, leg. & coll. Linder A., ETH; 1 ex., Bülchen (Olten), 21.VI.1936, leg & coll. Wittmer W., NMB; 1 ex., Meilen, Zch., 30.V.1937, leg & coll. Wittmer W., NMB; 1 ex., Kt. Bern, Uetligen, V.1942, leg. & coll. Linder A., ETH; 1 ex., Sattel SZ, 25.V.1958, leg & coll. Wittmer W., NMB; 1 ex., Villigen AG, 15.VI.1958, leg & coll. Wittmer W., NMB.

**Published data.** There are numerous records across the literature, but due to the difficult identification and recent taxonomic splits within the subgenus *Cyrtomoptila*, they are mostly unusable now, so we are not citing them here.

**Comment.** As pointed out by Constantin (2014), *Cantharis pagana* and *C. fibulata* had been recognised as separate species in much of the older literature until 1974. Then, however, Wittmer (1974) synonymised those two closely related species based on a rather superficial examination of their male genitalia. Švihla (2006) has correctly re-validated *C. fibulata* as a separate species. While Švihla (2006) confirms the presence of *C. fibulata* in Switzerland, he indicates the occurrence of *C. pagana* in Switzerland as in need of confirmation. The dissection of numerous males of this difficult group allows us to confirm the presence of both *C. fibulata* and *C. pagana* in Switzerland, with *C. pagana* being the less common of the two. *C. pagana* is known mainly from the northern part of the country, as a continuation of its range in southwest Germany (Bretzendorfer 2017), while *C. fibulata* is primarily found in the Alps, just like the third species of this group, *C. gemina*.



**Figure 1.** **A)** Habitus, **B)** aedeagus in ventral view, **C)** Swiss distribution of *Cantharis quadripunctata* (illustrated individual from Valsot GR); **D)** habitus, **E)** aedeagus in ventral view, **F)** Swiss distribution of *Cantharis montana* (illustrated individual from Russin GE). Only verified records based on male specimens were included in the distribution maps. Scale bar: 1 mm. (Photos by L. Magnin).

#### C6) *Rhagonycha (Rhagonycha) elongata* (Fallén, 1807)

**Examined material.** 1 ex., Vals, coll. Huguenin G., ETH; 4 ex., Chasseral, 22.VI.1896, coll. Wittmer W., ex coll. Rätzer A., NMB; 1 ex., Chasseral, 12.VI.1899, coll. Rätzer A., NMBE; 1 ex., Kt. Bern, Meinisberg, 2.IV.1939, leg. & coll. Pochon H., MHNF; 3 ex., Kt. Bern, Tramelan, VII.1939, leg. Linder A., ETH & NMB; 1 ex., Il Fuorn, 18.VII.1950, leg. & coll. Handschin E., BNM; 6 ex., Kt. Neuenburg, La Brévine, VI.1963, leg. Linder A., ETH & NMB; 3 ex., B. Finges VS, V.1969, leg. Toumayeff G., MHNG; 3 ex., Jura VD, Le Brassus, VI.1971, leg. Toumayeff G., MHNG; 28 ex., Le Chenit VD, 18.VI.2021, leg. & coll. Chittaro Y.

**Published data.** Several citations exist in the literature prior to Allenspach and Wittmer (1979), but these cannot be regarded as reliable since they were not based on dissected males (see below) and are therefore omitted here.

**Comment.** Even though this species was frequently recorded from Switzerland in the old literature, only a small number of records can be reliably assigned to this species, confirming the presence of a few scattered popu-

lations within the country. After 50 years without a single observation, this species was discovered in great numbers in Switzerland in 2021, by beating blossoming pine trees in a peat bog. For reliable identification, it is important to study the male genitalia, distinguishing it from the closely related *R. atra* and *R. gallica*. A number of older records are therefore uncertain. The published records from Baden-Württemberg all turned out to be wrong (Bretzen-dorfer 2010). The occurrence of this species from northern Italy is indicated as dubious (Fanti 2014) and there are no records from France (Constantin 2014a).

#### C7) [*Rhagonycha (Rhagonycha) femoralis* (Brullé, 1832)]

**Published data.** There are numerous citations in the older Swiss literature, but those were already indicated as wrong by Allenspach and Wittmer (1979) and are therefore not repeated here.

**Comment.** Allenspach and Wittmer (1979) already indicated that the specimens identified as *R. femoralis*

in Swiss collections, as well as all the literature records, refer to *R. improvisa* (currently *R. fuscitibia*), a species described only a few years before by Dahlgren (1976). The « true » *R. femoralis* is a species from Greece and the Balkans, not found in Switzerland.

**C8) *Rhagonycha (Rhagonycha) pedemontana* Baudi di Selve 1872**

**Examined material.** 1 ex., Camoghe, TI, VIII.1963, leg. & coll. Toumayeff G., MHNG; 8 ex., Bellinzona TI, Corneo Gesero, 16.VI.2006, leg. Liberti G., coll. Liberti G. & Chittaro Y.

**Published data.** 1 ex., Wallis, Binntal, 1953, coll. Lindberg, Zoologisches Museum, Helsingfors (Dahlgren 1968).

**Comment.** This species from the southwestern Alps is only known from very few Swiss specimens, a male identified and cited by Dahlgren (1968) and several other specimens collected by G. Toumayff and G. Liberti in Ticino. Constantin (2014a) cites it from the western French Alps, from the Savoie until the Maritime Alps. In Italy, Fanti (2014) cites it exclusively from the North-West (Piedmont and Aosta Valley), where it is rather localised and uncommon. Additional surveying in the Valais, particularly on the south side of the Simplon and in north-western Tessin may yield additional data on this species. *Rhagonycha pedemontana* is closely related to *R. maculicollis*, so the identifications should always be confirmed through examining the male parameres (particularly long and slender in *R. pedemontana*).

**C9) *Malthinus (Malthinus) bilineatus* Kiesenwetter, 1852**

**Examined material.** 1 ex., Chambrelieu, 12.VII.1949, leg. Anonymous, MHNG; 2 ex., Vaud, Buchillon, 30.VI.1951, leg. Besuchet C., MZL; 2 ex., Tessin, Rovio, 29.VII.1973, leg. & coll. Scherler P., NMBE; 1 ex., Vaud, Moiry, 18.VIII.1984, leg. & coll. Scherler P., NMBE; 3 ex., Meride TI, Serpiano, Wald, 21.VII.1995, 21.VII.1996, 11.VIII.1996, leg. Rezbanyai-Reser L., NMLU; 1 ex., Péry BE, 28.VI.–19.VII.2018, leg. & coll. Chittaro Y.

**Published data.** Bois de Chênes, Ferreyres-Moiry, 18.VIII.1984 by Scherler P. (Scherler et al. 1989); <sup>1</sup>Naturschutzgebiet Wildenstein BL, 2000 by Walter Thomas (Walter et al. 2003).

**Comment.** This species was only recorded from two Swiss localities (Buchillon and Rovio) by Allenspach and Wittmer (1979). Since that publication, some additional data allowed us to get a better picture of the distribution of this rare species. It is restricted to the southern Ticino and a few thermophilous localities of the Swiss plateau and the Jura. It is also present in the Centre and South of France (Constantin 2014a), northern Italy (Fanti 2014), but only known from a single record in Germany (Bretzendorfer 2017). The Palaearctic catalogue (Kazantsev and Brancucci 2007) also indicate it as present in Belgium and Luxemburg.

**C10) *Malthinus (Malthinus) rubricollis* Baudi di Selve, 1859**

**Examined material.** 1 ex., Suisse, Genève, Avully, 10.V.1993, leg. Besuchet C., MHNG; 1 ex., Suisse, Genève, Avully, 16.VI.1993, leg. Besuchet C., MHNG; 2 ex., Suisse, Genève, Avully, 29.VI.1994, leg. Besuchet C., MHNG.

**Comment.** This southern European species is known from certain regions of France, most notably around Lyon (Constantin 2014a). The above data from Geneva are therefore a continuation of its range in France. It is rare in Italy and only cited from the centre and the north (Fanti 2014) and from South Tyrol/Alto Adige (Kahlen and Hellrigl 1996), where it is, however, considered extinct. Further, there are also records from Croatia, Bulgaria, Greece, Tunisia and Syria (Kazantsev and Brancucci 2007). The two specimens from Geneva from 1993 were collected “on a pile of dead wood”, while the two specimens from 1994 were collected while sweeping at the same locality.

**C11) *Malthinus (Malthinus) sordidus sordidus* Kiesenwetter, 1871**

**Examined material.** 1 ex., Astano TI, 14.VII.1977, leg. & coll. Scherler P., NMBE; 1 ex., Castel S. Pietro TI, 29.VI.1984, leg. & coll. Scherler P., NMBE; 1 ex., Lugano TI, Mte Brè-Ost, 1.VIII.1984, leg. Rezbanyai-Reser L., NMLU; 1 ex., Meride TI, San Antonio, 21.–30.VII.1991, leg. Rezbanyai-Reser L., NMLU; 2 ex., Meride TI, Serpiano, 1.–10.VII.1995, leg. Rezbanyai-Reser L., NMLU; 1 ex., Vico Morcote TI, 1.VII.2013, leg. & coll. Chittaro Y.; 1 ex., Centovalli TI, 5.–13.VII.2017, leg. Pollini L., coll. Chittaro Y.; 2 ex., Centovalli TI, 20.VI.–4.VII.2018, leg. Pollini L., coll. Chittaro Y.; 1 ex., Losone TI, 5.–20.VI.2018, leg. Pollini L., coll. Chittaro Y.

**Published data.** 13 ex., Bosco di Maia TI, 2002–2004 by WSL (Kopetz and Duelli 2006); 1 ex., Vico Morcote TI, 1.VII.2013 by Chittaro Y. (Chittaro and Sanchez 2017).

**Comment.** Present in a large part of the Italian Peninsula (Fanti 2014), this species has only recently been recorded from Switzerland, in Ticino (Kopetz and Duelli 2006). Since its first mention, the revision of additional museum material and the capture of some additional specimens have provided a more specific understanding of its distribution in the south of that canton. In France, this species is known exclusively from a few localities in the Maritime Alpes and the Var department (Constantin 2014a, c).

**C12) *Malthodes (Malthodes) aemulus* Kiesenwetter, 1861**

**Examined material.** 1 ex., Dalpe TI, 17.VI.–2.VII.1957, leg. Allenspach V., coll. Wittmer W., NMB; 3 ex., Valais, Laquintal, 26.VII.1963, leg. & coll. Scherler P., NMBE; 2 ex., Alpjen s. Gondo VS, VII.1971, leg. Toumayeff G., NMB & MHNG; 1 ex., Laggintal VS, VII.1971, leg.

Toumayeff G., MHNG; 1 ex., A. di Neggia TI, VII.1971, leg. Toumayeff G., MHNG; 4 ex., Tessin, S. Carlo (V. Bavona), 13.VII.1975, leg. Besuchet C., NMB & MHNG; 8 ex., Tessin, Mte. Boglia, 14.VII.1978, leg. & coll. Scherler P., NMBE; 1 ex., Laggintal VS, VII.1979, leg. Toumayeff G., coll. Wittmer W., NMB; 1 ex., Tessin, Brè, 11.VII.1980, leg. & coll. Scherler P., NMBE; 10 ex., Tessin, Mte Lema, 17.VII.1980, leg. Scherler P., coll. Wittmer W., NMB & NMBE; 5 ex., Tessin, Pne. di Breno, 17.VII.1980, leg. Scherler P., coll. Wittmer W., NMB & NMBE; 6 ex., Tessin, Mte. Gambarogno, 23.VII.1980, leg. & coll. Scherler P., NMBE; 1 ex., Mte. Boglia TI, 14.VI.1982, leg. & coll. Scherler P., NMBE; 1 ex., s. Vergeletto TI, 22.VII.1983, leg. & coll. Scherler P., NMBE; 4 ex., Grisons, Bregaglia, V. Bondasca, 19.VII.1984, leg. Besuchet C., MHNG & leg. & coll. Scherler P., NMBE; 13 ex., Tessin, Alpe Brogoldone, s/Claro, 17.VII.1990, leg. Besuchet C., MHNG; 3 ex., Molinera TI, 19.VII.1990, leg. & coll. Scherler P., NMBE; 1 ex., Ticino, Sigirino, Alpe Cusello, VII.1993, leg. & coll. Focarile A., MSNL; 2 ex., Simplon VS, 30.VI.2018, leg. & coll. Chittaro Y.; 2 ex., Zwischbergen VS, 1.VII.2018, leg. & coll. Chittaro Y.

**Published data.** <sup>1,7)</sup>Mt-Rose by Stierlin G. (Favre 1890); Ticino, Brissago and Sigirino by Focarile A., Ticino, Cari, 2003 by Liberti G. (Liberti 2011).

**Comment.** *Malthodes aemulus* inhabits the French Alps (the Maritime Alps until the Savoie, according to Constantin 2014a), as well as the Alps of Italy (Liberti 2011, 2015, Kahlen and Hellrigl 1996) and Switzerland. In Switzerland, it is limited to the southern slope of the Alps (South of Simplon in Valais, Tessin, South of Grisons).

### C13) *Malthodes (Malthodes) bertolinii* Fiori, 1905

**Examined material.** 1 ex., Tessin, Generoso, Cragno, 4.VI.1969, leg. Besuchet C., MHNG; 1 ex., Tessin, Bruzella, 15.VII.1977, leg. & coll. Scherler P., NMBE; 1 ex., Tessin, Muggio, 22.VII.1980, leg. & coll. Scherler P., NMBE; 8 ex., Mt. Generoso TI, Bellavista, several dates between 1.VII.1982–1.VIII.1984, leg. Rezbanyai-Reser L., NMLU; 10 ex., Lugano TI, Mte Brè-Vetta, several dates between 21.VI.–20.VII.1983, leg. Rezbanyai-Reser L., NMLU; 1 ex., Riva S. Vitale TI, 4.VII.1984, leg. & coll. Scherler P., NMBE; 4 ex., Ticino, Tesserete, Gola di Lago, VI.1985, leg. & coll. Focarile A., MSNL; 11 ex., Casima TI, Südrand, several dates between 1.–30.VII.1988, leg. Rezbanyai-Reser L., NMLU; 6 ex., Lugano TI, Mte Brè-Ost, several dates between 11.VII.1984–10.VII.1986, leg. Rezbanyai-Reser L., NMLU; 10 ex., Somazzo TI, Torreta-O., several dates between 1.VII.1985–30.VII.1987, leg. Rezbanyai-Reser L., NMLU; 1 ex., s. Capolago TI, 5.VII.1986, leg. & coll. Scherler P., NMBE; 11 ex., Meride TI, San Antonio, several dates between 1.VII.1989–20.VII.1991, leg. Rezbanyai-Reser L., NMLU; 3 ex., Castel S. Pietro TI, Obino, Waldrand, several dates between 1.VII.1991–20.VI.1993, leg. Rezbanyai-Reser L., NMLU; 6 ex., Cragno TI, Pree, several dates between 11.VII.1994–20.VII.1996, leg. Rezbanyai-Reser L., NMLU; 1 ex., Mt.

Generoso TI, Bellavista-Ost, 12.VII.1994, leg. Rezbanyai-Reser L., NMLU; 1 ex., Gandria TI, Scapi, 21.–30.VI.1991, leg. Rezbanyai-Reser L., NMLU.

**Published data.** Tessin, Generoso-Cragno, 4.VI.1969, leg. Besuchet C., MHNG (Wittmer 1971).

**Comment.** This is a species from the central and south-eastern Alps, only known from Italy (Kahlen and Hellrigl 1996, Fanti 2014, Liberti 2015) and Switzerland, where it is recorded exclusively from Ticino. The majority of the Swiss records have been made by L. Rezbanyai-Reser, using light traps. In some localities, this species co-occurs with its close relatives *M. alpicola* and *M. guttifer*.

### C14) [*Malthodes (Malthodes) bifurcatus* Kiesenwetter, 1852]

**Published data.** <sup>1,8)</sup>1 ex., Sièrene GE [Sierne], MHNG (Allenspach and Wittmer 1979).

**Comment.** According to Allenspach and Wittmer (1979), there was a specimen of this species at MHNG. While there is a label and space dedicated to this species in the MHNG collection, no specimen was found there. The specimen cited by Allenspach and Wittmer (1979) probably turned out to be misidentified and has been moved to another species in the collection by V. Švihla in the years after 2000. Strangely, the only specimens from the same locality (Sierne) found at MHNG are all *M. spretus*. There may have been a confusion with that species. In any case, as already noted by Allenspach and Wittmer (1979), this species does not belong to the Swiss fauna, being endemic to Sicily (Fanti 2014) and Malta (Švihla and Mifsud 2006, Fanti 2014).

### C15) [*Malthodes (Malthodes) boicus* Kiesenwetter, 1863]

**Published data.** <sup>2)</sup>1 ex., Meride TI, 30.VI.1983, <sup>2)</sup>1 ex., Rancate TI, 30.VI.1983 and <sup>2)</sup>2 ex., Riva San Vitale TI, 4.VII.1984 by Scherler P. (Scherler 1986).

**Comment.** For Switzerland, this species is only cited from three localities in Ticino by Scherler (1986). We were able to revise those specimens in Scherler's collection and all of them turned out to be misidentified *M. umbrosus*. Before the publication of detailed illustrations by Liberti (2016), it was easy to mistake *M. umbrosus* for *M. boicus*. Kahlen and Hellrigl (1996) and Liberti (2016) cite *M. boicus* from Italy, but only from a few localities in the north-east, far from the Swiss border. *Malthodes boicus* is also cited from Austria and a few localities in Germany, from Bavaria to Baden-Württemberg (Bretzendorfer 2017).

### C16) *Malthodes (Malthodes) caudatus* J. Weise, 1892

**Examined material.** 3 ex., Cheville VD, coll. Bugnion E., NMB & MZL; 1 ex., Generoso, 27.VII., leg. Anonymous, MHNG; 1 ex., Pont de Nant, 14.VII.1940, leg. Demole W., MHNG; 1 ex., Tessin, Generoso, 12.VII.1961, leg. & coll. Scherler P., NMBE; 1 ex., Trogen, 7.VII.1963, leg.

Spälti A., MHNG; 1 ex., Les Haudères VS, 6.VIII.1980, leg. & coll. Scherler P., NMBE; 1 ex., Suisse, BE, Lenk, Hahnenmoos, VII.1983, leg. Toumayeff G., MHNG; 1 ex., CH, TI, Mt. Generoso, Vetta, Wald, 13.VII.1990, leg. Rezbanyai-Reser L., NMLU; 3 ex., CH, LU, Romoos, Neumatt, 21.-30.VI.1991, leg. Rezbanyai-Reser L., NMLU; 1 ex., CH, LU, Romoos, Neumatt, 1.-10.VI.1993, leg. Rezbanyai-Reser L., NMLU; 1 ex., Oberems VS, 4.VII.2013, leg. & coll. Chittaro Y.; 1 ex., Zermatt VS, 2.VII.2019, leg. & coll. Chittaro Y.

**Published data.** 2 ex., Waadt, Cheville (Pas de Cheville, Diablerets), coll. Bugnion E. and <sup>1</sup>1 ex., Saxon, Erzgebirge, coll. Wittmer W., ex coll. Hicker R. (Wittmer 1970, 1971); <sup>1</sup>Scatlè [Breil/Brigels GR], 2013 by Huber B. (Huber and Büche 2014); 3 ex., Romoos, Neumatt, 21.-30.VI.1991 and 1 ex., 1.-10.VI.1992 (Herger and Germann 2015).

**Comment.** Liberti (2015) considers this as a rare species from the Alps, present from France (where it was only recently recorded by Constantin 2014c) until the Czech Republic and Slovenia (Drovenik 2001). While also quite rare in Switzerland, there are scattered records from various parts of the Swiss Alps.

#### C17) *Malthodes (Malthodes) crassicornis* (Maeklin, 1846)

**Examined material.** <sup>3,4,6</sup>1 ex., Helvetia, leg. Anonymous, NMB; 1 ex., T. [Chiasso, Tannino], 7.VI.1930, coll. Fontana P., MSNL.

**Published data.** <sup>1</sup>“Schweiz” by K. (Breimi-Wolf 1856); <sup>1</sup>Genf by Tournier H. and <sup>1</sup>Schaffhausen by Stierlin G. (Stierlin and Gautard 1867); <sup>1</sup>Valais by Stierlin G. (Favre 1890); <sup>1</sup>Schweiz, leg. Rey, nach Kiesenwetter (1860) (Horion 1953).

**Comment.** All Swiss literature records of this species are very old and not verifiable, while the data of the old specimen deposited at NMB are too imprecise to be retained. The only more or less reliable record of this species in Switzerland is based on a specimen collected by P. Fontana in southern Ticino, in 1930, now deposited at MSNL (Fig. 2A–C). This specimen had already been seen by Wittmer, and we were now able to extract its aedeagus to confirm its identity beyond any doubt. The data labels in P. Fontana’s collection can generally be regarded as reliable, so we are, at least provisionally, retaining this species on the Swiss list based on this single specimen. In a larger biogeographical context, the present record close to the Italian border is quite interesting, after all the records from Italy were considered doubtful and « pending confirmation » by Fanti (2014) and Liberti (2015). Though generally rare, this species from northern and central Europe is nonetheless known from south-western Germany, where Bretzendorfer (2017) even listed some recent verified records. It is therefore possible that *M. crassicornis* also occurs in the North of Switzerland. It would be important to confirm the occurrence of *M. crassicornis* in Switzerland through additional surveys in the future.

#### C18) *Malthodes (Malthodes) debilis debilis* Kiesenwetter, 1852

**Examined material.** 4 ex., Suisse, Tessin, Magadino, 16.VII.1969, leg. Scherler P., MHNG & leg. & coll. Scherler P., NMBE; 3 ex., Suisse, Tessin, Magadino, 30.VII.1974, leg. Scherler P., MHNG & leg. & coll. Scherler P., NMBE; 1 ex., CH, LU, Romoos, Neumatt, 11.-20.VII.1992, leg. Rezbanyai-Reser L., NMLU.

**Published data.** <sup>1</sup>1 ex., Schaffhausen, DEI (Horion 1953); Magadino, 16.VII.1969 by Scherler P. (Wittmer 1971); <sup>1</sup>Val Bavona, 2003 by Focarile A. (Focarile 2003); 1 ex., Romoos, Neumatt, 11.-20.VII.1992 (Herger and Germann 2015).

**Comment.** Only a very small number of specimens from two localities confirm the occurrence of this species in Switzerland, where it appears to be rare. With more research in the future, it may well be discovered in other parts of Switzerland. Widely distributed within the Palearctic Region, it is known from all the regions adjacent to Switzerland: Ain in France (Constantin 2014a); Baden in Germany (Bretzendorfer 2017); Vorarlberg in Austria (Brandstetter and Kapp 1998); northern Italy (Liberti 2015). With the assistance of Gianfranco Liberti, we were able to confirm that the taxon that occurs in Switzerland is the nominal subspecies and not the recently described subspecies *pedemontanus* Liberti, 2018. This taxon differs from the nominotypical form in the structure of the aedeagus and is known from a handful of specimens from Piedmont, Liguria, the northwestern Apennines and a single specimen from Calabria (Liberti and Poggi 2018).

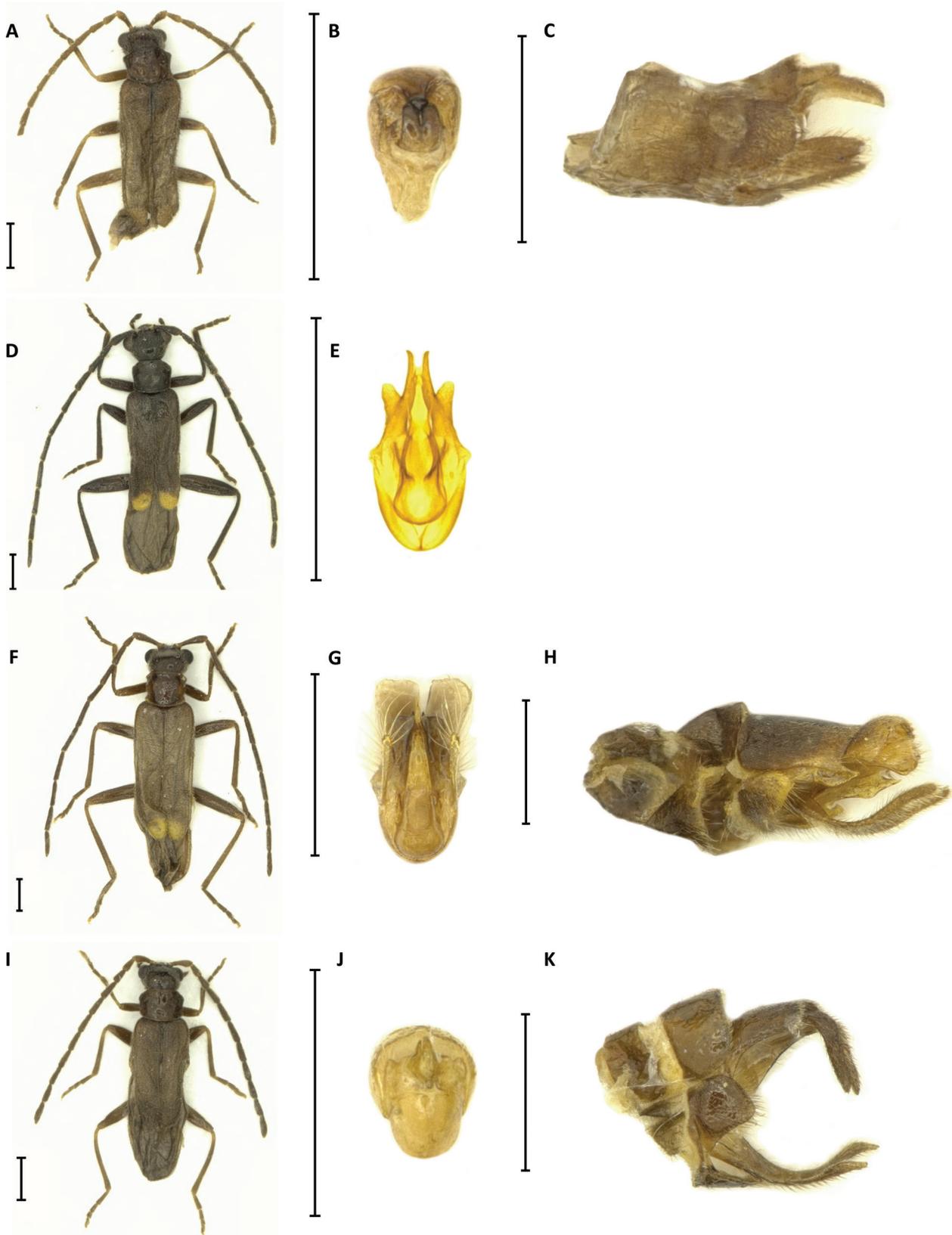
#### C19) [*Malthodes (Malthodes) dimidiaticollis dimidiaticollis* (Rosenhauer, 1847)]

**Published data.** <sup>1</sup>“Schweiz” (Breimi-Wolf 1856).

**Comment.** This species was included in the checklist of Swiss Coleoptera by Breimi-Wolf (1856) under the now synonymous name *Malthodes pulicarius* (Redtenbacher, 1849). Known from Central Europe and even from Turkey, Lebanon, Israel, Jordan and Kazakhstan, the species could not be confirmed for Italy (Fanti 2014), and the records from Germany are also dubious or at least very old (Köhler and Klausnitzer 1998). For Switzerland, only this single, old and imprecise literature citation is available. We therefore advise the removal of this species from the list of the Swiss fauna.

#### C20) *Malthodes (Malthodes) facetus* Kiesenwetter, 1863

**Examined material.** 1 ex., Bruzella TI, 15.VII.1977, leg. & coll. Scherler P., NMBE; 1 ex., Mte. San Giorgio TI, 10.VII.1978, leg. & coll. Scherler P., NMBE; 1 ex., Tessin, Besazio, 18.VII.1980, leg. & coll. Scherler P., NMBE; 9 ex., Suisse, Tessin, Mte San Giorgio, 14.VII.1980, leg. Scherler P., MHNG & leg. & coll. Scherler P., NMBE; 3 ex., Suisse, Tessin, Muggio,



**Figure 2.** A) Habitus, B) aedeagus (dorsal view) and C) last abdominal segments (lateral view) of *Malthodes crassicornis* (Tannino, Chiasso); D) habitus and E) aedeagus (dorsal view) of *Malthodes kahleni* (Hasle, Entlebuch) (last abdominal segments damaged); F) habitus, G) aedeagus (dorsal view) and H) last abdominal segments (lateral view) of *Malthodes stolzi* (Bruzella); I) habitus, J) aedeagus (dorsal view) and K) last abdominal segments (lateral view) of *Malthodes umbrosus* (Riva S. Vitale). Scale bar: 0.5 mm. (Photos by Y. Chittaro).

22.VII.1980, leg. Scherler P., MHNG & leg. & coll. Scherler P., NMBE; 3 ex., Suisse, Tessin, Bruzzela, 26.VII.1980, leg. Scherler P., MHNG & leg. & coll. Scherler P., NMBE; 4 ex., Meride TI, 15.VI.1982, leg. & coll. Scherler P., NMBE; 3 ex., s. Capolago TI, 23.VI.1983, leg. & coll. Scherler P., NMBE; 4 ex., Meride TI, 30.VI.1983, leg. & coll. Scherler P., NMBE; 1 ex., Castel S. Pietro TI, 29.VI.1984, leg. & coll. Scherler P., NMBE; <sup>8</sup>1 ex., Berne, Jochpass, 28.VII.1986, leg. & coll. Scherler P., NMBE; 2 ex., Arzo TI, 13.VI.1990, leg. & coll. Scherler P., NMBE; 1 ex., Melano TI, 19.VI.2019, leg. Guidotti G., coll. Chittaro Y.

**Published data.** 1 ex., Bruzella, 15.VII.1977, 1 ex., Monte San Giorgio, 10.VII.1978, 8 ex., Monte San Giorgio, 14.VII.1980, 2 ex., Besazio, 18.VII.1980, 2 ex., Muggio, 22.VII.1980 and 2 ex., Bruzella, 26.VII.1980 by Scherler P. (Scherler 1981).

**Comment.** Reported as new to Switzerland by Scherler (1981), based on several records from Ticino, this species also exists in the southeast of France (Var, Alpes-Maritimes, Alpes-de-Haute-Provence, see Constantin 2014a), as well as northern and central-western Italy (Liberti 2011, 2015). After its discovery in Switzerland, several more yet unpublished records from southern Ticino, mainly made by Pierre Scherler, have helped to provide more detail about its distribution within the country. Considering its overall distribution, we strongly suspect that the single specimen labelled as coming from North of the Alps (Jochpass, Bern) is mislabelled.

#### C21) *Malthodes (Malthodes) fibulatus* Kiesenwetter, 1852

**Examined material.** 1 ex., Zürich Umgb., Killwangen, 22.V.1941, leg. Wolf J.-P., MHNG; 2 ex., Waldegg ZH, 29.IV.1943, leg. & coll. Allenspach V., NMB; 1 ex., Schaffhausen SH, 10.V.2020, leg. Kessler D., coll. Chittaro Y.

**Published data.** <sup>2</sup>Strada, S., 23.V.1961 by Handschin E. (Handschin 1963); <sup>1</sup>Schaffhausen, coll. Stierlin G., DEI, <sup>2</sup>Yvonand VD, 16.V.1952, leg. Besuchet C., MZL; <sup>2</sup>Sierre, coll. Bugnion E., MZL and Waldegg ZH, 29.IV.1948, leg. Allenspach V. (Wittmer 1970); <sup>1</sup>1 ex., Mt. Jorat VD, MZL (Allenspach and Wittmer 1979); <sup>2</sup>1 ex., Romoos, Neumatt, 11.–20.VI.1992 (Herger and Germann 2015).

**Comment.** This species is found in almost all of Europe, from Scandinavia to Italy and from France to Poland (Liberti 2015). A few scattered data confirm its presence in Switzerland, where it seems to be scarce. Some of the citations of this species in the Swiss literature have however turned out to be based on misidentified specimens (the specimen from Romoos LU turned out to belong to *M. maurus*, the one from Strada GR is *M. misellus*, the one from Sierre VS is *M. europaeus*).

#### C22) *Malthodes (Malthodes) holdhausi* Kaszab, 1955

**Examined material.** 2 ex., Schweiz, AG, Untersiggenthal, Iflue, 21.V.1998, leg. Walter T., MHNG & NMB; 4 ex., Schaffhausen SH, 7.V.2009, 7.VI.2009, leg. & coll.

Pankow W.; 1 ex., Schaffhausen SH, 13.V.2009, leg. & coll. Pankow W.

**Published data.** 5 ex., Untersiggenthal, 21.V.1998 by Walter T. & Weber P. (Walter and Weber 1999).

**Comment.** Only recently recorded from Switzerland from a single locality in the canton of Aargau (Walter and Weber 1999), this species was later found in the canton of Schaffhausen, from where F. Bretzendorfer identified a number of specimens collected by W. Pankow. Most likely, this species is only present in the northern part of the country. It is also known from the South-West of Germany (Bretzendorfer 2017), Austria, Czech Republic, Hungary, Romania and Slovakia (Kazantsev and Brancucci 2007).

#### C23) *Malthodes (Malthodes) icaricus* Wittmer, 1940

**Examined material.** 1 ex., Terre di Pedemonte TI, Cavigliano, 21.IV.2015, leg. & coll. Chittaro Y.

**Published data.** <sup>2</sup>Berninapass, 6.VIII.1896, Albulapass, 30.VII.1908 (Wittmer 1970, 1971); <sup>2</sup>Hohtälli, 12.VIII.1982 by Besuchet C. (Besuchet 1983).

**Comment.** *M. icaricus* was only recently elevated to full species rank by Liberti (2015), having been treated as a subspecies of *M. penninus* before. The entirety of the specimens found identified in collections (mainly by W. Wittmer) as *M. penninus icaricus* turned out to in fact belong to the high-altitude morph of *M. penninus* (after Liberti 2015) after closer scrutiny. At this moment, only a single specimen collected in Ticino at Cavigliano in 2015 can be attributed to *M. icaricus*, confirmed by G. Liberti. The specimen was collected in a flight intercept trap at an altitude of 600 m. There are also records from Austria and several parts of Italy: Prealps of Piedmont, Lombardy and Trentino (Liberti 2015) and South Tyrol / Alto Adige (Kahlen and Hellrigl 1996).

#### C24) *Malthodes (Malthodes) kahleni* Wittmer, 1982

**Examined material.** 1 ex., Hasle im Entlebuch, Entlen-Ufer, 20.VII.1990, leg. Kiener S., NMBE.

**Published data.** 1 ex., Hasle im Entlebuch, 20.VI.1990 by Kiener S. (Kiener 1995).

**Comment.** The type locality of this species, described by Wittmer (1982) is Stams in Tyrol, Austria. Liberti (2016) indicates that this could be a very rare relict species, distributed across a vast area including at least Central Europe, the East Alps and the Pyrenees. It was only recently recorded from Italy, from Amaro in Udine province (Kahlen 2010). Liberti (2016) also cites localities in Czech Republic and Spain, while Kazantsev and Brancucci (2007) also list it from Austria and Slovakia. This species is also present in Switzerland: one specimen (Fig. 2D, E), from the canton of Lucerne, was collected by S. Kiener in 1990 and identified by W. Wittmer. Kiener (1995) simply indicated that his specimen was found in an “Auengebiet” (riparian woodland), same as the type material, which led him to suppose that this species may be restricted to that kind of habitat.

**C25) [*Malthodes (Malthodes) montanus* Kiesenwetter, 1863]**

**Published data.** <sup>2</sup>Saas-Almagell, VII.1942 by Lautner J.; <sup>2</sup>Schuls, VI.1938 by Toumayeff G. (Linder 1968); <sup>1</sup>Scuol, Innufer, 31.V.1953 by Handschin E. (Handschin 1963); <sup>1</sup>Jonschwil, Lee, am Tümpel, VII.1960 by Hugentobler H. (Hugentobler 1966); <sup>2</sup>Poschiavo [Val Poschiavo] by Jörger J.B. (Linder 1967); <sup>2</sup>Bissone, Lugano by Lautner J. and <sup>2</sup>8 ex., Büren a/Aare BE, VI.1894, NMBE (Allenspach and Wittmer 1979); <sup>2</sup>1 ex., Romoos, Neumatt, 1.-10.VI.1993 (Herger and Germann 2015).

**Comment.** Liberti (2016) treats this as a species limited to the eastern Alps, from north-eastern Italy to Austria and Slovenia. It is also recorded from Germany (Bavaria and Weser-Ems region, historically also from Nordrhein, according to Köhler and Klausnitzer 1998), Belgium and Hungary (Kazantsev and Brancucci 2007). For Switzerland, all of the literature citations turned out to be misidentifications (confusions with *M. spathifer* in case of the specimens from Schuls and Büren, with *M. cyphonurus* for those from Poschiavo and Bissone and with *M. hexacanthus* for that from Romoos), after the study of the relevant material. Based on the currently available data, this species does not occur in Switzerland.

**C26) *Malthodes (Malthodes) penninus raeticus* Wittmer, 1970**

**Examined material.** 2 ex., Vals, VIII.1909, leg. Jörger J.B., coll. Wittmer W., NMB.

**Published data.** Vals, Graubünden, 31.VIII.1909, ex coll. Jörger J.B., holotype and paratype NMB (Wittmer 1970, 1971).

**Comment.** This subspecies of *M. penninus* is hitherto only known from the holotype and a single paratype, both collected by Jörger J.B. in Vals, in the canton of Grisons. Its taxonomic status needs to be critically examined.

**C27) *Malthodes (Malthodes) siculus* Kiesenwetter, 1852**

**Examined material.** 1 ex., Vaud, Prangins, 17.V.1956, leg. Besuchet C., MZL; 2 ex., Buchillon VD, 21.V.1956, leg. Besuchet C., NMB & MHNG; 3 ex., Suisse, Vaud, Buchillon, 29.5.1956, leg. Besuchet C., MZL; 1 ex., Vaud, La Sarraz, 19.V.1968, leg. & coll. Scherler P., NMBE; 1 ex., Eclépens VD, V.1972, leg. Toumayeff G., MHNG; 1 ex., Vaud, Bretonnières, 14.V.1972, leg. & coll. Scherler P., NMBE; 4 ex., Suisse, Vaud, Mormont, 14.V.1972, leg. Scherler P., MHNG & leg. & coll. Scherler P., NMBE; 1 ex., Vaud, Pompaples, 22.V.1976, leg. & coll. Scherler P., NMBE; 4 ex., Vaud, Moiry, 30.V.1982, leg. & coll. Scherler P., NMBE; 4 ex., Vaud, s. L'Isle, 29.V.1983, leg. & coll. Scherler P., NMBE; 1 ex., Vaud, Moiry, moitié NO de la réserve à partir de la route Moiry-Envy, 11.VII.1985, leg. Scherler P., MZL; 4 ex., Vaud, Ferreyres, 25.V.1986, leg. & coll. Scherler P., NMBE; 4 ex.,

Orny VD, V.1989, leg. Toumayeff G., MHNG; 1 ex., La Sarraz VD, 9.V.2017, leg. & coll. Chittaro Y.

**Published data.** Buchillon (Vaud), 29.V.1956 by Besuchet C. and La Sarraz (Vaud), 19.V.1968 by Scherler P. (Wittmer 1970, 1971); Bois de Chênes, Ferreyres-Moiry, 25.V.1985, 11.VII.1985 by Scherler P. (Scherler et al. 1989).

**Comment.** This species is widely distributed in Italy, most notably in the Centre and South of the country (Fanti 2014, Liberti 2015), but also present in a few localities in France (Constantin 2014a), as well as western Switzerland.

**C28) *Malthodes (Malthodes) stolzi* Hicker, 1915**

**Examined material.** 1 ex., Tessin, Bruzella, 26.7.1980, leg. & coll. Scherler P., NMBE.

**Published data.** 1 ex., Bruzella, 26.7.1980 by Scherler P. (Scherler 1981).

**Comment.** This species was recorded as new to Switzerland by Scherler (1981), based on a single specimen (Fig. 2F–H) from the Val Muggio, Ticino, which was verified by W. Wittmer. We were able to find the respective voucher specimen in Scherler's collection and confirm its identity. *M. stolzi* has been considered a rare endemic of the Bergamasque Prealps, only known from a small area on the southern slope of Mt. Menna, near Oltre il Colle (Fanti 2014, Liberti 2015). The single known Swiss locality in southern Ticino, 50 km apart from the type locality, therefore considerably extends the known range of this species. Scherler (1981) indicated that the Swiss locality lies at 700 m altitude and that it was collected « in a sparse chestnut woodland with grassy and bushy undergrowth ».

**C29) *Malthodes (Malthodes) umbrosus* Kiesenwetter, 1871**

**Examined material.** 2 ex., Meride TI, 30.VI.1983, leg. & coll. Scherler P., NMBE; 1 ex., Rancate TI, 30.VI.1983, leg. & coll. Scherler P., NMBE; 3 ex., Suisse, TI, Riva San Vitale, 4.VII.1984, leg. Scherler P., MHNG & leg. & coll. Scherler P., NMBE; 1 ex., Suisse, Tessin, Lago d'Origlio, 24.VI.1987, leg. Besuchet C., MHNG; 3 ex., Meride TI, San Antonio, 11.–20.VII.1991, leg. Reser L., NMLU.

**Comment.** Some specimens from southern Ticino allow us to record this species as new to Switzerland here. The three specimens from 1991 were collected at a light trap, while those from 1987 were found « under bark of an alder trunk ». The specimens from 1983 and 1984 (Fig. 2I–K) were erroneously recorded as *M. boicus* by Scherler (1986), but turned out to belong to *M. umbrosus*.

**C30) *Malthodes (Malthodes) vincens* Gredler, 1870**

**Examined material.** 1 ex., CH, TI, Mte Generoso, Bellavista, IX.1982, leg. Rezbanyai-Reser L., MHNG; 2 ex., Mt. Generoso TI, Bellavista, 1.–10.IX.1982, leg. Rezbanyai-Reser L., NMLU; 1 ex., Mt. Generoso TI, Bellavista, 1.–10.IX.1983, leg. Rezbanyai-Reser L., NMLU;

2 ex., Mt. Generoso TI, Bellavista, 21.–30.IX.1983, leg. Rezbanyai-Reser L., NMLU; 1 ex., Mt. Generoso TI, Bellavista, 21.–30.IX.1984, leg. Rezbanyai-Reser L., NMLU; 1 ex., Cragno TI, Pree [Salorino], 1.–10.X.1995, leg. Rezbanyai-Reser L., NMLU; 1 ex., Cragno TI, Pree [Salorino], 11.–20.X.1995, leg. Rezbanyai-Reser L., NMLU; 2 ex., Meride, Serpiano TI, Wald, 1.–10.X.1995, leg. Rezbanyai-Reser L., NMLU; 1 ex., CH, TI, Mte Generoso, Valle d. Giascia, Zoca, 2.X.1995, leg. Rezbanyai-Reser L., MHNG; 1 ex., Cragno TI, Pree [Salorino], 1.–10.X.1996, leg. Rezbanyai-Reser L., NMLU; 1 ex., Meride, Serpiano TI, Wald, 11.–20.IX.1997, leg. Rezbanyai-Reser L., NMLU.

**Published data.** 2 ex., Brusio Arsizio, Serpiano, 1.–10.X.1995 and 1 ex., 11.–20.IX.1997 (Herger et al. 2015).

**Comment.** This phenologically late species has a scattered distribution across the central and eastern Italian Alps and into Austria and Slovenia (Kahlen and Hellrigl 1996, Liberti 2016), as well as the Swiss canton Ticino. The closely related sister species *M. fiorii* Ganglbauer, 1906 replaces *M. vincens* in Liguria and the Maritime Alps (Liberti 2016). This species was firstly recorded from Switzerland by Herger et al. (2015), based on specimens collected in a light trap and deposited at NMLU. Here, we can add a few more records collected earlier, based on specimens at MHNG and NMLU. All of the specimens were collected by the lepidopterist L. Rezbanyai-Reser at light traps.

### C31) [*Autosilis nitidula* (Fabricius, 1792)]

**Examined material.** <sup>3,4,6</sup>2 ex., Schweiz, leg. Anonymous, NMB; <sup>3,4,7</sup>1 ex., Suisse, Macugnaga [IT] coll. Maerky C., MHNG.

**Published data.** <sup>1</sup>“Schweiz” by Stierlin G. (Bremi-Wolf 1856); <sup>1,7</sup>Macugnaga by Stabile G. (Stierlin and Gautard 1867).

**Comment.** The data available to us are insufficient to retain this species as part of the Swiss fauna. Only two specimens, labelled simply “Schweiz” [Switzerland], without precise localities, exist in Swiss collections. Regarding the record from “Macugnaga”, a locality also cited in the Swiss literature, we have to point out that this is located in Italy, close to the Swiss border, but not in Switzerland! Additionally, the label data in the collection to which those specimens belong to (coll. C. Maerky) have often proven to be unreliable (Monnerat et al. 2015). Despite being widely distributed in central, northern and eastern Europe, including parts of Italy (Monte Rosa area and Carnian Alps, according to Fanti 2014), this species doesn’t appear (yet) to be part of the Swiss fauna.

## Discussion

This commented list on the Swiss Cantharidae and Lycidae is in keeping with other syntheses on various beetle families published in the past years (see for example Chittaro and Sanchez 2019a, b; Sanchez et al. 2020). It thus improves the overall understanding of Swiss fauna.

Thanks to the distribution maps based on the collected data (available on the info fauna – CSCF cartographic server, www.cscf.ch), this work provides a thorough faunistic overview of the current understanding of the species of Cantharidae and Lycidae.

Cantharidae (100) and Lycidae (6) are represented by 106 species in Switzerland. Compared to the previous national list (Allenspach and Wittmer 1979), several species have been added (*Cantharis fibulata*, *C. liburnica*, *C. paradoxa*, *Malthinus rubricollis*, *M. sordidus*, *Malthodes facetus*, *M. holdhausi*, *M. kahleni*, *M. stolzi*, *M. umbrosus*, *M. vincens*, *Rhagonycha pedemontana*), while one has been removed (*Malthodes montanus*). Another species recorded later on by Scherler (1986), *M. boicus*, has also been deleted from the Swiss checklist. The species added since Allenspach and Wittmer (1979) were mostly possible thanks to more intense surveying that led to the discovery of more taxa, although in a few cases they were the result of species being “split”, i.e. taxa that were initially understood to be single species were later recognised as a group of cryptic species (e.g. Švihla 2006). Additionally, we are now able to provide additional data for some species only known from a small handful of data points at the time of Allenspach and Wittmer (1979), e.g. *Malthodes bertolinii* and *M. setifer*, thanks to numerous surveys conducted during the past 40 years.

While our knowledge on the distribution of Cantharidae and Lycidae in Switzerland is based on a solid foundation of data and can be considered solid, at least compared to other countries, there are nevertheless a number of species in urgent need of additional documentation. This is particularly the case for some *Malthodes*, *Malthinus* and *Rhagonycha*, where reliable identifications are only possible through the examination of the male terminalia, while the females are often impossible to identify with any certainty.

Targeted sampling of certain species or species groups in the future, while systematically extracting the genitalia of those specimens where necessary, is still likely to add some new discoveries to our fauna, as exemplified by the new country records of *Cantharis paradoxa* and *Malthodes umbrosus* in the present paper. Several species present in areas adjacent to Switzerland could be added in the future, most notable in the Ticino. For example, *Malthodes tetraglyphis* Hicker, 1953 and *M. caudatomimicus* Wittmer, 1970 are present in northern Italy not far from the Swiss border (Liberti 2015). *Ancistronycha occipitalis*, present in southwestern Germany (Bretzen-dorfer 2017), could easily also occur in northern Switzerland. It is also not impossible that there could be undescribed cryptic species or subspecies currently mixed up with known Swiss species. Hendrich et al. (2015) showed the existence of multiple distinct genetic lineages within what is currently considered a single species of Cantharidae (in *Cantharis terminata*, *C. tristis* and *Malthodes mysticus*), based on their study on mitochondrial DNA. The above paper also managed to confirm that many closely related cantharid species, distinguished only by

their genitalia and currently indistinguishable by external characters, are indeed genetically separate species. As for Lycidae, *Benibotarus taygetanus* Pic, 1905 is a species which could be discovered in Switzerland in the future, being present in Alsace (Callot 2001, Callot et al. 2010).

While adult cantharids are rather easily encountered when sweeping herbaceous vegetation, beating trees and shrubs, or searching on umbellifer flowers, our knowledge on the larval ecology of Swiss Cantharidae and Lycidae is still extremely fragmentary, and often completely lacking (Allenspach and Wittmer 1979). As a general rule, around half of the Cantharidae and the whole of Lycidae have been considered saproxylic, at least according to data from France (Bouget et al. 2019). Saproxylic Cantharidae are mainly within the genera *Malthinus* and *Malthodes*, whose larvae are predators inside rotting wood (Koch 1989), while the larvae of the other Cantharidae genera are active predators in the soil and in leaf litter (Constantin 2014a).

From a conservation point of view, it can be said that Switzerland harbors a number of species considered rare at a European or global scale (e.g. *Malthodes kahleni*), despite not having any strictly endemic taxa (with the possible exception of *Malthodes penninus raeticus*, whose taxonomic status requires further study). A number of the species found in Ticino, while only marginally distributed in Switzerland, have limited overall ranges, such as *Malthodes bertolinii*, *M. vincens* and, even more so, *M. stolzi*. Unfortunately, the life history and habitat requirements of many species, particularly in the genus *Malthodes*, are very much unknown, making it impossible to make an accurate assessment of their conservation status and highlighting particularly endangered species. Due to their small body size, short adult lifespan and difficult identification, it is easily possible that some “rare” *Malthodes* species are simply being overlooked, in Switzerland and elsewhere, and might not be as rare as currently thought. On the other hand, there is a risk that some of those species could “silently” be moving towards extinction while our knowledge about them is still not sufficient to even notice their decline, let alone plan appropriate conservation measures.

Unlike other families of Coleoptera, Cantharidae and Lycidae don't seem to contain any highly specialised alpine endemics within the borders of Switzerland, even though there are some in adjacent countries, e.g. the apterous local endemic *Podistra rupicola* Kiesenwetter, 1863 in Austria (Carinthia) and adjacent Slovenia. A number of Swiss cantharid species are restricted to higher altitudes, though often covering a relatively wide altitudinal range from the sub-alpine conifer forest zone up until the edge of alpine scree slopes and glaciers (e.g. *Cantharis tristis*, *Cratosilis distinguenda*, *Malthodes trifurcatus*, *M. penninus*, *Rhagonycha nigripes*). Most of these species have relatively wide ranges within the Alps, with some even occurring in other high mountain ranges of Europe. All of those species have winged adults, at least for the males. Brachypterous females do, however, occur at least

in higher altitude populations of *Malthodes trifurcatus*, *M. penninus* and *M. caudatus* group. Apterous females are common in *Malthodes lobatus*, but this is a species of low altitudes.

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## Supplementary material 1

### File S1

Authors: Yannick Chittaro, Andreas Sanchez, Michael Geiser

Data type: word document

Explanation note: Publications for which data have been fully collected, but which are not explicitly quoted in the text.

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# Female accessory gland fluid promotes sperm survival in yellow dung flies

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## Abstract

Female and male reproductive traits co-evolve through pre- and post-copulatory sexual selection and sexual conflict. Although males typically transfer many sperm during copulation, only a small proportion reach the fertilization site because females often actively or passively reduce sperm number in their reproductive tract. Males may transfer accessory substances to protect their ejaculates against female selective processes, which benefits males but can harm females. In turn, females may use accessory gland fluids to control paternity or sperm storage. Female yellow dung flies (*Scathophaga stercoraria*) have paired accessory glands that produce fluids involved in fertilization and egg laying. One proposed function for these fluids is spermicide. Alternatively, female accessory gland fluid may help keep sperm alive to avoid fertilization failure or encourage sperm competition. Using yellow dung flies, we investigated the interaction of female accessory gland fluid with sperm *in vitro*. Significantly more sperm remained alive when exposed to accessory gland fluid compared to buffer only (63% vs. 44%). We conclude that female accessory gland fluid in yellow dung flies can help nourish rather than kill male sperm, although selective nourishment of sperm is as consistent with cryptic female choice as is selective spermicide.

## Key Words

Reproduction, sexual conflict, *Scathophaga stercoraria*, sexual selection, sperm competition, spermicide

## Introduction

In species with internal fertilization, only a fraction of the vast numbers of sperm transferred by males tend to ever reach the fertilization site (Chang 1951; Hartman 1957; Bedford 1970; Austin 1975; Suarez 1987; Williams et al. 1993; Suarez and Pacey 2006). This sperm loss can result from physiological or biochemical challenges within the female reproductive tract (Birkhead et al. 1993) and, if their tract is large, from additional dilution effects (Immler et al. 2011; Lüpold and Fitzpatrick 2015). Further, females of a diversity of species actively reduce sperm numbers in their reproductive tract by extrusion, dissolution or degradation (Davey 1985; house flies: Degrugillier 1985; bruchid beetles: Eady 1994; spiders: Peretti and Eberhard 2010; *Drosophila* fruit flies: Snook and Hosken

2004; Holman and Snook 2008; Lüpold et al. 2013; Manier et al. 2013; fowl: Pizzari and Birkhead 2000; Dean et al. 2011), implying female influences on sperm storage and paternity that may or may not be adaptive. Therefore, sperm are often short-lived within the female reproductive tract, although there are exceptions such as bees, ants, or bats (Hosken 1997; den Boer et al. 2008; King et al. 2011). In response, males of several insects produce and transfer various accessory substances to protect their ejaculates against female enzymatic attack and digestion (Leopold et al. 1971; Merritt 1989; Duvoisin et al. 1999; Chapman et al. 2001; Lung et al. 2002; Poiani 2006; Holman and Snook 2008; den Boer et al. 2008; King et al. 2011; Avila 2011). These male substances may benefit the males even if to the detriment of the females (i.e., indicating potential sexual conflict; Chapman et al. 2003; Arnqvist and Rowe

2005), for example by decreasing female receptivity to further mating, by accelerating egg laying, storage and use of sperm, or by reducing female life span (Chen 1996; Wolfner 2002; Chapman et al. 1995, 2001).

The female reproductive tract of insects typically includes a pair of ovaries from which the oviducts emanate to further join and form a common oviduct, one to several spermathecae (i.e., sperm storing organs), and paired accessory glands (Wigglesworth 1967; Gillott 1988; Chapman 1998). Davey (1985) documented various functions of female accessory glands: lubrication during copula and oviposition for faster mating and egg laying, production of oviposition pheromones, or protective secretions to coat the eggs. In *Musca domestica*, accessory gland fluid moves along with the spermatozoa to the fertilization chambers and is used to dissolve the cap of the mature egg to allow fertilization (Leopold and Degrugillier 1973; Leopold et al. 1978). Female accessory gland fluid may also facilitate cryptic female choice by creating a selective insemination site (Birkhead et al. 1993; Eberhard 1996; Hellriegel and Ward 1998; Hosken et al. 2001). Several studies have hypothesized or shown that female accessory gland fluids can selectively kill sperm, thus acting as a spermicide (Greeff and Parker 2000; Bernasconi et al. 2002; Holman and Snook 2008). A female may benefit from such sperm killing by promoting male competition (Birkhead et al. 1993; Bernasconi and Keller 2001), countering antagonistic male adaptations (Chapman et al. 1995; Rice 1996; Andrés and Arnqvist 2001), or simply by biasing paternity in favour of males of high genetic quality (Birkhead et al. 1993; Greeff and Parker 2000). However, while the number of sperm stored is generally lower than the number transferred (Hosken et al. 2001; Bernasconi et al. 2002), this does not necessarily mean that females actively kill or eject sperm; sperm may simply get lost in the female reproductive tract (Arthur et al. 2008).

The yellow dung fly *Scathophaga stercoraria* L. (Diptera: Scathophagidae) is a cool-climate species that is common around livestock (especially cattle) pastures in cold-temperate regions of the northern hemisphere (Blanckenhorn et al. 2010). In Switzerland, this species abounds up to high altitudes beyond the treeline (Kraushaar et al. 2002). Females lay their eggs into vertebrate dung, which the larvae consume. Consequently, males are usually found in large numbers on and around cow dung pats, waiting for females to mate with (Parker 1970). Due to the pioneering work of Geoff Parker and colleagues, the yellow dung fly has become the classic species for studies of sexual selection, sexual conflict, and sperm competition (Parker 1970, 1978; Simmons et al. 2020). Following copulation with a male, some sperm are stored and partitioned among typically three storage organs (spermathecae) within the female reproductive tract, potentially allowing some level of sperm choice by sorting (Otronen et al. 1997; Ward 2000; Bussière et al. 2010; Demont et al. 2021). Although sperm viability varies in different parts of the female reproductive tract, Bernasconi et al. (2002) found no evidence for female acces-

sory gland fluid affecting sperm viability. One limitation of their approach, however, was that they used previously frozen accessory gland fluid for their *in vitro* experiments. Thus, there is no direct evidence yet that accessory gland products can debilitate sperm in this species (cf. Holman and Snook 2008). To the contrary, it is also conceivable that female accessory gland fluid may actually promote sperm survival (King et al. 2011). Killing sperm by degradation or keeping sperm alive are thus two contrasting functions of female accessory gland products that are both consistent with a female influence on paternity.

Here, we revisited the potential role of accessory gland fluid of female yellow dung fly in sperm viability by using fresh accessory gland fluid to circumvent the possibility of inactivating some important substances by freezing. We predicted two contrasting observations for sperm viability depending on which, if any, of the alternative hypothetical functions for accessory gland fluids is true: compared to a control treatment, we should find more (rather than fewer) live sperm after exposure to accessory gland fluid if accessory glands nourish sperm. In contrast, if the glands promote spermicide, fewer sperm should be alive after exposure to accessory glands than in controls.

## Materials and methods

We collected flies from a pasture in Fehraltorf, Switzerland (47°23'N, 8°44'E) and maintained them for multiple generations in the laboratory using standard conditions (Ward 2000; Blanckenhorn et al. 2010). For our experiment we used offspring of the 6<sup>th</sup> laboratory generation, dissecting a total of 50 females (of which three had to be discarded as dissection was unsuccessful) and 30 males after flies reached sexual maturity (>10 d after adult emergence for females, >4 d for males: Blanckenhorn and Henseler 2005). We performed these dissections in five temporal blocks no more than 12 minutes apart to provide equally fresh sperm, with 10 females and 6 males per block. The fluid of both female accessory glands of each female was extracted by rupturing each gland in a micro-centrifuge tube containing 20 µl buffer (Schneider's *Drosophila* medium; this solution is henceforth referred to as "accessory gland fluid suspension"). We then mixed the extracted accessory gland fluid from all 10 females (i.e., 20 accessory glands) per block so that all sperm samples of the 6 males within a block received the same accessory gland product. To obtain live sperm samples, we dissected individual males and extracted sperm from the proximal end (adjacent to the ejaculatory duct) of one of their testes by piercing the testis and pressing it lightly with a needle until approximately one third of the testis content was released into 100 µl buffer onto a glass slide (Schneider's *Drosophila* medium plus 10% heat-inactivated fetal calf serum: see Bernasconi et al. 2002; this solution is henceforth referred to as "sperm suspension"). All dissections were performed after flies had been anesthetized with CO<sub>2</sub>.

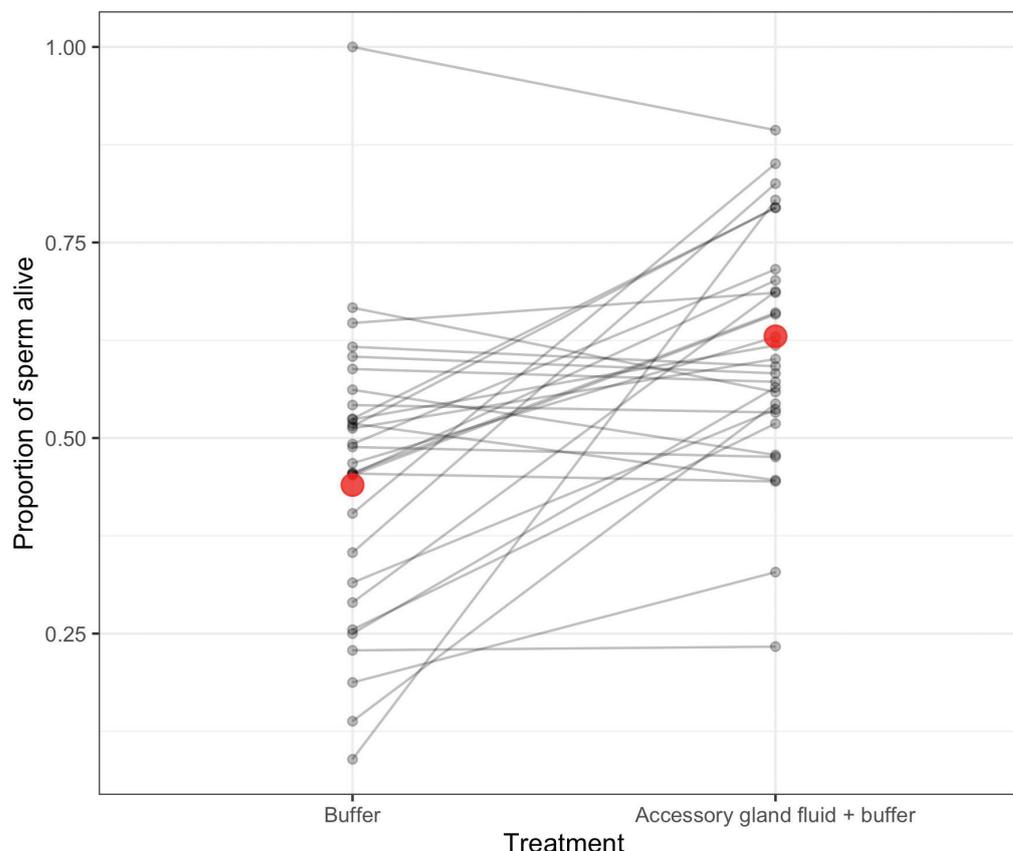
To ascertain whether the female accessory gland fluid affects sperm viability, we exposed sperm samples from 30 individual males to both fresh accessory gland fluid mixed with buffer or to buffer alone in a paired design. We incubated 15  $\mu\text{l}$  of the (male) sperm suspension with 30  $\mu\text{l}$  of buffer plus 15  $\mu\text{l}$  of the female accessory gland fluid suspension (or 45  $\mu\text{l}$  of buffer in the control treatment) for a total of 60  $\mu\text{l}$  for  $11 \pm 2$  min at room temperature. Subsequently, we released 30  $\mu\text{l}$  of these mixtures on a glass slide and examined them under a fluorescent microscope. We assessed sperm viability using the LIVE/DEAD Sperm Viability Kit (L-7011, Molecular Probes), which consists of a green membrane-permeant (live) nucleic acid stain (SYBR14, 1 mM in DMSO, diluted 1:50; emission max. 516 nm) and a red stain that penetrates only the damaged membranes of dead sperm (propidium iodide, 2.4 mM in water; emission max. 617 nm). After incubation, we added 5  $\mu\text{l}$  of each stain, vortexed lightly, and incubated the suspension in the dark for 5 min before viewing the sample under the fluorescent microscope. In the rare cases that cells took on both stains, we scored them as dead (Bernasconi et al. 2002). The fluorescent microscope contains three filter sets, allowing the viewing and recording of digital photographs under green light only, red light only, and green plus red light to clearly distinguish dead from live sperm.

We calculated sperm viability as the proportion of live sperm among all sperm counted in the sample (for plot-

ting), based on 20 randomly taken images (frames) per male at  $20\times$  magnification within  $20 \pm 2$  min of dissection (corresponding to  $9 \pm 1$  min after adding the stains). Data were analysed with a binomial generalized linear mixed model with logit-link, implemented in the lme4 package (Bates et al. 2015) of R version 4.04 (R Core Team 2021): the two-vector response variable was the absolute number of sperm that were alive versus dead (summed across the 20 frames taken for each male), and the lone fixed predictor was the experimental treatment. We fitted a random effect for male identity in recognition of the paired nature of the design, and an additional observation level random effect to account for overdispersion in the response. We used parametric bootstrapping (implemented in the pbkrtest package for R: Halekoh and Højsgaard 2014) to assess the significance of treatment.

## Results

We counted a mean of  $258 \pm 53$  (SD) sperm per male (sums by treatment: buffer dead: 1819; buffer alive: 1453; accessory gland dead: 1520; accessory gland alive: 2955). The proportion of live sperm was higher when sperm were exposed to accessory gland fluid (mean [ $\pm 95\%$ CI]: 0.63 [0.57, 0.68]) than in plain buffer (0.44 [0.38, 0.50]; parametric bootstrap P-value = 0.001; Fig. 1).



**Figure 1.** Proportion of sperm from 30 random *Scathophaga stercoraria* males remaining alive after *in vitro* paired treatment with female accessory gland fluid vs. buffer control (red dot = overall mean). Proportions were based on absolute counts of live and dead sperm, which could be distinguished by stain colour, across 20 equal-sized images per male.

## Discussion

Bernasconi et al. (2002) had previously shown for yellow dung flies that after mating sperm viability was significantly reduced in spermathecae compared to a male's testes. Nevertheless, *in vitro* exposure of sperm to several parts of the female reproductive tract, including the accessory glands, showed no sperm degradation (Bernasconi et al. 2002). Here, using fresh rather than frozen female accessory gland fluid, we found that this fluid contains substances that apparently increase sperm survival, at least *in vitro*. However, we cannot exclude the possibility that other organs or their secretions may additionally affect sperm viability either inside the spermathecae or in other parts of the female reproductive tract.

Unless there is strict monogamy, which is rare (Birkhead and Møller 1998), the sexes have different reproductive interests, potentially leading to sexual conflict (Chapman et al. 2003). A selective female environment could kill or absorb some incoming sperm before (actively or passively) transferring the remaining sperm to her spermathecae (Hellriegel and Ward 1998). Selective spermicide could be a mechanism to reduce adverse effects of genetic incompatibility (Bishop 1996; Stockley 1999), but could also provide females with a mechanism to bias paternity through cryptic female choice (Birkhead 1998). It is thus possible that accessory gland fluid components with spermicidal functions are female adaptations that arose in the context of sexual conflict, but we found no evidence for this process here.

Sperm are often short-lived within the female reproductive tract. Sperm survival is primarily a function of sperm quality, motility and longevity, and secondarily depends on the female environment such as her accessory gland fluids. Our experiment supports the latter mechanism (without addressing the first). Studies of bees and ants have shown that male accessory fluids can also prolong sperm viability in the female reproductive tract (den Boer et al. 2008; King et al. 2011). The number of sperm transferred by male yellow dung flies during copulation increases with copula duration (Parker and Simmons 1994), and in principle any effect of accessory gland fluid could change with the ratio of sperm-to-fluid. As we diluted the accessory gland fluid in buffer following Bernasconi et al. (2002), we may also have diluted important effects of accessory gland fluid on sperm. However, it seems highly unlikely that the direction of the effect of accessory gland fluid on sperm reverses depending on the concentration of the fluid.

Other studies of insects have found positive effects of female accessory gland fluids on sperm viability and fertilization success. Hosken et al. (2002) showed for *S. stercoraria* that gland extract does not inhibit bacterial growth, suggesting that accessory gland fluid is more likely involved in fertilization functions rather than antimicrobial immunological processes. We stress, however, that selective provisioning of sperm could in principle serve the same function as selective spermicide by creating conditions of sperm storage that favour some males over others. But whether a sperm nourishing function of accessory gland fluid can actively favour certain ejaculates over others remains unclear.

Because there is almost always a surfeit of males at the dung, females might not need to keep sperm alive unless they want to impose competition on males they are forced to mate with at the oviposition site. Nevertheless, because keeping sperm alive for weeks inside the reproductive tract may be energetically costly, females may benefit from selective nutrient provisioning of sperm. Females should store only as many sperm as are needed in the short term, and kill or absorb any unnecessary or disfavoured sperm (Birkhead 2000). In yellow dung flies, far fewer sperm are released from the spermathecae during fertilization of individual eggs than was previously thought based on theory (Sbilordo et al. 2009). Along with the abundance of available males willing to mate, this makes sperm limitation unlikely in this species (Simmons et al. 2020).

While our study has clarified one aspect of the function of female accessory glands in yellow dung flies, more work on the physiological and biochemical interactions involved in sperm storage and use, as well as on the reproductive consequences of sperm mortality for male fertilization success and female fitness, is clearly needed to elucidate the multiple facets of sexual conflict and postmating sexual selection in insects.

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## Supplementary material 1

### Table S1

Authors: Karin Thüler, Wolf U. Blanckenhorn, Paul I. Ward, Stefan Lüpold, Luc F. Bussière

Data type: excel table

Explanation note: Sperm counts for 30 males under two conditions, buffer (control) & accessory gland suspension (AG), generated by this study.

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Link: <https://doi.org/10.3897/alpento.5.68501.suppl1>

# Relict populations of *Lyonetia ledi* Wocke, 1859 (Lepidoptera, Lyonetiidae) from the Alps indicate postglacial host-plant shift to the famous Alpenrose (*Rhododendron ferrugineum* L.)

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## Abstract

*Lyonetia ledi* Wocke, 1859 (Lyonetiidae), was hitherto considered as a boreal species with a circumpolar distribution pattern and relict populations in isolated peat bogs north-east of the Alps (Austria, Czech Republic, Germany). In Europe it is known as a leaf-miner on *Rhododendron tomentosum* Stokes ex Harmaja (Ericaceae) as the primary host-plant and also *Myrica gale* L. (Myricaceae). The first record of *L. ledi* from the Swiss Alps on *Rhododendron ferrugineum* L., the famous Alpenrose, indicates an ancient host-plant switch during postglacial periods when *R. tomentosum* and *R. ferrugineum* shared habitat in the prealps. Conspecificity with northern populations is supported by the adult morphology and supplementing DNA barcodes (mtDNA COI gene). *L. ledi* is the first obligatory leaf-mining species on *R. ferrugineum*. Details of the life-history and habitat are described and figured. The record finally substantiates the probability of an autochthonous population in Carinthia (Austria), from where the species was recently published as new to the Alps.

## Key Words

*Lyonetia ledi*, new host-plant, new record, faunistics, Switzerland, boreo-montane, circumpolar, DNA barcoding

## Introduction

Although new national records are of considerable faunistic interest in Europe *per se*, they are often disregarded of only limited scientific value. Here we report an exceptional observation of a species of microlepidoptera which is not only of faunistic but also of considerable ecological interest as the first specialized leaf-miner on *Rhododendron ferrugineum*. The species discussed, *Lyonetia ledi*, was previously known in the Alps only from a single specimen from Carinthia, whose origin seemed questionable, especially because the known host-plants *Rhododendron tomentosum* (Ericaceae) and *Myrica gale* (Myricaceae) are absent from that area. On a visit to the Lower Engadine, Switzerland, on the 29<sup>th</sup> of July 2021 as part of the surveys for Biodiversity Monitoring Switzerland (Koordinationsstelle BDM 2014), occupied mines of an unidentified species were discovered on *Rhododendron ferrugineum*

by PH and subsequently confirmed by JS. The find was immediately surprising, as no specialized leaf-miners were previously known from this plant (Hering 1957) and therefore usually this plant remains disregarded by lepidopterists. The suspicion that it was a member of the family Nepitculidae was rejected from larval habits. The final instar larva made, after leaving the leaf-mine, a spinning typical of the genus *Lyonetia* with the pupa suspended by silken threads. The subsequently emerged moths were identified as *Lyonetia ledi* both according to external morphological features and by subsequent DNA barcoding.

## Material and methods

A total of 19 male and 6 female specimens of *Lyonetia ledi* from Switzerland have been examined. Material is preserved in the research collection of Tiroler

Landesmuseum Ferdinandeum (Hall, Austria) and of Jürg Schmid (Ilanz, Switzerland). Material is either pinned or alternatively set traditionally.

Species identification was based firstly on phenotypic characteristics of adults (wing markings, colour, size) using comparative collection specimens of *L. ledi* from the Tyrolean State Museums as well as on available online illustrations (Rennwald and Rodeland 2021). Despite considerable individual variation, sometimes with complete reduction of dark markings in the basal two-thirds of the forewing, *L. ledi* cannot be confused with any European congeners. Specific characteristics of the male and female genitalia are described and illustrated by Bengtsson and Johansson (2011), for example, but were not examined in the context of the present study. Finally, three samples were used for molecular analysis.

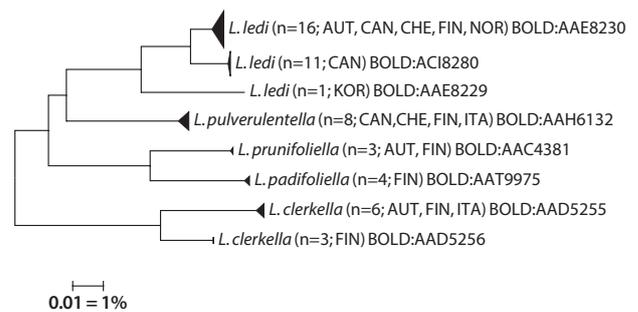
Tissue samples (a single hind leg) from 3 specimens of the suspected *Lyonetia ledi* were prepared according to prescribed standards to obtain DNA barcode sequences of a 658 base-pair long segment of the mitochondrial COI gene (cytochrome c oxidase subunit 1) and successfully processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) using the standard high-throughput protocol described in deWaard et al. (2008). We furthermore analysed 49 public supplementary barcode sequences > 500 bp from BOLD, covering all four of the other European species of the genus: *L. pulverulentella* Zeller, 1839, *L. prunifoliella* (Hübner, 1796), *L. padifoliella* (Hübner, 1813) and *L. clerkella* (Linnaeus, 1758).

All sequences were submitted to GenBank, and further details including complete voucher data and images can be accessed in the public dataset “Lepidoptera of the Alps - *Lyonetia ledi* [DS-LYONLEDI]” <https://doi.org/10.5883/DS-LYONLEDI> in the Barcode of Life Data Systems BOLD (Ratnasingham and Hebert 2007). Degrees of intra- and interspecific variation of DNA barcode fragments were calculated using the Kimura two-parameter model on the platform of BOLD systems v. 4.0. (<http://www.boldsystems.org>). A COI Neighbor-Joining tree was constructed using under the Kimura two-parameter model in MEGA 6 (Tamura et al. 2013). A three-letter code (ISO 3166-1 alpha-3, [https://en.wikipedia.org/wiki/ISO\\_3166-1\\_alpha-3](https://en.wikipedia.org/wiki/ISO_3166-1_alpha-3)) was used to abbreviate country names.

## Results

### Molecular analysis

The length of obtained DNA barcodes in three Swiss specimens of *L. ledi* was 586, 632 and 658 bp respectively. A considerable intraspecific divergence was detected in DNA barcodes of *L. ledi* (Fig. 1). European populations and four Canadian *L. ledi* specimens formed one cluster and assigned to BIN BOLD:AAE8230 (n=14), with a mean intraspecific distance of 0.39% and a maximum divergence of 1.22% but 2.24% to the nearest



**Figure 1.** COI Neighbor-Joining tree of species in the studied *Lyonetia*. Note: the scale bar only applies to internal branches between species. Width of triangles represent sample size, depth the genetic variation within the cluster.

neighbour. However, except for a single weakly deviating sequence from Lower Austria, all specimens from Europe including Swiss samples share the same haplotype, whereas Canadian samples belong to a distinct haplotype. Two additional BINs which include the nearest neighbour of European *L. ledi* from Canada and a unique sequence from South Korea may suggest potential cryptic diversity. Similarly, the considerable intraspecific variability (6.65%) detected in *L. clerkella* in Europe (table 1) must also be tested for potential cryptic diversity.

However, apart from exceptions, DNA barcode distances to nearest neighbours are much higher than intraspecific divergence in European *Lyonetia* ranging from c. 6% to 12% (Table 1).

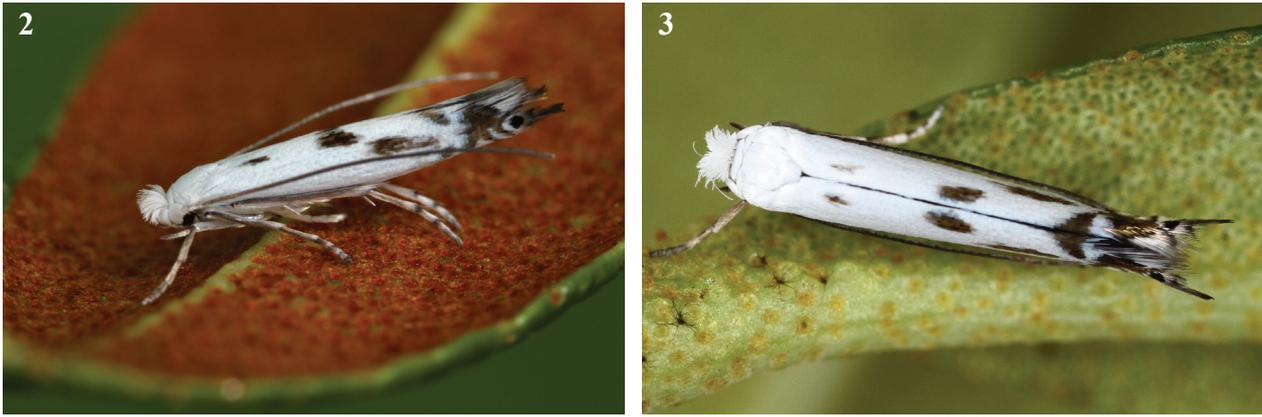
**Table 1.** Intra- and interspecific divergence in the studied *Lyonetia* species (%).

Species	Mean Intra-Sp	Max Intra-Sp	Nearest Species	Distance to NN
<i>Lyonetia clerkella</i>	2.69	5.49	<i>Lyonetia ledi</i>	12.13
<i>Lyonetia ledi</i>	1.68	6.65	<i>Lyonetia pulverulentella</i>	8.76
<i>Lyonetia padifoliella</i>	0.43	0.79	<i>Lyonetia prunifoliella</i>	5.75
<i>Lyonetia prunifoliella</i>	0.16	0.17	<i>Lyonetia padifoliella</i>	5.75
<i>Lyonetia pulverulentella</i>	0.54	1.2	<i>Lyonetia ledi</i>	8.76

### Alpine population of *Lyonetia ledi*

**Material examined.** 1♂: Switzerland, Graubünden, Ardez, SE Sur En, 1760 m, 46°45'38"N, 10°11'11.7"E, 6.8.2021 ex larva (*Rhododendron ferrugineum*), leg. Huemer; 3♂: same data, but DNA Barcode TLMF 30911, DNA Barcode TLMF 30912, DNA Barcode TLMF 30913; 4♂: same data, but 21.8.2021 ex pupae, all leg Huemer coll. TLMF. 11♂, 6♀ same locality, 8.2021 e.l., e.p. leg. et coll. JS.

**Adult (Figs 2, 3).** Head, tuft, and eye-cap as well as thorax glossy white; labial palpus white with some fuscous on outer surface; antenna about length of forewing, pale grey. Wingspan c. 7–9 mm; forewings glossy white; short oblique dark brown streak from tornus at half-length of wing, longitudinal patch at about 2/3, two dorsal streaks from tornus converging in disc at 3/4;



Figures 2, 3. *Lyonetia ledi* adults resting on leaves of *Rhododendron ferrugineum* (Switzerland, Graubünden, Ardez).



Figures 4, 5. Leaf-mines of *Lyonetia ledi* on *Rhododendron ferrugineum* (Switzerland, Graubünden, Ardez).

large ochre-brown patch in distal fifth; costal ciliae with four blackish strigulae, large black apical dot followed by black line and apical scale-pencil. Hindwings grey. The variation of forewing markings is considerable, i.e. a short sub-basal streak below fold at about 1/5 or a complete medial streak as figured by Bengtsson and Johansson (2011) could not be observed, whereas the medial and postmedial markings are completely reduced in one specimen.

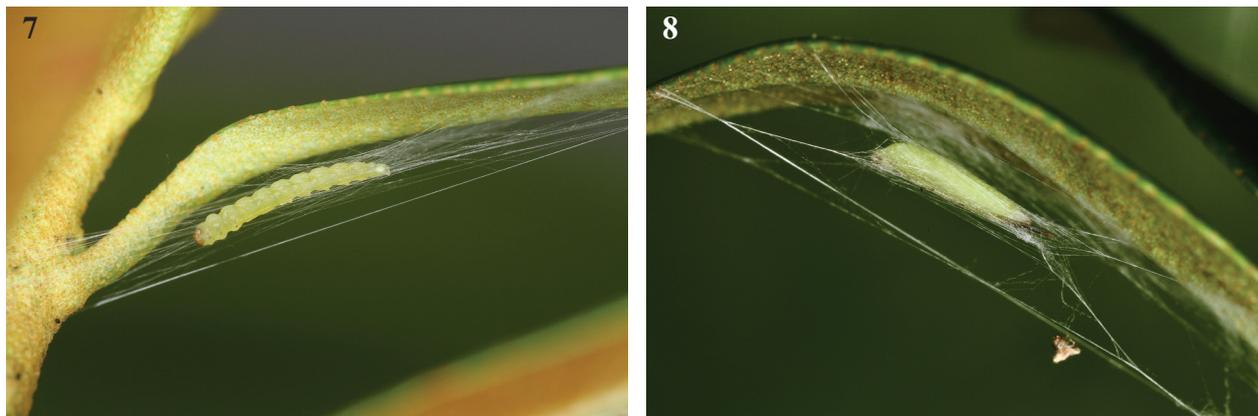
For exhaustive description of the adults including genitalia of both sexes see Bengtsson and Johansson (2011).

**Biology.** In Europe, *Lyonetia ledi* is a widespread leaf-miner of *Rhododendron tomentosum* (Ericaceae), but in the northern part of the continent it is also regularly recorded from the unrelated *Myrica gale* (Myricaceae), a species absent from large parts of Central Europe. Larvae of the newly discovered population from the Engadine mine the leaves of *R. ferrugineum*. The egg is laid on the upper side of a leaf. The tunnel-mine initially extends towards the base of the leaf, then turns and continues alongside the leaf rim towards the leaf tip, where a spacious blotch mine is formed. Only current year leaves, recognizable by their green underside are infested, while older leaves with the plant's name-giving rusty underside may contain mines from previous years only (Figs 4, 5). The mine is hardly visible on the underside. Frass is firstly deposited in



Figure 6. Final instar larva of *Lyonetia ledi* on *Rhododendron ferrugineum* (Switzerland, Graubünden, Ardez).

continuous line which later fills the complete tunnel-mine, whereas it is deposited in irregular flawy patches in the blotch-mine. According to Kuroko (1964) frass may also be ejected through semicircular lateral slits along the border of the blotch mine on the lower side. The same author also reports the larva moving to a new leaf and starting to produce a new mine, an observation unconfirmed in alpine habitats. The final instar larva is light yellow with a light brown head and a brownish mottled thoracic shield and ca. 4.8 mm long (Fig. 6). On the underside of a nearby



**Figures 7, 8.** Characteristic cocoon with final instar larva and pupa of *Lyonetia ledi* on *Rhododendron ferrugineum* (Switzerland, Graubünden, Ardez).



**Figure 9.** Habitat of *Lyonetia ledi* in Engadine/Switzerland with *Rhododendron ferrugineum*.

leaf, it constructs a X-shaped silken scaffold in the center of which it then pupates like in a hammock (Figs 7, 8). The ca. 4.4 mm long pupa can be easily found when examining the underside of mined or adjacent leaves. First larvae were detected on the 29<sup>th</sup> of July 2021, two weeks later on the 12<sup>th</sup> of August 2021 only pupae were found. In captivity the adults emerged after about a week to 10 days between 6<sup>th</sup> and 21<sup>st</sup> of August. These data suggest hibernation of the adults as it is also reported from Sweden, with a flight period lasting from mid-August to October and again from April to May (Bengtsson and Johansson 2011).

The larvae seem to be regularly infested by parasitic wasps of *Diadegma cf. semiclausum*, (Ichneumonidae) (barcoded) and an unidentified species of Ichneumonidae

as we found a number of their cocoons that were already empty.

**Habitat (Fig. 9).** *Lyonetia ledi* is considered as a tyrphobiontic species (Spitzer et al. 1996) because it is restricted to peat bogs. The Swiss habitat is completely different and can be characterized as a northern exposed subalpine Larici-Piceetum plant-association dominated by *Larix decidua* Mill. and *Picea abies* (L.) H. Karst and interspersed *Pinus cembra* L., *Betula pendula* Roth and *Alnus alnobetula* (Ehrh.) K. Koch are also present in the adjacent area. This biotope is located in a north-facing, steep avalanche gully at the bottom of which remaining snow masses may persist into early summer and provide unique microclimatic conditions. Furthermore, the most

infested *Rhododendron* shrubs are often rather puny specimens, growing in very shady places and thus unable to produce flowers.

## Discussion

In Europe, *Lyonetia ledi* is a leaf-miner mainly of *Rhododendron tomentosum* (formerly *Ledum palustre*) (Ericaceae), whereas in Asia it has also been recorded from *R. dauricum* L., *R. indicum* (L.) Sweet, *R. kaempferi* Planch., *R. mucronulatum* Turcz., *R. occidentale* Torr. & A. Gray, *R. japonicum* (A. Gray) Suringar and *R. pentandrum* (Maxim.) Craven and in North America from *R. albiflorum* Hook. (Kuroko 1964; Robinson et al. 2010), giving a potentially much broader host-plant spectrum. This is also indicated by regular records from the unrelated *Myrica gale* (Myricaceae) in Northern Europe and the now detected records on *R. ferrugineum* in the Alps. In particular *Myrica* includes a weird selection of species feeding otherwise on other plants, e.g. *Coleophora cornutella* Herrich-Schäffer, 1861 (in Finland only on *Myrica*), *C. uliginosella* Glitz, 1872, *C. vacciniella* Herrich-Schäffer, 1861 (Mutanen in litt.), and *Pseudotelphusa paripunctella* (Thunberg, 1794). Interestingly, however, the congeneric species *L. myricella* Kuroko, 1964 from Japan also feeds on *Myrica* and the genus may contain common metabolite plant additives with *R. tomentosum*. In contrast, *R. tomentosum* has a specialized fauna of Lepidoptera, e.g. *Stigmella lediella* (Schleich, 1867), *Coleophora ledi* Stainton, 1860 (also observed on *R. canadense* (L.) Torr. at the botanical garden in Oulu, Finland, Mutanen in litt.), *Coleophora obscuripalpella* Kanerva, 1941, *Carpatolechia epomidella* (Tengström, 1869) and *Argyroploce lediana* (Linnaeus, 1758). Both hitherto known European host-plants of *L. ledi* are characteristic of peat bogs and show a circumpolar distribution pattern. Whereas *R. tomentosum* is becoming increasingly rare towards the South, with only a few relict populations in peat bogs of Central Europe north of the Alps, *Myrica gale* is completely absent from the southern part of Central Europe. Following its host-plants *L. ledi* is widely distributed from northern Europe to the Far East (Aarvik et al. 2017; Baryshnikova 2019), with an increasingly patchy distribution pattern in northern Central Europe (Spitzer et al. 1996), and isolated populations in southern Czech Republic and northernmost Austria (Lower Austria) (Laštůvka and Liška 2011; Huemer 2013). The newly detected mountainous population of *L. ledi* from Switzerland is highly isolated at a distance of about 440 km from the closest confirmed records in the northern part of Lower Austria (Huemer 2013). However, records of the host-plant *R. tomentosum* have been published from southern Germany (Allgäu) at a distance of only about 100 km from the Swiss population (Dörr 2007). On the other hand, *R. ferrugineum* is known from sub-recent observations on the border of peat bogs of the Allgäu district (Dörr and Lippert 2004; Bundesamt für

Naturschutz 2021). At the maximum stage of the last ice-age some 22'000 years BP, the northern rim of the alpine glaciers extended over today's lake Constance and even approached what is now the city of Munich (Seguinot et al. 2018). It may be hypothesized that *Rhododendron ferrugineum* and *R. tomentosum* both coexisted in the glacier's foreland of this region. Once *Lyonetia ledi* had switched to *R. ferrugineum*, it followed its new hostplant with the receding glaciers in the post glacial period into the alpine valleys where it survives to the present day at very specific sites. As the Lower Engadine became ice-free only at around 14'000 years BP, *L. ledi* was not isolated long enough to develop marked genetic differences to other European colonies. If this hypothesis holds true, *L. ledi* has a part in a group of species like *Exaeretia alisella* Stainton, 1849, *Depressaria leucocephala* Snellen, 1884, and possibly *Agonopterix subtakamukui* Lvovsky, 1998 (all Elachistidae, Depressariinae) which postglacially colonized the northeastern part of the Alps from northeastern glacial refugia and are found there in sparse, isolated colonies. In comparison, several mutations in COI gene are already occurring in Canada's populations with 4 diagnostic and 33 partial characters, which must have been separated for much longer, and the divergence compared with European *L. ledi* is already more than 1%. The observed geographical variation of host-plants seems to be a more widespread phenomenon in tyrphobiotic species and has also been recorded e.g. for *Eupithecia gelidata* Möschler, 1860 (Spitzer et al. 1991).

A unique record of *L. ledi* from the southern Alps in the absence of one of the known host-plants remained unexplained (Wieser 2018). The single adult specimen was collected at light nearly 300 km from the next known population of *Lyonetia ledi* in Lower Austria, whereas the nearest relict population of the host-plant from Allgäu is about 250 km away. Thus, if not accidentally introduced, this specimen may indicate another population from an alpine *Rhododendron*. The habitat is a stream bed at about 650 m above sea level with typical alpine alluvial plants on limestone such as *Dryas octopetala* L. and probably also (unchecked) *R. hirsutum* L. as a potential host-plant (Wieser in litt.).

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# On some *Ctenarytaina* species (Hemiptera, Psylloidea) from Gunung Kinabalu (Malaysia, Sabah)

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## Abstract

Gunung Kinabalu is famous for its exceptionally diverse fauna and flora, rich in endemism. An example is the psyllid genus *Ctenarytaina* that is represented by four, apparently endemic species. Here two new *Ctenarytaina* species, *C. lienhardi* sp. nov. and *C. smetanai* sp. nov., are described from Gunung Kinabalu. The new taxa are diagnosed, illustrated and their relationships to other species in the genus are discussed. *Ctenarytaina daleae* Burckhardt is redescribed. The species develops on *Leptospermum* species (Myrtaceae) and not *Syzygium* as previously suggested.

## Key Words

Sternorrhyncha, Aphalaridae, Spondyliaspinae, systematics, phytophagy, distribution

## Introduction

Gunung (=Mount) Kinabalu, with an elevation of around 4100 m, is the highest mountain between the peaks of the eastern flank of the Himalaya in Burma and Mount Wilhelm in Papua New Guinea. It is famous for its exceptionally diverse flora, rich in endemism. The lower slopes were originally covered in lowland dipterocarp forest, most of which has disappeared through human activities. The lowland and montane forests up to about 2500 m altitude are characterised by Oriental floral elements. At altitudes above 2500 m, plant taxa shared with the Himalayan (e.g. Ericaceae) and Australian floras (e.g. Myrtaceae) become more dominant (Cockburn 1978; Corner 1978; Beaman and Beaman 1990). Similar but less well-documented relationships can also be found in phytophagous insects such as the phloem feeding, generally host specific psyllids. This group of Sternorrhyncha includes over 4000 described species worldwide. It is most species-rich in the tropics and south temperate regions (Burckhardt et al. 2021).

Fifteen psyllid species have been reported from Gunung Kinabalu. Four *Paurocephala* species (Liviidae,

Liviinae) are associated with species of *Pterospermum* (Malvaceae), *Artocarpus* and *Ficus* (Moraceae) (Mifsud and Burckhardt 2002). They are characteristic Oriental taxa. The other 11 species are members of the subfamily Spondyliaspinae (Aphalaridae) and are associated with Myrtaceae. They belong to the genera *Boreioglycaspis* (7 spp. on *Syzygium* and *Tristaniopsis*) (Burckhardt 1991) and *Ctenarytaina* (4 spp. presumed to be associated with *Syzygium*) (Burckhardt et al. 2020). As their hosts, these psyllids represent Australian biogeographical elements.

The Spondyliaspinae is a species-rich subfamily of 23 recognised genera (Burckhardt et al. 2021) mostly restricted to the Australian biogeographical realm and associated with hosts in the Myrtaceae (Burckhardt 1991). *Boreioglycaspis* and *Ctenarytaina* are exceptional in that they occur also outside the Australian region. *Ctenarytaina* comprises 29 described species originating from tropical Asia (12 spp.), Australia (9 spp.), Oceania (6 spp.) and Africa (2 spp.) (Burckhardt et al. 2020). Two Australian species, *C. eucalypti* (Ferris & Klyver) and *C. spatulata* Taylor, are economically important invasive pests in eucalypt plantations in Africa, Europe and the Americas where they are adventive (Queiroz et al. 2012; Makunde et al.

2020). Host plants are mostly Myrtaceae, but one species each develops on *Boronia* (Rutaceae), *Eurya* (Theaceae) and *Fuchsia* (Onagraceae), respectively.

Apart from the four species allegedly associated with *Syzygium* (Burckhardt et al. 2020), two undescribed *Ctenarytaina* species were collected on Gunung Kinabalu that are described in the present paper. The taxonomy of *Ctenarytaina daleae* Burckhardt is revised and its host relationships are discussed.

## Material and methods

Material is deposited in the Muséum d'histoire naturelle, Genève, Switzerland (MHNG) and Naturhistorisches Museum, Basel, Switzerland (NHMB). The morphological terminology follows Halbert and Burckhardt (2020). Measurements were taken as follows: adult body length from dry mounted specimens measuring the distance between fore margin of head and tip of forewings when folded over body; the other measurements were taken from slide mounted specimens. The measurements and ratios are given as range. The plant nomenclature accords with the World Flora Online (2021).

## Results

### Taxonomy

#### *Ctenarytaina daleae* Burckhardt, 2020

Figs 1, 4, 5, 10–14

*Ctenarytaina daleae* Burckhardt: Burckhardt et al. (2020: 44), p.p. [description and figures ♂, key]

**Type locality.** Malaysia, Sabah, Ranau, Gunung Kinabalu, 6.0428°N, 116.5587°E, 2600 m.

**Material examined.** Malaysia: *Holotype* ♂, Sabah: Ranau, Gunung Kinabalu, 6.0428°N, 116.5587°E, 2600 m, 2.v.1987, *Syzygium korthalsianum* (D. Burckhardt & I. Löbl) #8751 (MHNG, slide mounted). – Malaysia: 6 ♂, 8 ♀, same but summit trail, 3230 m, *Leptospermum* sp., 29.iv.1982, *Leptospermum* scrub (D. Burckhardt) #8277; 10 ♂, 12 ♀, same but 3230 m, *Leptospermum recurvum*, #8278; 1 ♂, 1 ♀, same but 2600 m, 1.v.1987 (D. Burckhardt & I. Löbl) #8735; 21 ♂, 36 ♀, same but 2600 m, 2.v.1987, *Leptospermum recurvum*, #8747, #8748, #8749; 6 ♂, 6 ♀, same but 2600 m, 2.v.1987, general sweeping of vegetation, #8752; 2 ♂, 9 ♀, same but 2600 m, 2.v.1987, *Leptospermum javanicum*, #8753; 12 ♂, 13 ♀, same but 3300 m, 4.v.1987, *Leptospermum recurvum*, #8756; 4 ♂, 4 ♀, same but below Layang Layang, 2600 m, 2–8.v.1987, interception trap (A. Smetana); 7 ♂, 11 ♀, same but below Laban Rata, 3155 m, 5.v.1987; 1 ♂, 5 ♀, same but Laban Rata, 3200 m, 4–8.v.1987, interception trap; 8 ♂, 7 ♀, same but 3200 m, 9–20.v.1987, interception trap (MHNG, NHMB, dry and slide mounted).

**Diagnosis.** Genal processes 0.3 times as long as vertex along mid-line, irregularly rounded anteriorly. Forewing oblong oval, widest in the middle, 2.3–2.7 times as long as broad, broadly rounded apically; vein C+Sc mostly straight, weakly concave in proximal third, cell c+sc narrow. Surface spinules present in all cells, forming cellular pattern; in cell  $r_2$  above bifurcation of vein M, the cells are irregularly hexagonal consisting of two indistinct rows of spinules. No extra pore fields developed on abdominal intersegmental membrane. Basal segment of proctiger weakly curved posteriorly, hind margin with a row of stout setae; apical segment 0.2–0.3 times as long as basal segment. Paramere digitiform. Distal segment of aedeagus cuneate. Female terminalia strongly narrowed medially, bearing each an apical process on proctiger and subgenital plate, female proctiger dorsally serrate.

**Redescription.** Adult. Colouration. Head and thorax light reddish brown. Vertex with dark brown dot in the middle of either half; genal processes dark brown at base, yellow apically. Antenna light orange brown at base, getting gradually darker from segment 6 to apex which is dark brown or black. Pronotum with each two submedian dark dots and mesopraescutum with each one submedian dark dot along fore margin on either side. Legs yellow; profemora light greyish brown. Forewings light ochreous or amber-coloured, slightly lighter along fore margin; veins concolourous with membrane. Abdomen yellow or orange; base of female proctiger light brown. Younger specimens with less extended dark colour.

**Structure.** Conforming to the generic description of Burckhardt et al. (2020). Body length ♂ 1.4–1.5 mm, ♀ 1.5–1.9 mm (6 ♂, 6 ♀). Head deflexed 45° from longitudinal axis of body. Vertex rhomboidal, weakly concave at base; preocular sclerite forming flat tubercule; genal processes 0.3 times as long as vertex along mid-line, irregularly rounded anteriorly, contiguous medially; eyes weakly ‘stalked’ (Fig. 1). Antenna 0.6–1.0 times as long as head width. Metatibia 0.5–0.7 times as long as head width, weakly widening to apex, with 5 irregularly spaced apical spurs. Forewing (Fig. 4) oblong oval, widest in the middle, 2.3–3.0 times as long as head width, 2.3–2.7 times as long as broad, broadly rounded apically; pterostigma, at base narrower than adjacent part of cell  $r_1$ , regularly narrowing to apex, ending at apical fifth of wing; vein C+Sc mostly straight, weakly concave in proximal third, cell c+sc narrow; vein Rs almost straight, vein M long, with short, weakly diverging branches, vein  $Cu_{1a}$  relatively straight, reaching the wing margin distinctly distal to bifurcation of vein M. Surface spinules present in all cells, forming cellular pattern; in cell  $r_2$  above bifurcation of vein M, the cells are irregularly hexagonal consisting of two indistinct rows of spinules (Fig. 5). No extra pore fields developed on abdominal intersegmental membrane. Male terminalia as in Figs 10–12. Proctiger 0.4–0.6 times as long as head width; basal segment, in profile, weakly curved posteriorly, irregularly beset with fine setae, hind margin with a row of stout setae; apical segment tubular, 0.2–0.3 times as long as basal segment. Subgenital plate,

in profile, triangular, with almost straight dorsal margin; sparsely beset with short setae. Paramere, in profile, digitiform, almost straight anteriorly, wavy posteriorly, broadly rounded apically; inner face densely covered in moderately long bristles. Distal portion of aedeagus slender in basal half, widening towards apex which is rounded; sclerotised end tube of ductus ejaculatorius small, weakly curved. Female terminalia as in Fig. 13. Proctiger 0.8–1.0 times as long as head width, 2.3–3.7 times as long as circumanal ring, cuneate; strongly narrowed medially, bearing an apical process, apical third serrate dorsally, subacute apically; sparsely beset with short setae, with a longitudinal lateral row of slightly longer setae in apical third and 2 longitudinal rows of peg setae near ventral margin in apical half. Subgenital plate 0.7–0.8 times as long as proctiger, in profile, bearing narrow, apically pointed process. Valvulae dorsalis and ventralis straight (Fig. 14); valvula lateralis pointed apically.

Measurements in mm (5 ♂, 6 ♀). Head width 0.44–0.58; antenna length 0.34–0.50; forewing length 1.08–1.48; length of male proctiger 0.20–0.24; paramere length 0.16–0.18; length of distal portion of aedeagus 0.10–0.14; female proctiger length 0.42–0.46.

Fifth instar immature unknown.

**Distribution.** Malaysia: Sabah, probably endemic to Gunung Kinabalu.

**Host plant, biology and habitat.** Adults were collected in large numbers on *Leptospermum javanicum* Blume (= *L. flavescens* auct.) and *L. recurvum* Hook.f. (Myrtaceae) suggesting that these two species constitute hosts. *Leptospermum javanicum* is widely distributed from Burma and southern Thailand to the Philippines, Maluku and Lesser Sunda Islands, and *L. recurvum*, is endemic to Gunung Kinabalu (Thompson 1989). It has been suggested that *L. recurvum* has split from the former after the last Pleistocene glaciation (Lee and Lowry 1980). The species occurs as a tree and at high altitudes as prostrate shrub on an outcrop of ultra basic rocks. It is one of the main shrub species of the summit zone above 3200 m altitude (Cockburn 1978; Corner 1978). A single male was collected also on *Syzygium korthalsianum* (Miq.) Miq. (Myrtaceae), which is an unlikely host contrary to the statement by Burckhardt et al. (2020).

**Comments.** *Ctenarytaina daleae* is most similar to *C. insularis* Martoni & Armstrong in the posteriorly weakly lobed male proctiger, the digitiform paramere, the female terminalia, which are strongly narrowed medially and bear each an apical process on the proctiger

and subgenital plate as well as the dorsally serrate female proctiger. It differs from the latter in the surface spinules forming rings consisting of two rows of spinules, the distal aedeagal segment which is evenly widening to apex rather than with a slender stalk and inflated apical part, the dorsally less concave female proctiger and the host plant: *Leptospermum* versus *Syzygium*.

*Ctenarytaina daleae* was described based on the male holotype and two female paratypes (Burckhardt et al. 2020). The examination of a long series of material from the summit region of Gunung Kinabalu collected on *Leptospermum* spp. shows that the holotype of *C. daleae* corresponds to the species from *Leptospermum* but not the females which belong to *C. smetanai* sp. nov. described below. *Ctenarytaina daleae* and *C. smetanai* sp. nov. are similar in the head and forewing structure (Figs 1, 3, 4, 8) but differ in the male and female terminalia (Figs 10–14, 18–20, 23, 24).

#### *Ctenarytaina lienhardi* sp. nov.

<http://zoobank.org/A84EAD53-7419-4D7B-89C8-26811D4493A4>

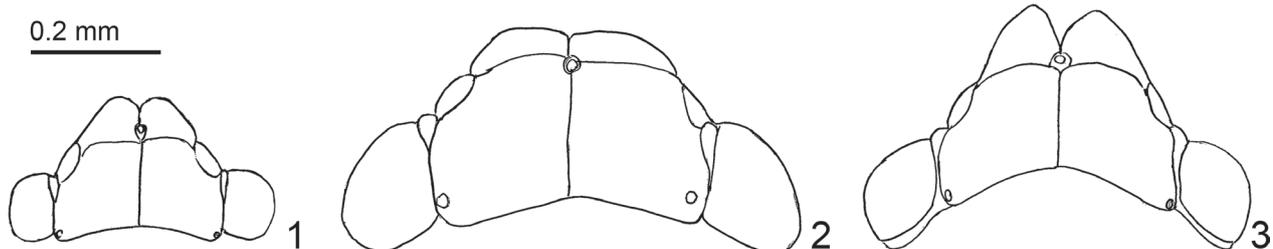
Figs 2, 6, 7, 15–17, 21, 22

**Type locality.** Malaysia, Sabah, Ranau, Gunung Kinabalu, 1750–1800 m.

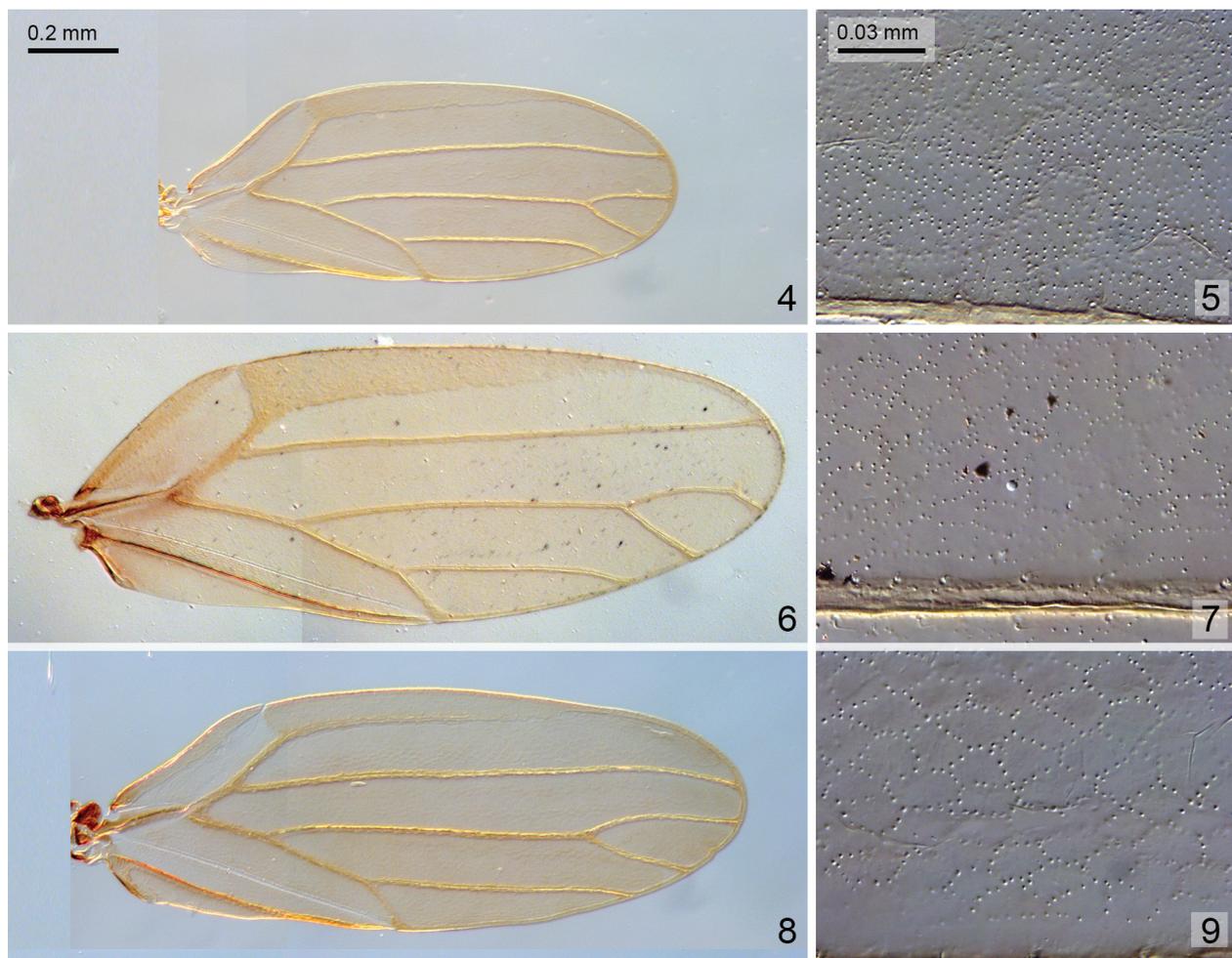
**Material examined.** *Holotype* ♂, Malaysia: Sabah: Ranau, Gunung Kinabalu, 1750–1800 m, 22.iii.1983 (C. Lienhard) #Pal-83/47 (MHNG, dry mounted).

**Paratypes:** Malaysia: 1 ♂, 2 ♀, same data as holotype; 1 ♀, same but, 1750 m, 27.iv.1987, *Tristaniopsis* (D. Burckhardt and I. Löbl) #8722; 1 ♀, same but, 1750–1850 m, 20.iii.1983 (C. Lienhard) #Pal-83/34 (MHNG, NHMB, dry and slide mounted).

**Diagnosis.** Genal processes 0.3 times as long as vertex along mid-line, irregularly rounded anteriorly. Forewing oblong oval, widest in the middle, 2.3–2.5 times as long as broad, narrowly rounded apically; vein C+Sc mostly straight, cell c+sc narrow. Surface spinules present in all cells, forming cellular pattern; in cell  $r_2$  above bifurcation of vein M, the cells are irregularly hexagonal consisting of one or two indistinct rows of spinules. Extra pore fields developed on abdominal intersegmental membrane. Basal segment of proctiger weakly curved posteriorly, hind margin with a row of stout setae; apical segment 0.2 times as long as basal segment. Paramere weakly cuneate; inner face densely beset with long bristles. Distal portion of aedeagus slender in basal half, weakly inflated in apical



Figures 1–3. *Ctenarytaina* spp., head, in dorsal view. 1. *C. daleae*; 2. *C. lienhardi* sp. nov.; 3. *C. smetanai* sp. nov.



**Figures 4–9.** *Ctenarytaina* spp. **4, 6, 8.** Forewing; **5, 7, 9.** Surface spinules in cell  $r_2$  above bifurcation of vein M. **4, 5.** *C. daleae*; **6, 7.** *C. lienhardi* sp. nov.; **8, 9.** *C. smetanai* sp. nov.

half. Female terminalia cuneate; proctiger blade-shaped distal to circumanal ring, smooth dorsally, blunt apically.

**Description.** Adult. Colouration. Head and thorax light reddish brown. Vertex with dark brown dot in the middle of either half; genal processes dark brown at base, yellow apically. Antenna light orange brown at base, getting gradually darker from segment 6 to apex which is dark brown or black. Pronotum with each two submedian dark dots and mesopraescutum with each one submedian dark dot along fore margin on either side. Legs yellow; profemora light greyish brown. Forewings light ochreous or amber-coloured, slightly lighter along fore margin; veins concolourous with membrane. Abdomen yellow or orange; base of female proctiger light brown. Younger specimens with less extended dark colour.

**Structure.** Conforming to the generic description of Burckhardt et al. (2020). Body length ♂ 2.0 mm, ♀ 2.4 mm (1 ♂, 1 ♀). Head deflexed 45° from longitudinal axis of body. Vertex rhomboidal, weakly concave at base; preocular sclerite forming small tubercule; genal processes 0.3 times as long as vertex along mid-line, irregularly rounded anteriorly, contiguous medially; eyes weakly ‘stalked’ (Fig. 2). Antenna 0.8 times as long as head width. Metatibia 0.5–0.6 times as long as head width, weakly widening to apex, with 5 irregularly spaced apical spurs. Forewing

(Fig. 6) oblong oval, widest in the middle, 2.3–2.5 times as long as head width, 2.5–2.6 times as long as broad, narrowly rounded apically; pterostigma, at base wider than adjacent part of cell  $r_1$ , regularly narrowing to apex, ending at apical quarter of wing; vein C+Sc mostly straight, cell c+sc narrow; vein Rs almost straight, vein M long, with short, weakly diverging branches, vein  $Cu_{1a}$  relatively straight, reaching the wing margin at bifurcation of vein M. Surface spinules present in all cells, forming cellular pattern; in cell  $r_2$  above bifurcation of vein M, the cells are irregularly hexagonal consisting of one or two rows of surface spinules (Fig. 7). Extra pore fields present on abdominal intersegmental membrane. Male terminalia as in Figs 15–17. Proctiger 0.5 times as long as head width; basal segment, in profile, weakly curved posteriorly; irregularly beset with fine setae, bearing a row of short bristles along hind margin; apical segment tubular, 0.2 times as long as basal segment. Subgenital plate, in profile, triangular, slightly elongate, with weakly concave dorsal margin; sparsely beset with short setae. Paramere, in profile, weakly cuneate, relatively straight, narrowly rounded apically; inner face densely beset with long bristles. Distal portion of aedeagus slender in basal half, weakly inflated in apical half; sclerotised end tube of ductus ejaculatorius small, almost straight. Female ter-

minalia as in Fig. 21. Proctiger 1.0 times as long as head width, 2.7–2.8 times as long as circumanal ring, cuneate; dorsal margin of proctiger concave, blade-shaped distal to circumanal ring, smooth dorsally, blunt apically; sparsely beset with short setae, with a longitudinal lateral row of slightly longer setae in apical half and 3 longitudinal rows of peg setae near ventral margin in apical half. Subgenital plate 0.7–0.8 times as long as proctiger, in profile, forming narrow process in apical half, pointed apically. Valvulae dorsalis and ventralis weakly curved (Fig. 22); valvula lateralis narrowly rounded apically.

Measurements in mm (1 ♂, 2 ♀). Head width 0.64–0.74; antenna length 0.60; forewing length 1.54–1.84; length of male proctiger 0.38; paramere length 0.28; length of distal portion of aedeagus 0.16; female proctiger length 0.64–0.72.

Fifth instar immature unknown.

**Etymology.** Named after C. Lienhard, Genève, eminent specialist of Psocodea and collector of most of the type series.

**Distribution.** Malaysia: Sabah, probably endemic to Mount Kinabalu.

**Host plant, biology and habitat.** Unknown; a single female was collected on *Tristaniaopsis* (Myrtaceae).

**Comments.** *Ctenarytaina lienhardi* sp. nov. shares with *C. daleae*, *C. insularis* and *C. taylori* the narrow forewings and the posteriorly weakly curved male proctiger. It differs from the two former species in the blade-shaped, dorsally smooth female proctiger and from the latter in the lack of a dark brown basal patch on the forewing.

### *Ctenarytaina smetanai* sp. nov.

<http://zoobank.org/092F93CA-08C5-4D4A-90D7-5EC57A98B9F0>  
Figs 3, 8, 9, 18–20, 23, 24

*Ctenarytaina daleae* Burckhardt: Burckhardt et al. (2020: 44), p.p., mis-identification [description and figures ♀, key]

**Type locality.** Malaysia, Sabah, Ranau, Gunung Kinabalu, below Layang Layang, 2600 m.

**Material examined.** *Holotype* ♂. Malaysia: Sabah: Ranau, Gunung Kinabalu, below Layang Layang, 2600 m, 2–8.v.1987, interception trap (A. Smetana) (MHNG, slide mounted).

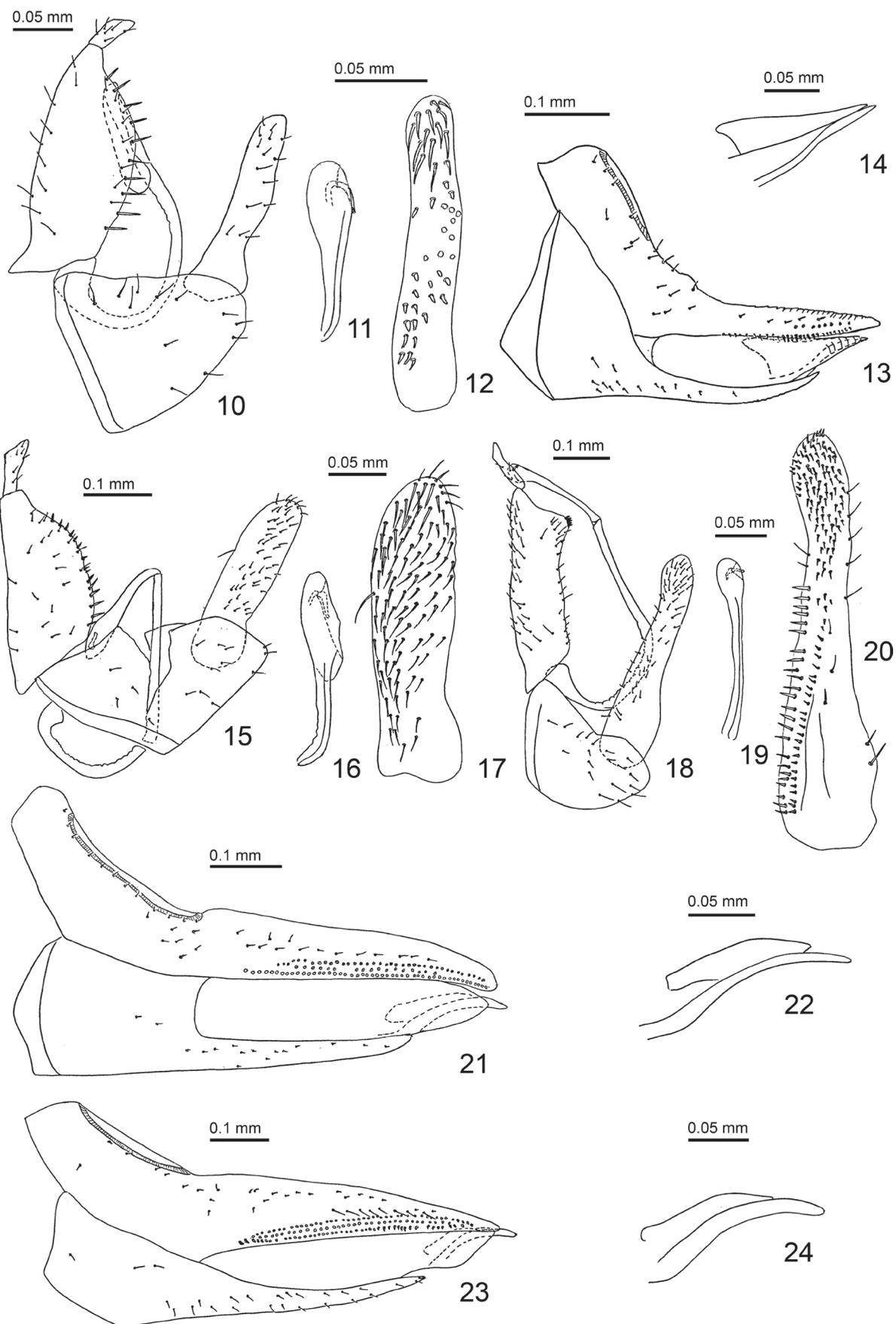
**Paratypes.** Malaysia, 1 ♀, Sabah, Ranau, Gunung Kinabalu, same as holotype (dry mounted); 1 ♀, same but 2600 m, 1.v.1987, *Syzygium punctilimum* (D. Burckhardt & I. Löbl) #8737 (MHNG, slide mounted); 1 ♀, same but Gunung Kinabalu, 6.0195°N, 116.5385°E, 1700 m, 22.iii.1983 (S. Nagai) #Pal-83/46 (MHNG, dry mounted).

**Diagnosis.** Genal processes 0.5 times as long as vertex along mid-line, irregularly rounded anteriorly. Forewing oblong oval, widest in the middle, 1.9–2.8 times as long as broad, narrowly rounded apically; vein C+Sc mostly straight, weakly concave in proximal third, cell c+sc narrow. Surface spinules present in all cells, forming cellular pattern; in cell  $r_2$  above bifurcation of vein M, the cells are irregularly hexagonal consisting of one row of

spinules. No extra pore fields developed on abdominal intersegmental membrane. Basal segment trapezoidal, hind margin with subapical angle bearing 5 short peg setae; apical segment 0.2–0.3 times as long as basal segment. Paramere very long and slender. Distal portion of aedeagus slender, weakly inflated apically. Female terminalia cuneate; dorsal margin of proctiger angularly concave at caudal end of circumanal ring, from there to pointed apex weakly convex, smooth.

**Description.** Adult. Colouration. Head and thorax dark reddish brown to almost black. Genal processes lighter than vertex, ochreous to brown. Antennal segments 1 and 2 light brown, segments 3–5 and basal third of segment 6 yellow to ochreous, apical two thirds of segment 6 and segments 7–10 dark brown to almost black. Mesoscutum with a broader median and two narrower submedian reddish brown longitudinal stripes. Fore and mid legs brown, tarsi and hind legs, including metacoxae, dirty yellowish. Forewings amber-coloured or light brown; veins concolourous with membrane. Hindwings whitish. Abdomen reddish brown to almost black dorsally, black ventrally; male and female terminalia light brown.

**Structure.** Conforming to the generic description of Burckhardt et al. (2020). Body length ♂ 1.9 mm, ♀ 2.0–2.2 mm (1 ♂, 2 ♀). Head deflexed 45° from longitudinal axis of body. Vertex rhomboidal, concave at base; preocular sclerite forming small tubercle; genal processes 0.5 times as long as vertex along mid-line, irregularly rounded anteriorly, well separated medially; eyes moderately ‘stalked’ (Fig. 3). Antenna 0.9–1.1 times as long as head width. Metatibia 0.5 times as long as head width, weakly widening to apex, with 5 irregularly spaced apical spurs. Forewing (Fig. 8) oblong oval, widest in the middle, 2.3–2.4 times as long as head width, 1.9–2.8 times as long as broad, narrowly rounded apically; pterostigma, at base narrower than adjacent part of cell  $r_1$ , regularly narrowing to apex, ending at apical third of wing; vein C+Sc mostly straight, weakly concave in proximal third, cell c+sc narrow; vein Rs almost straight, vein M long, with short, weakly diverging branches, vein  $Cu_{1a}$  relatively straight, reaching the wing margin distinctly distal to bifurcation of vein M. Surface spinules present in all cells, forming cellular pattern; in cell  $r_2$  above bifurcation of vein M, the cells are irregularly hexagonal consisting of one row of spinules (Fig. 9). No extra pore fields developed on abdominal intersegmental membrane. Male terminalia as in Figs 18–20. Proctiger 0.7 times as long as head width; basal segment, in profile, trapezoidal; irregularly beset with setae along anterior and posterior margins, hind margin with subapical angle bearing 5 short peg setae; apical segment tubular, 0.3 times as long as basal segment. Subgenital plate, in profile, elongate, with wavy dorsal margin; sparsely beset with short setae. Paramere, in profile, very long and slender, slightly narrowed in apical third, narrowly rounded apically; inner face with moderately long bristles in apical third and with two rows of bristles in basal two thirds. Distal portion of aedeagus slender, weakly inflated apically; sclerotised end tube of ductus ejaculatorius small, relatively straight.



**Figures 10–24.** *Ctenarytaina* spp., terminalia. **10, 15, 18.** Male terminalia, in profile; **11, 16, 19.** Distal portion of aedeagus; **12, 17, 20.** Inner face of paramere; **13, 21, 23.** Female terminalia, in profile; **14, 22, 24.** Dorsal and ventral valvulae. **10–14** *C. daleae*; **15–17, 21, 22.** *C. lienhardi* sp. nov.; **18–20, 23, 24.** *C. smetanai* sp. nov.

Female terminalia as in Fig. 23. Proctiger 1.1 times as long as head width, 2.9 times as long as circumanal ring, cuneate; dorsal margin of proctiger angularly concave at caudal end of circumanal ring, from there to pointed apex weakly convex, smooth; weakly beset with short setae, with a longitudinal lateral row of long setae in apical third and 2–3 longitudinal rows of peg setae near ventral margin in apical half. Subgenital plate 0.7 times as long as proctiger, in profile, evenly narrowing to pointed apex. Valvulae dorsalis and ventralis curved (Fig. 24).

Measurements in mm (1 ♂, 1 ♀). Head width 0.62–0.72; antenna length 0.64–0.66; forewing length 1.46–1.68; length of male proctiger 0.46; paramere length 0.44; length of distal portion of aedeagus 0.20; female proctiger length 0.82.

Fifth instar immature unknown.

**Etymology.** Named after the late A. Smetana, Ottawa, eminent staphylinid specialist and collector of the holotype.

**Distribution.** Malaysia: Sabah, probably endemic to Mount Kinabalu.

**Host plant, biology and habitat.** One female was swept from *Syzygium punctilimum* (Merr.) Merr. & L.M.Perry (Myrtaceae), a possible host, in moss forest. One male and one female were collected in an interception trap and one female was taken by sweeping vegetation.

**Comments.** *Ctenarytaina smetanai* sp. nov. differs from other congeners in the basal segment of the male proctiger which is trapezoidal and bears 5 short peg setae on the subapical angle of hind margin (Fig. 18).

## Discussion and conclusions

Within the subfamily Spondyliaspidae, which is almost entirely restricted to Australia, *Ctenarytaina* is exceptional in that it occurs also in Asia, Africa and Oceania. In fact, more than a third of the known species are native to Asia and only slightly less than a third is Australian. Among the 12 species known from Asia, the following four are apparently endemic to Gunung Kinabalu: *Ctenarytaina baliota* Burckhardt (on *Syzygium punctilimum*), *C. daleae* (on *Leptospermum javanicum* and *L. recurvum*), *C. loebli* Burckhardt (on *Syzygium* sp.) and *C. taylori* Burckhardt (on *Syzygium* sp.). Here another two species are added, viz. *C. lienhardi* sp. nov. and *C. taylori smetanai* sp. nov. (both without host records), reflecting the species richness of the fauna of Gunung Kinabalu. All six *Ctenarytaina* species from this mountain appear to be endemic, a feature that is relatively rare in psyllids (Burckhardt and Queiroz 2021).

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Bänziger H (2021)

## Vampire moths. Behaviour, ecology and taxonomy of blood-sucking *Calyptra*.

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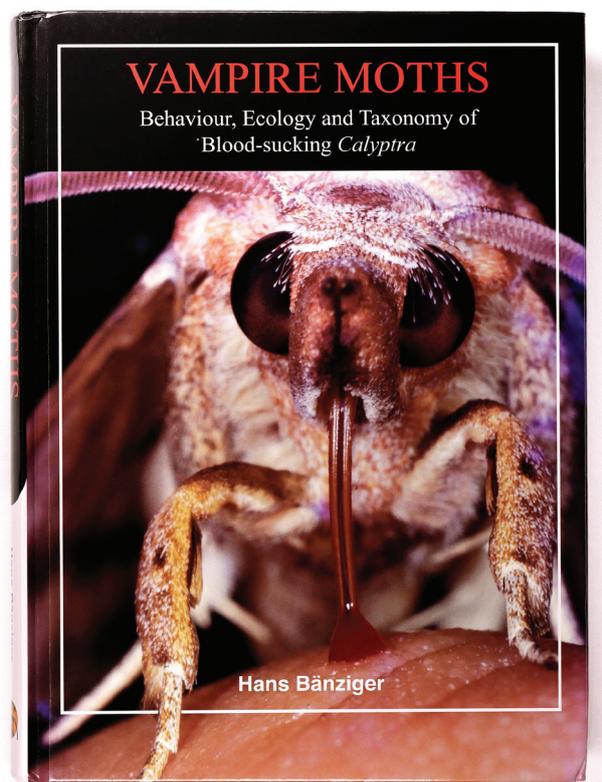
<http://zoobank.org/002B936D-ECB7-427C-964F-2A1C01F4FEF0>

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26 × 19.3 cm, 232 pp. (including 2 short taxonomic appendices), hardbound, glossy paper, 263 colour photos (including close-ups), 1 b/w photo, 114 b/w drawings and diagrams, in English; ISBN 978-983-812-199-6, Natural History Publications (Borneo), Kota Kinabalu, Malaysia, 2021; price 50 US\$ (shipment not included), available from the author, e-mail: [hans.baenziger@cmu.ac.th](mailto:hans.baenziger@cmu.ac.th), or 250 RM (Malaysian ringgit; costs of shipment not included and presumably almost as much as the book price) from the publisher.

Lepidoptera not only visit flowers and feed on nectar – many of us have also seen them sucking on less pleasant things like pus, urine and faeces – but it is not widely known that some of them are true blood suckers. Eight of the 17 currently recognized species (one of them containing two newly reinstated subspecies) of the genus *Calyptra* (Erebidae) in Asia are known to penetrate the skin of mammals – including humans – with a specialized proboscis and imbibe fresh blood. Hans Bänziger, a Swiss entomologist living in Thailand and a long-time member of the Swiss Entomological Society, has studied these enigmatic moths in their natural environment since 1967 and provides a summary of his findings and of the current state of knowledge in this newly published book. It is mostly based on the author's patient and meticulous observations during 545 nights in Papua New Guinea, West Malaysia, Thailand, Laos, Sri Lanka, India



and Nepal. Hans Bänziger is a field entomologist par excellence, who spent countless hours, often under harsh conditions and alone at night, watching (more than catching) tear-sucking moths and fruit-piercing moths. During the day he concentrated on caterpillars, tear-drinking bees and pollinators of *Paphiopedilum* slipper orchids, *Aristolochia*, *Rafflesia* and *Rhizanthus* flowers.

In the first three chapters of this book the reader learns about how the author moved to that part of the world, about his diverse entomological activities and how he operated in the field, all nicely dressed with reminiscences

and anecdotes. This is followed by a taxonomic treatment of the genus *Calyptra* and its close relatives, which includes an identification key to all species and subspecies, one lectotype designation, one generic synonymy, and the re-instatement of two subspecies. Four tables provide additional morphological characters and measurements. Furthermore, a detailed presentation of each taxon is given along with a list of the specimens examined, illustrations of the male genitalia, photos of habitus, larvae and their inconspicuous and often quite scarce food plants, as well as information on seasonality and habitat preferences.

The largest part of the book is an extensive and beautifully illustrated account of the author's observations (in the wild, in local zoos and enclosures for domestic animals) on how and on what these moths feed exactly. The human victim in all observed cases was the author himself. The specialized mechanism of skin-piercing by a modified proboscis is explained and illustrated, as is the evolution from fruit-piercing and sap-sucking to skin-piercing and blood-drinking. A surprising fact

about this unusual (for moths) behaviour – about which we do not want to give away too much here – is that only *Calyptra* males feed on blood, and it is not for the most likely reason. Of note here is the convincingly presented argument that *C. thalictri*, the only species of the genus occurring in Europe, is not naturally haematophagous although it may draw mammal blood under constrained conditions.

We are not only impressed by the exotic nature of the book's subject and the presented wealth of difficult-to-obtain observations, but also by the high quality of the colour photos, almost all of which were taken with analogous cameras, in some instances over 30 years ago. The book ends with a topic that puts these so-called "vampire" moths in a very current spotlight: the potential transmission of pathogens (which is unlikely and still unproven).

This fascinating book, written in a rich vocabulary, is highly recommended for all lepidopterists, as well as entomologists, biologists, ecologists, veterinarians and medical doctors with an interest in exotic species and unusual animal behaviour.

## In memoriam Professor Dr. Georg Benz (14. Juli 1926 – 15. Juni 2021)

Daniel Burckhardt<sup>1</sup>

<sup>1</sup> Naturhistorisches Museum, Augustinergasse 2, 4001 Basel, Switzerland

<http://zoobank.org/A9DD9E46-0F76-4C95-9E01-7E84EE6FB4DF>

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Academic editor: Thibault Lachat ♦ Received 30 August 2021 ♦ Accepted 4 November 2021 ♦ Published 22 November 2021

Kurz vor seinem 95. Geburtstag ist Professor Dr. Georg A. Benz am 15. Juni 2021 nach einem langen, erfüllten Leben verstorben. Seit 1991 war er Ehrenmitglied der SEG in Anerkennung seiner Verdienste um unsere Gesellschaft, der er seit 1960 als Mitglied angehörte. Im Vorstand war er von 1977–1982 Bibliothekar, von 1982–1991 Redaktor der Mitteilungen, von 1986–1988 Präsident und von 1989–1991 Vizepräsident. Während dieser Zeit war er auch Gastgeber mehrerer Jahresversammlungen sowie Organisator der ersten gemeinsamen Tagung mit der Deutschen Gesellschaft für allgemeine und angewandte Entomologie und der Österreichischen Entomologischen Gesellschaft 1981 in St. Gallen.

Georg Benz stammte aus Marbach SG, wo er auch aufwuchs. Sein Zoologie-Studium absolvierte er an der Universität Zürich. Dort erwarb er 1951 ausserdem das Diplom für das höhere Lehramt. Anschliessend arbeitete er über Insektenphysiologie bei Prof. V.B. Wigglesworth in Cambridge, UK. Von 1952–1956 war er Doktorand und Assistent von Prof. E. Hadorn an der Universität Zürich. Auf seine Promovierung mit der Dissertation über zwei Letalfaktoren von *Drosophila melanogaster* folgten drei Jahre als Forschungsassistent bei Prof. F.E. Lehmann am Zoologischen Institut der Universität Bern. Eine im Auftrag des Entomologischen Instituts der ETH absolvierte Ausbildung in Insektenpathologie führte ihn 1959–1960 nach Nordamerika (Insect Pathology Research Institute in Sault Ste. Marie, Ontario, Kanada und Department of Insect Pathology der University of California, Berkeley, bei Prof. E.A. Steinhaus). Seine dort geführten Untersuchungen über den Nukleinsäure Stoffwechsel gesunder und viröser Fichtenblattwespen bildeten die Basis für seine spätere Habilitationsarbeit.

Georg Benz trat 1960 als Mitarbeiter des Lärchenwickler-Projektes, in dem er die Pathologie und Physiologie betreute, ins Entomologische Institut der ETH Zürich ein. Mit dem 1963 erhaltenen Lehrauftrag für Insektenpathologie begann seine erfolgreiche Dozenten-

laufbahn. Es folgten die Habilitation an der Abteilung X der ETH für Pathologie und Physiologie der Insekten (1966), die Ernennung zum ausserordentlichen (1968) und zum ordentlichen (1972) Professor für Entomologie. Von 1972 bis zu seiner Emeritierung am 1. Oktober 1993 leitete er das Entomologische Institut (von 1972–1980 zusammen mit V. Delucchi). In seiner 30-jährigen Lehrtätigkeit an der ETH deckte er ein grosses und vielseitiges Angebot von Vorlesungen, Kursen und Exkursionen, die bei den Studenten besonders beliebt waren, ab. Seine Vorlesungen an den Abteilungen für Naturwissenschaften, Forstwirtschaft, Landwirtschaft, Pharmazie und Umweltwissenschaften reichten von Allgemeiner Biologie und Entomologie über Insektenpathologie, Insektenphysiologie und Insektenökophysiologie zu Forstentomologie. Seine pädagogische Ausbildung und sein gutes Gedächtnis halfen ihm, die Entomologie einem grossen Kreis von Studierenden näher zu bringen. Ähnlich vielfältig waren auch die Themen der vielen von ihm betreuten Diplomarbeiten und der 40 Doktorarbeiten. Neben dem Unterricht an der ETH hielt er zudem Gastvorlesungen an verschiedenen Universitäten in der Schweiz, Deutschland, Österreich und den USA. Als Forscher hinterlässt Georg Benz ein beachtliches Werk von 175 wissenschaftlichen Publikationen, das sein breites Interesse und seine grosse Kompetenz in verschiedenen Fachgebieten der Biologie reflektiert. Seine gute Beobachtungsgabe und der Sinn für relevante Fragen prägen seine Arbeiten. Eine Liste seiner Publikationen, die auch diverse Beiträge für mehrere internationale Standardwerke enthält, findet sich in einer anlässlich seines 80. Geburtstags publizierten Schrift (Burckhardt und Keller 2006). Neben Unterricht und Forschung war er zudem Redaktor und Fachberater mehrerer wissenschaftlicher Zeitschriften und Redaktor von drei Büchern. Ebenso war er Mitglied diverser Gremien: FAO-Experte in der Türkei, in Ruanda und Burundi, Council Member der ICIPE-Foundation (Stockholm), Mitglied

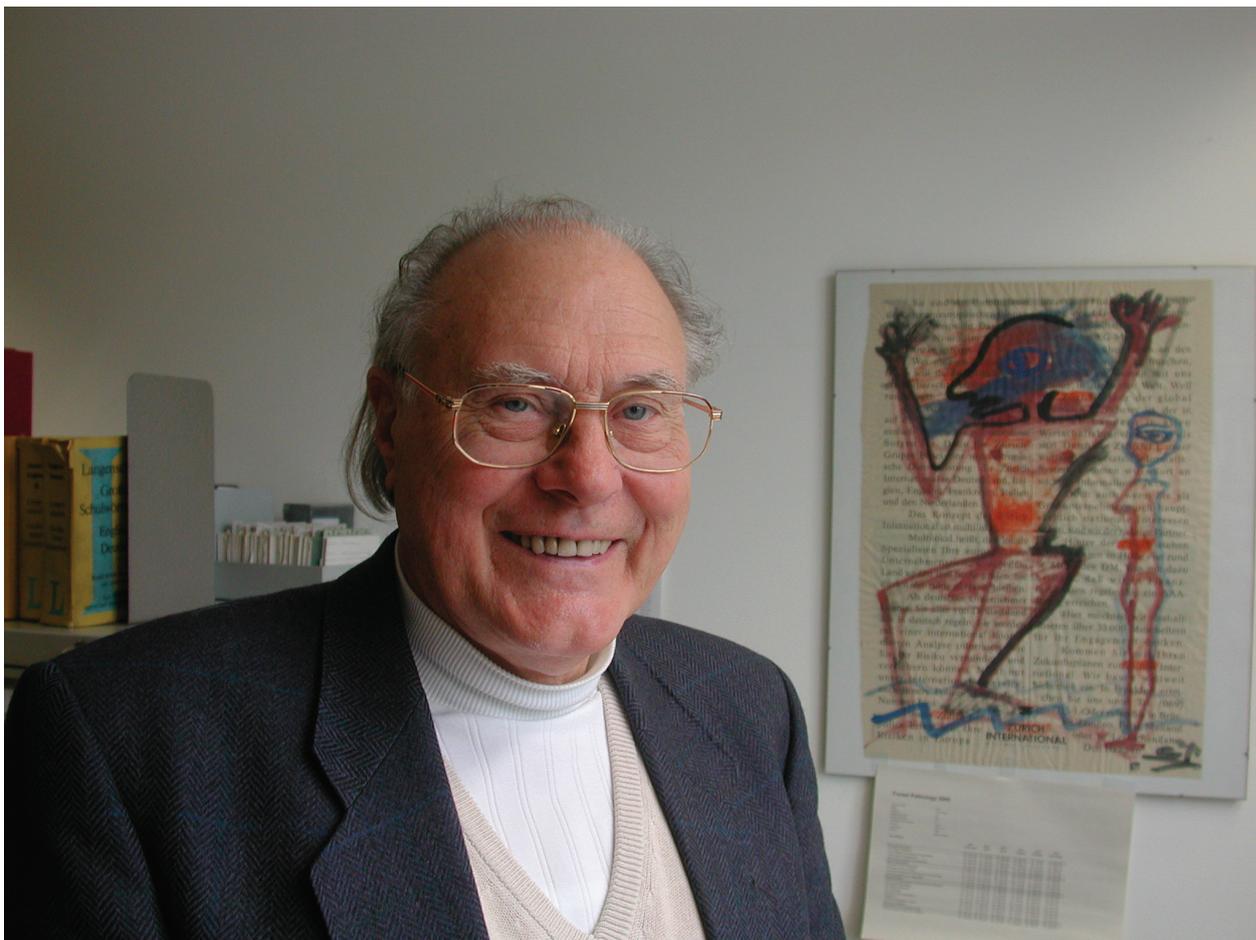


Abbildung 1. Georg Benz am 25. Februar 2005 in der ETH Zürich (Foto Ottmar Holdenrieder).

der OILB, in der er die Arbeitsgruppe «Virus Control of Orchard Tortricides» leitete und 1993 die Tagung der Arbeitsgruppe «Insect Pathogens and Insect Parasitic Nematodes» organisierte, sowie langjähriger Präsident der Forschungskommission der Schweizerischen Naturforschenden Gesellschaft (heute Akademie der Naturwissenschaften Schweiz).

Auch privat interessierte sich Georg Benz immer für die Zusammenhänge in der Natur, sei es auf Spaziergängen oder in seinem geliebten Garten, belegt durch die in seinem «Gartentagebuch» festgehaltenen Beobachtungen, das er seit seiner Emeritierung bis 2015 geführt hat. Neben den Naturwissenschaften war er an Politik interes-

siert und der Kunst zugetan. So war er ein guter Zeichner und Sänger, hörte gerne Musik und las gerne.

Das Interesse und die Faszination für die Natur begleiteten ihn durch das ganze Leben bis ins hohe Alter. Als enthusiastischen und engagierten Entomologen werden wir Georg Benz in Erinnerung behalten.

## Literatur

Burckhardt D, Keller S (2006) Zum 80.Geburtstag von Professor Dr. Georg Benz. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 79: 149–165. <https://doi.org/10.5169/seals-402917>

# Protokoll der Jahresversammlung der Schweizerischen Entomologischen Gesellschaft vom 5. März und 21. Juni 2021 via Videokonferenz

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Aufgrund der anhaltenden Corona-Pandemie musste die Jahresversammlung leider auf einen Tag reduziert werden und ohne physische Präsenz stattfinden. Sie wurde daher per Videokonferenz abgehalten. Der Präsident Oliver Martin hatte dafür ein Meeting via Zoom organisiert, das reibungslos ablief.

Trotz der erschwerten Umstände konnte ein interessantes Vortragsprogramm für die Jahresversammlung zusammengestellt werden. Den Themenschwerpunkt bildete die experimentelle Forschung mit Hymenopteren, jedoch aus ganz unterschiedlichen Fachgebieten. Das Programm startete mit dem Hauptvortrag von Yuko Ulrich, Professorin an der ETH Zürich, zum Thema Sozialverhalten und Krankheitsdynamik bei Ameisen. Darin gab sie einen Einblick, wie im Labor soziale Interaktionen und die Mechanismen der Entstehung von Arbeitsteilung untersucht werden. Als Modellorganismus diente die räuberische Ameisenart *Ooceraea biroi*, die keine Königinnen ausbildet. Stattdessen vermehren sich alle Individuen parthenogenetisch, was den Faktor der genetischen Varianz in Experimenten deutlich reduziert. Mittels Kameras über mehreren Dutzend Ameisenkolonien und Farbcodes auf den Tieren konnte das Verhalten und der Aufenthaltsort (im Nest oder ausserhalb des Nests) jedes Individuums analysiert werden. Dann wurde der Einfluss der Koloniegrosse, sowie der Mischung von Genotypen und Körpergrössen innerhalb einer Ameisengruppe auf das Verhalten der Tiere untersucht. Abschliessend berichtete Frau Ulrich über die neueste Forschung mit experimentell infizierten Ameisen. Von Pilzsporen befallene Tiere werden intensiver von Artgenossen betreut, wodurch ihre Überlebensrate stark steigt. In zukünftigen Studien sollen die genannten Untersuchungen über mehrere Generationen von Ameisen hinweg ausgedehnt werden.

Folgende fünf Vorträge wurden gehalten:

- Social behaviour and disease dynamics in clonal ant colonies.  
Yuko Ulrich, ETH Zürich
- Defensive symbionts protect aphids from parasitoid wasps depending on stable genotype-by-genotype interactions.  
Elena Gimmi, Eawag / ETH Zürich
- *Megachile sculpturalis* Smith, 1853 (Hymenoptera: Megachilidae), an Asian wild bee populates Europe.  
Julia Lanner, Universität für Bodenkultur Wien / Universität Bern
- Homemade or take away: Where do the cuticular hydrocarbons of parasitoid wasps come from?  
Corinne Hertäg, ETH Zürich
- Entwicklungsbiologische Ursachen sexueller Merkmale bei Mistkäfern: Wie macht man lange Beine?  
Patrick Rohner, Indiana University

Der ETH Zürich sei für das Zurverfügungstellen des Videokonferenzraums herzlich gedankt.

## Generalversammlung

### Begrüssung

Der Präsident Oliver Martin eröffnet die Generalversammlung um 13:30 Uhr und begrüsst die anwesenden 24 Mitglieder. Er kommuniziert eine

Änderung des Programms: Da der Bericht der Quästorin nicht vorliegt und an der ordentlichen Generalversammlung nicht präsentiert werden kann, wird zu diesem Punkt ein ausserordentlicher Teil der Generalversammlung per Videokonferenz später im Jahr abgehalten.

## Protokoll der Generalversammlung 2020 in Basel

Das Protokoll wird kommentarlos und unverändert genehmigt.

### Bericht des Präsidenten, Oliver Martin

#### Administratives

Im administrativen Bereich wurden wir 2020 wiederum durch das Centre Suisse de Cartographie de la Faune (CSCF) in Neuchâtel unterstützt. Die SEG ist Mitglied der Plattform Biologie der Akademie der Naturwissenschaften Schweiz (SCNAT) in Bern, und wird dort von der Geschäftsleiterin Pia Stieger betreut. <https://biol.scnat.ch/de>

#### Finanzielle Unterstützung

Die Gesuche des Präsidenten um finanzielle Unterstützung wurden von den angefragten Institutionen vollumfänglich bewilligt. Es handelt sich dabei um folgende Beträge: Akademie der Naturwissenschaften Schweiz (SCNAT) in Bern: CHF 13'155.–, Biedermann-Mantel-Stiftung in Zürich: CHF 6'000.– und Syngenta AG in Basel: CHF 6'000.–. Wir sind diesen drei Geldgebern für ihre wichtigen Beiträge sehr dankbar.

#### Jahresversammlung, Generalversammlung und Vorstandssitzungen

Die entomo.ch, die traditionell zweitägige Jahresversammlung fand am Freitag, 6. und Samstag, 7. März 2020 am Naturhistorischen Museum Basel statt. Wir danken Matthias Borer und seinem Team am Museum ganz herzlich für die hervorragende Organisation des Anlasses. Die Generalversammlung der SEG fand am Samstag, 7. März 2020 von 10 bis 11 Uhr ebenfalls am Naturhistorischen Museum Basel statt. Die beiden regulären halbjährlichen Vorstandssitzungen fanden am Freitag, 6. März am Naturhistorischen Museum in Basel und am Mittwoch, 4. November 2020 online via Zoom statt.

#### Website

Die Website der SEG, u.a. mit Information zur Jahrestagung entomo.ch, war auch dieses Jahr wieder im Portal Naturwissenschaften Schweiz der Akademie der Naturwissenschaften Schweiz (SCNAT) abrufbar. Für

die Betreuung danke ich Mariella Hobi, Nicola Frieden (beide Support) und Andres Jordi (Webredaktion). <https://entomo.ch/de>

#### Digitalisierung von entomologischen Zeitschriften

Die Projekte der SEG zur Digitalisierung von entomologischen Zeitschriften laufen weiter. Zusätzlich zu den bisher digitalisierten Zeitschriften, werden künftig auch sämtliche Bände der folgenden Zeitschriften im pdf-Format online zugänglich sein: "Entomologica Basiliensia" und "Entomologica Basiliensia et Collectionis Frey" (in Kollaboration mit dem NHM Basel), "Bulletin Romand d'entomologie", und "Entomo Helvetica". Die Ansprechpartnerin für die SEG war weiterhin Regina Wanger, Leiterin des DigiCenters der ETH-Bibliothek in Zürich. [www.e-periodica.ch](http://www.e-periodica.ch)

#### Insekt des Jahres

In Zusammenarbeit mit Entomologen aus Deutschland und Österreich wurde die Dänische Eintagsfliege (*Ephemera danica*, Ephemeroptera) zum Insekt des Jahres für das Jahr 2021 bestimmt. Dazu wurde wiederum ein Flyer publiziert, welcher über die SEG bezogen werden kann. [https://entomo.ch/de/portrait/insect\\_of\\_the\\_year/insect\\_of\\_the\\_year\\_2021](https://entomo.ch/de/portrait/insect_of_the_year/insect_of_the_year_2021)

Im Namen des Vorstandes und der Mitgliedschaft der SEG danke ich allen erwähnten Institutionen, Gremien und Personen nochmals ausdrücklich für ihre wertvolle Unterstützung und ihren Einsatz!

### Bericht des Bibliothekars, Philippe Jeanneret

En 2020, il n'y a pas eu d'activité de la bibliothèque de la Société.

### Bericht des Redaktors der Fauna Helvetica, Daniel Burckhardt

Im Berichtsjahr wurde kein Band publiziert, es sind aber zwei Manuskripte schon weit fortgeschritten. Für die gute Zusammenarbeit mit dem CSCF möchte ich dem Leiter Dr. Yves Gonseth und seinen Mitarbeiterinnen und Mitarbeitern ganz herzlich danken.

### Bericht des Chefredaktors von Alpine Entomology, Thibault Lachat

The fourth edition of Alpine Entomology was delivered at the beginning of 2021. The new issue of our journal included 18 articles across 194 pages: 13 research articles, 1 checklist, 1 short communication, 1 book review, 1 in memoriam, and the yearly report of the SES. Ten different nationalities were represented among the authors of the

published articles, fitting our goal to gain importance at the international level. However, authorships remain dominated by Swiss entomologists.

Two new subject editors have joined the editorial board, which is now composed of 24 specialists. Thanks to the excellent contributions of the subject editors and the permanent support of Pensoft, we could significantly reduce the mean duration for acceptance of a manuscript.

Since late autumn 2020, we have experienced a strong decrease in submitted manuscripts, which might impact on the number of published manuscripts for the next issue. Different measures have already been discussed with Pensoft and the editorial board in order to secure a consistent flow of manuscripts.

## Bericht der Quästorin, Emanuela Leonetti

Da der Bericht nicht zur regulären Generalversammlung im März vorlag, wurde am 21. Juni 2021 eine ausserordentliche Versammlung per Videokonferenz abgehalten.

Aus der Jahresrechnung 2020 von Frau Leonetti ist folgende Tabelle entnommen:

Positionen / Objets	Ausgaben / Dépenses	Einnahmen / Revenus
Publikationskosten / Charges de publications:		
Publikation AE - impression	6'618,73	
Pensoft: Website, Open access	16'260,75	
Publikation „Fauna Helvetica“	70,84	
Verwaltung / Administration	5'518,40	
Beitrag sc nat / Cotisation sc nat	1'673,00	
Arbeitsgruppenförderung / Groupes soutien de travail	1'463,12	
Verkauf Mitteilungen / Ventes bulletins		1'403,50
Mitgliederbeiträge / Cotisations		13'925,70
Verkauf Fauna Helvetica / Ventes Fauna Helvetica		8'809,78
Beiträge / Subventions :		
sc nat		4'688,12
Syngenta		6'000,00
Biedermann-Mantel-Stiftung		6'000,00
Spenden und sonstige Einnahmen / Dons et autres produits		135,40
Zinsen / Intérêts :		
SEG-Konten / Comptes SEG	51,60	
Fauna Helvetica-Konto / Compte Fauna Helvetica	60,00	
Erhöhung von Rücklagen / Augmentation de réserve (résultat Fauna Helvetica)	8'678,94	
Total / Total	<b>40'395,38</b>	<b>40'962,50</b>
Jahresgewinn / Bénéfice annuel 2020	<b>567,12</b>	
	40'962,50	40'962,50

Die Erfolgsrechnung für das Jahr 2020 schloss mit einem Gewinn von CHF 567,12.- und einem Vermögen von CHF 109'983,31.-.

## Bericht der Rechnungsrevisoren, Michel Sartori und Christian Monnerat

Sehr geehrte Damen und Herren

Als Kontrollstelle der Schweizerischen Entomologischen Gesellschaft und der Entomo Helvetica haben

wir die Jahresrechnung 2020 geprüft. Dabei stellten wir fest, dass:

- die Eröffnungsbilanz, der Jahresabschluss und die Betriebsrechnung der Rechnungserlegung entsprechen
- die Belege konform und genau sind und den gewöhnlichen Aktivitäten der SEG entsprechen
- das Vermögen der Gesellschaft dem Aktivkonto der Bilanz (Liquidität + Transitorische) entspricht.

Für ihren Teil gewährleistet die Kassiererin, dass die Buchführung, im Rahmen ihrer Befugnisse, korrekt und nach den Prinzipien der Formel des Obligationencodes (CO 959 t 662a/2) durchgeführt wurde.

Deshalb beantragen wir der Mitgliederversammlung, die vorliegende Jahresrechnung zu genehmigen und der Quästorin Entlastung zu erteilen.

Der Quästorin wird von den anwesenden Mitgliedern einstimmig Decharge erteilt.

## Budget und Mitgliederbeiträge

### Budget

Der Präsident stellt das Budget für 2021 vor, welches wiederum einen Gewinn von CHF 0.- vorsieht.

### Mitgliederbeiträge 2021

Die Beiträge bleiben erneut gleich: Mitglieder in der Schweiz zahlen CHF 60.-, Studierende oder sich anderweitig in Ausbildung befindende Mitglieder zahlen während drei Jahren nur die Hälfte des ordentlichen Beitrags (CHF 30.-). Mitgliedern im Ausland, die die gedruckte Version von Alpine Entomology wünschen, werden zusätzlich CHF 15.- Versandkosten verrechnet.

Das Budget und die Mitgliederbeiträge werden einstimmig genehmigt.

## Personelles

### Todesfälle

Den verstorbenen SEG-Mitgliedern Michele Aberhalden (Mitarbeiter Info Fauna und Naturhistorisches Museum Lugano; 1969–2020), Claude Henri Besuchet (Konservator Naturhistorisches Museum Genf; 1930–2020), Renate Gyax-Däppen (1937–2020), Charles Maquelin (Mitarbeiter Zentrum für Bienenforschung Liebefeld; 1933–2019), Willi Sauter-Niederer (Professor ETH Zürich, ehem. Vorstandsmitglied, Präsident und Ehrenmitglied der SEG; 1928–2020), Jean-Michel Studer (1944–2020) und Erwin Steinmann-Gredinger (1923–2020) wird mit einer Schweigeminute gedacht.

## Jahresversammlung 2022

Ende der Generalversammlung um 14:13 Uhr.

Die nächste Jahresversammlung, die entomo.ch 2022, soll am 4. und 5. März im Museo cantonale di storia naturale in Lugano stattfinden.

Walterswil SO im Oktober 2021,  
der Sekretär Marc Neumann.

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# Five years of *Alpine Entomology*, the international journal on mountain insects

Thibault Lachat<sup>1,2</sup>, Oliver Y. Martin<sup>3</sup>

<sup>1</sup> Editor in Chief, Bern University of Applied Sciences, Zollikofen, Switzerland

<sup>2</sup> Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland

<sup>3</sup> President of the Swiss Entomological Society and member of the editorial board, Department of Biology & Institute of Integrative Biology, ETH Zürich, Switzerland

<http://zoobank.org/102545FC-A303-4328-88C0-B2BB2022032F>

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Published 22 November 2021

With this new issue, our journal *Alpine Entomology* celebrates its 5<sup>th</sup> anniversary. From the very beginning, it was clear for the Swiss Entomological Society that our journal would not solely focus on insects from the Alps. *Alpine Entomology* should be very much perceived as an international journal for mountain entomology worldwide. At first sight, the term mountain seems to be simple to define. Nevertheless, in reality, these rugged structures in the landscape are not that easy to delineate, and mountains can be defined in different ways (see e.g., Körner et al. 2021). For this reason, when we evaluate each manuscript submitted, we also consider the landscape and taxonomic context of the study. It is important to note that our journal is not restricted to insects, because articles focusing on other mountain arthropods are also welcome. In summary, *Alpine Entomology* publishes articles on all aspects of arthropods from the Alpine region and other mountainous regions all over the world.

Similar to many other species groups, insects are affected by the biodiversity crisis caused by land use and climate changes, over or under use of resources, pollution, and invasive alien species (IPBES 2019). After the famous Krefeld study, which highlighted a loss of 75% of the insect biomass over the last 27 years in protected areas in Germany (Hallmann et al. 2017), further scientific articles and reviews have been published on this topic (e.g., Seibold et al. 2019; Wagner 2020). Nowadays, it is obvious, that the diversity and biomass of insects are strongly threatened globally. Nevertheless, not all insect populations are decreasing. Some thermophilous species can benefit from climate change and hence expand their population size and their distribution (e.g., Roth et al.

2021). There are also examples of increasing insect populations due to successful conservation measures (e.g., Walter et al. 2017).

A comprehensive recent study published in a Swiss Academic Report (Widmer et al. 2021) concluded that conservation measures are urgently needed to avoid dramatic losses of insects and the valuable ecosystem services they provide. This is necessary for all activity sectors such as agriculture, forestry, and energy production. Among other measures, this report recommends an intensification of species monitoring and research activities in entomology, and an improvement in knowledge transfer. Our journal, *Alpine Entomology*, fulfills this goal extremely well. As an open-access journal, we aim at publishing *inter alia* research and review articles, short communications and checklists on arthropods not only from the Alps but also from other mountainous regions. In doing so, we contribute to the dissemination of knowledge on insects to a broad audience. For example, more than twenty articles published in *Alpine Entomology* since 2017 have acquired more than 2'000 unique views.

To improve the international impact and scientific quality of *Alpine Entomology*, we can now count on our recently formed editorial board. The board members will act as ambassadors for our journal outside of Switzerland, as well as support us in our strategic decisions.

Our Editorial board is currently composed of the following people:

Prof. Dr. Thibault Lachat, Editor in chief, Bern University of Applied Sciences

Dr. Oliver Martin, President of the Swiss Entomological Society, ETH Zurich  
 Dr. Yves Basset, Smithsonian Tropical Research Institute, Panama  
 Prof. Dr. Inon Scharf, Tel Aviv University  
 PD Dr. Seraina Klopstein, Natural History Museum, Basel  
 Prof. Dr. Lyubomir Penev, Managing Director and Founder of Pensoft Publishers

We are open to extending this board by inviting a few additional members, and especially hope to recruit international researchers working in regions not currently represented.

A few weeks ago, we launched our first topical collection, a step that should also help to increase the attractiveness of our journal. This collection is focused on arthropods associated with aquatic ecosystems in mountainous regions.

Aquatic ecosystems and especially running waters represent some of the most impacted environments on the planet. Furthermore, aquatic invertebrates are key indicators of global or local changes, and many aquatic ecosystems are closely linked to mountains as they originate in them.

With this open collection, *Alpine Entomology* now provides authors with an opportunity to submit manuscripts based on already available data with clear evidence for changes/trends in aquatic arthropods (even where sampling designs were not initially conceived for this goal). Such studies would be highly relevant to improving our understanding of developments concerning arthropod populations and knowledge of aquatic species.

With this initiative, we aim to provide a platform for scientists to publish research articles or short notes on trends and/or changes in biogeography, species community or distribution, as well as behavior, or morphology of aquatic arthropods from mountainous regions. The editors of this collection (Jean-Luc Gattolliat and Dávid Murányi) will be inviting authors to submit their manuscript and will offer a fee waiver for invited contributions. The topical collection is also open to relevant additional contributions (for details see [https://alpineentomology.pensoft.net/special\\_issues](https://alpineentomology.pensoft.net/special_issues)).

Over the next months, we plan to launch further topical collections and therefore hope to offer attractive avenues for researchers to publish their results in our journal. The editorial board will be involved in evaluating suggestions for future topics, as well as recruiting new topics in a targeted fashion.

After five years of existence, *Alpine Entomology* has already surmounted different challenges. Since 2019, our journal has been indexed in Emerging Sources Citation by

Clarivate Analytics and since 2020, we are also indexed by Scopus. One of our goals for the next years will be to obtain an impact factor from Clarivate. This would provide a clear signal that our journal is well established and recognized in the scientific community. To reach this goal, we need to recruit and secure a consistent flow of manuscripts aiming at *ca.* 20–25 published papers per year. Of course, the quality of our published articles must also be guaranteed. Fortunately, for this we can continue to count on the strong support of our expert subject editors and the numerous reviewers. Here, we would like to take the opportunity to thank all those involved for their essential contributions to our journal over the years since its creation.

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