Alpine Entomology

7 2023

PENSOFT.

The Journal of the Swiss Entomological Society

Alpine Entomology

Editor-in-Chief

Jessica Litman
Muséum d'histoire naturelle de Neuchâtel
Neuchâtel, Switzerland
jessica.litman@unine.ch

Editorial Secretary

Boryana Ovcharova
Pensoft Publishers, Sofia, Bulgaria
e-mail: journals@pensoft.net

Editorial Board

Jessica Litman, Neuchâtel, Switzerland
Yves Basset, Washington, DC, United States of America
Hannes Baur, Bern, Switzerland
Seraina Klopfstein, Basel, Switzerland
Dominique Mazzi, Cadenazzo, Switzerland
Lyubomir Penev, Sofia, Bulgaria
Inon Scharf, Tel Aviv, Israel

Subject Editors

Hannes Baur, Bern, Switzerland
Christophe Bouget, Nogent-Sur-Vernisson, France
Stève Breitenmoser, Nyon, Switzerland
Claudia Buser, Zürich, Switzerland
Yannick Chittaro, Neuchâtel, Switzerland
Stefan Dötterl, Salzburg, Austria
Peter Duelli, Birmensdorf, Switzerland
Jean-Luc Gattolliat, Lausanne, Switzerland
Christoph Germann, Basel, Switzerland
Peter Huemer, Innsbruck, Austria
Philippe Jeanneret, Zürich, Switzerland
Christian Kropf, Bern, Switzerland
Thibault Lachat, Zollikofen, Switzerland
Bernard Landry, Geneve, Switzerland
Jessica Litman, Neuchâtel, Switzerland
Oliver Martin, Zürich, Switzerland
Marco Moretti, Birmensdorf, Switzerland
Roland Mühlethaler, Berlin, Germany
Andreas Müller, Wädenswil, Switzerland
Dávid Murányi, Eger, Hungary
Patrick Rohner, San Diego, United States of America
Andreas Sanchez, Neuchâtel, Switzerland
Stefan Schmidt, Munich, Germany
Dagmara Żyła, Hamburg, Germany

Alpine Entomology

2023. Volume 7

ISSN: 2535-0889 (online)

Photo
The cover picture shows the predatory beetle *Licinus depressus* holding onto a prey snail (*Chondrina arcadica*) with its forelegs and breaking through the shell wall with its asymmetrical mandibles. Drawing: Armin Coray. See paper of **Baur B, Gilgado JD, Coray A** Prey handling and feeding habits of the snail predator *Licinus depressus* (Coleoptera, Carabidae).

Alpine Entomology

Content of volume **7** 2023

The Journal of the Swiss Entomological Society (SES)
Die Mitteilungen der Schweizerischen Entomologischen Gesellschaft (SEG)
Le Bulletin de la Société Entomologique Suisse (SES)
Il Bollettino della Società Entomologica Svizzera (SES)

Alpine Entomology

Content of volume **7** 2023

Alpine Entomology 7 2023, 1–11 | DOI 10.3897/alpento.7.98799

PENSOFT.
Alpine Entomology

On the occurrence of relict populations of *Pytho abieticola* J. R. Sahlberg, 1875 in Switzerland (Coleoptera, Pythidae)

Yannick Chittaro[1], Andreas Sanchez[1], Alexander Szallies[2], Martin M. Gossner[3,4], Thibault Lachat[3,5]

1 *info fauna, Avenue de Bellevaux 51, CH-2000 Neuchâtel, Switzerland*
2 *ZHAW Zürcher Hochschule für Angewandte Wissenschaften, Wädenswil, IUNR, Grüenthalstrasse 14, CH-8820 Wädenswil, Switzerland*
3 *Forest Entomology, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*
4 *Department of Environmental Systems Science, Institute of Terrestrial Eco-systems, ETH Zurich, Universitätstrasse 16, CH-8006 Zürich, Switzerland*
5 *School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences, Länggasse 85, CH-3052 Zollikofen, Switzerland*

https://zoobank.org/5013AEC9-A199-4B40-92D2-909F7F8E5CC6

Corresponding author: Yannick Chittaro (yannick.chittaro@infofauna.ch)

Academic editor: C. Bouget ♦ **Received** 13 December 2022 ♦ **Accepted** 7 February 2023 ♦ **Published** 8 March 2023

Abstract

Several adults and larvae of *Pytho abieticola* were discovered in 2021 and 2022 at three different localities in two regions of Switzerland, the Jura mountains and the Swiss National Park in the Eastern Alps. This very rare saproxylic beetle has not been detected in Switzerland so far. Considered a relict of primeval forests, it is in strong decline or has already disappeared from large areas of Central Europe. The isolated Swiss populations are the westernmost in its distributional range. Information on the ecology and distribution of *P. abieticola* in Switzerland and Europe is provided and criteria to distinguish *P. abieticola* from the congeneric and syntopic *P. depressus* are defined.

Key Words

log, conifer, subcortical, deadwood, faunistics, new record, distribution

Introduction

Within the family Pythidae, the genus *Pytho* Latreille, 1796 includes ten species, six of which are found in the Palaearctic region (Háva and Zahradník 2021). All species of the genus are saproxylic, with larvae and adults living under the bark of dead conifers (Pollock 1991). Three of them occur in Europe: *Pytho depressus* (Linnaeus, 1767), which is fairly widespread, and the rare *P. abieticola* J. R. Sahlberg, 1875 and *P. kolwensis* C. R. Sahlberg, 1833, which mainly occur in Fennoscandia and Russia (Pollock 2008, 2020). In Central Europe, *P. abieticola* is only represented by very isolated populations. Its sharp decline, relict distribution, and specific ecological requirements justify its presence on the list of primeval forest relict species of Central Europe in category 1, which includes species restricted to a few remnants of natural forests (Eckelt et al. 2017).

In Switzerland, only *P. depressus* was known until now (Chittaro and Sanchez 2016). However, in 2021 and 2022, several specimens of *P. abieticola* were found at different localities. These first Swiss data are presented here and the situation of the species in Europe is discussed. Furthermore, information on its ecology and identification criteria are provided.

Materials and methods

In 2021 and 2022, the authors carried out different independent inventories of saproxylic beetles at three localities in Switzerland (the precise locations of these sensitive sites are not provided here, but the data have been deposited in the national database info fauna, www.infofauna.ch).

Ponts-de-Martel Valley

This site is located in the Ponts-de-Martel Valley in the canton of Neuchâtel, in the heart of the Jura mountains. It is a peat bog of national importance, located about 1000 m above sea level. Scattered stands of birch (*Betula pendula* Roth, *B. pubescens* Ehrh., *B. nana* L.) are present (Fig. 1A) but the site also includes denser forest areas consisting largely of Swiss mountain pine (*Pinus mugo uncinata* (DC.) Domin), and spruce (*Picea abies* (L.) H. Karst.) (Fig. 1B). These coniferous forests have existed for a long time: they were already marked on the first edition of the Siegfried National Map published in 1886 (Federal Office of Topography swisstopo; Journey through time – Topographic maps) and possibly also on the Dufour map of 1849 (but the symbolism used at that time was not always clear).

Between April and September 2022, ten "Polytrap" flight interception traps (Brustel 2012) were placed in different forest associations (according to Richard 1961), in particular in *Pino mugo-sphagnetum* (climax forest association of the peat bogs) and in *Sphagno-piceetum betuletosum* (sphagnum-rich waterlogged spruce forests, typical of undisturbed peat bog belts).

Saignelégier region

This site is located in the region of Saignelégier in the canton of Jura, about 40 km from the Ponts-de-Martel Valley. It is also a peat bog of national importance. Situated at about 1000 m a.s.l., its vegetation is identical to that of the first site (Fig. 2) and also shows significant temporal continuity. This site was studied precisely because it was very similar to the first one, which had proved to be of great faunistic interest. Here, research was conducted for only one day in the fall. Larvae and adults in pupal cells of *Pytho* species were searched for under the bark of spruce (Fig. 2) and Swiss mountain pine logs.

Swiss National Park

The third record site is the Swiss National Park in the eastern Alps of Switzerland, a high-altitude region near the borders with Austria and Italy. The Swiss National Park is a strict nature reserve left to its own natural development (no habitat management since 1914 (Parolini 2012)). One third of its 170 km^2 area is forested (Baur and Scheurer 2014). The higher elevations and southern slopes are dominated by Swiss mountain pine, interspersed with Arolla pine (*Pinus cembra* L.), while in the lower and northern exposed parts spruce, Scots pine (*Pinus sylvestris* L.) and European larch (*Larix decidua* Mill.) are the main forest-forming trees.

Sampling sites investigated with "Polytrap" flight interception traps were established in various regions of the national park in 2021 and 2022, e.g. at Plan Praspöl (1650 m a.s.l., Fig. 3, from May to August 2021) and in various mountain spruce sites such as Stabelchod (1900 m a.s.l., from May to August 2021 and 2022). Several days each year were also spent actively searching for individuals to supplement the list of species obtained by trapping.

Results

A total of 29 adults and several dozen larvae of *Pytho abieticola* (Figs 5, 7) were found in 2021 and 2022 at the three sampled localities. The species is new to the Swiss fauna.

Ponts-de-Martel Valley

Switzerland • 3 ♂, Neuchâtel, Ponts-de-Martel Valley, 1000 m a.s.l, 29 Apr.–23 May 2022 (2 ♂) and 23 May–22 Jun. 2022 (1 ♂), Chittaro Y. leg., flight interception traps, Chittaro Y. coll.

These specimens were intercepted at three trap sites about 50 m apart in the *Sphagno-piceetum betuletosum* forest association. The traps were placed near trunks of cut Swiss mountain pine and spruce that had been felled in previous years (to limit public access to this site) and placed on the ground. The traps were hung directly on spruce trees, including one on a dead standing tree.

Further searches in the summer and autumn in the immediate vicinity of the traps where adults had been captured revealed several dozen larvae as well as about ten adults of the congeneric *P. depressus* in pupal cells under the bark of pine and spruce logs on the ground, but no other pre-imaginal stages (larvae and pupae) or adults of *P. abieticola* were found.

Saignelégier region

Switzerland • 1 ♂, 1 ♀, Jura, Saignelégier region, 970 m a.s.l., 20 Oct. 2022, Sanchez A. and Chittaro Y. leg. and coll., under decayed bark of a spruce trunk.

Both specimens were found in a small spruce forest at the edge of a peat bog (*Sphagno-piceetum betuletosum* forest association). They were in pupal cells under the bark of a spruce trunk of about 30 cm diameter, cut in previous years along a forest path and partially lying above the ground, supported by its branches. The bark was missing for about one half of the length of the trunk (Figs 2, 4). The remaining bark could be easily detached by hand. Eight specimens of *P. depressus* were also found under the same bark (Fig. 4), as well as several specimens of *Ips typographus* (Linnaeus, 1758) (Curculionidae), *Rhagium inquisitor* (Linnaeus, 1758) (Cerambycidae) and *Rhizophagus dispar* (Paykull, 1800) (Monotomidae).

Figure 1. General views of the study site of the Ponts-de-Martel Valley. **A.** Deciduous forest clusters, mainly composed of birch; **B.** Denser forest areas composed of Swiss mountain pine and spruce. (Photos: A. Sanchez).

Figure 2. General view of the study site in the region of Saignelégier. (Photo: A. Sanchez).

Swiss National Park.

Switzerland, Grisons, Swiss National Park • 8 ♂, 6 ♀, Plan Praspöl, 1680 m a.s.l., 2–23 Jun. 2021, WSL leg., flight interception traps • 1 ♂, 1 ♀, Stabelchod, 1900 m a.s.l., 28 May–17 Jun. 2021 (1 ♂), 17 Jun.–7 Jul. 2021 (1 ♀), Abenis AG leg., flight interception traps • 1 ♂, 1 ♀, several larvae, Laj dad Ova Spin, southeastern end, 1670 m a.s.l., 18 May 2022, Szallies A. leg., under decayed bark of Swiss mountain pine • 5 ♂, 1 ♀, several larvae, Plan Praspöl, slope towards Laj dad Ova Spin, 1670 m a.s.l., 12 Oct. 2022, Szallies A. leg., under decayed bark of three different spruce trees of about 25 cm diameter. Voucher specimen will be deposited in the collections of A. Szallies, the Bündner Naturmuseum Chur and the Naturhistorisches Museum Basel.

Figure 3. General view of the study site in Plan Praspöl. (Photo: B. Wermelinger).

Figure 4. A. Spruce trunk in the Saignelégier region where adults of *P. abieticola* and *P. depressus* were found under the bark; **B.** A close-up to show the appearance under the bark. (Photos: A. Sanchez).

At Plan Praspöl, the specimens were sampled in 5 of 11 installed polytraps running from May to August 2021. Four of these 5 traps were installed at sites with high amount of lying and standing dead wood (Fig. 3). At Stabelchod, a Swiss mountain pine forest with a southern exposure, no additional specimens were found, despite an intensive active search, and it is likely that the trapped specimens originated in the wetter neighbouring forests.

The four trees with larvae of *P. abieticola* (three spruce and one Swiss mountain pine) were lying horizontally just above ground in a very humid and moist environment on the steep slope to the Spöl stream near Laj dad Ova Spin. The bark was heavily infested with fungi and no other beetle species were present. In the areas above the wet steep Spöl slope, only *P. depressus* was found, which apparently lives in drier habitats with fewer fungi.

Discussion

Diagnosis

Identification keys for adults of *Pytho* species were proposed by Kaszab (1969), Burakowski (1976), Iablokoff-Khnzorian (1985), Pollock (1991) and Háva and Zahradník (2021). *Pytho abieticola* differs from *P. depressus* on the basis of several characters, the most relevant of which are listed below:

1 Body black, elytra black without any metallic lustre, brown when immature. Abdomen blackish or brown, sometimes dark reddish. Pronotum more evenly rounded, its greatest width at midlength (Fig. 5). Aedeagus short, with short parameres (Fig. 6A). Last segment of maxillary palpi hardly widened (Fig. 6C). Labrum 2.5 times wider than long. Small body size (7–11 mm) .... *P. abieticola* (Fig. 5A, B)

– Body black, elytra with blue or green metallic lustre, sometimes testaceous or bicoloured, very rarely black or brown. Abdomen yellowish. Pronotum unevenly rounded, its greatest width well before the middle, in the upper third (Fig. 5). Aedeagus long with long parameres (Fig. 6B). Last segment of maxillary palpi enlarged (Fig. 6D). Labrum three times wider than long. Large body size (7–16 mm, but usually 10–14 mm)........ *P. depressus* (Fig. 5C, D)

Identification keys of larvae are provided by Burakowski (1976), Iablokoff-Khnzorian (1985) and Pollock (1991). These are modified below to discriminate *P. abieticola* larvae from those of *P. depressus*. Additional criteria were provided by Siitonen J. (pers. comm.).

1 Inner margin of urogomphi arched with two teeth, the anterior (closer to base) twice as large as the posterior (closer to tip). Posterior margin of tergite 9 with 7–9 (mostly 8) tubercles of different sizes which are unevenly spaced, so that the middle pair of teeth is further from the group of three other teeth (Fig. 7C). The tips of tubercles are directed backwards (Fig. 7E). Abdominal terga 1–8 mesally with paired, raised, parabasal ridge processes weakly marked and short, occupying less than one-fifth of the length of the terga (Fig. 7A). The chitin plate (urogomphal lip) between the urogomphi is slightly curved, often slightly incurved in the middle. Body greyish pale, reaching 18–28 mm (according to Iablokoff-Khnzorian (1985))........ *P. abieticola* (Fig. 7A)

– Inner margin of urogomphi arched, each urogomphus with two small, equal teeth. Posterior margin of tergite 9 with 11–16 (mostly 12) almost identical tubercles, arranged in a regular and very smoothly curved arc (Fig. 7D). The tips of tubercles are directed forwards (Fig. 7F). Abdominal terga 1–8 mesally with paired, raised, parabasal ridge processes, clearly marked, occupying one third of the length of the terga (Fig. 7B). The chitin plate (urogomphal lip) between the urogomphi straight-edged. Body yellowish pale, reaching 22–30 mm .... *P. depressus* (Fig. 7B)

Distribution and status

To place our records in a broader geographical context, we sought as much data as possible. Data published on GBIF.org (2022), which are very complete for Fennoscandia and Austria, were used as a basis. Additionally, we searched for further data from various Central European publications. Other data certainly exist in museums or in scattered publications, but the map below (Fig. 8) gives a good overview of the general distribution of *P. abieticola* in Europe. Although data for the Eastern Palaearctic region is scarce, the species appears to be widespread in Russia, from Karelia (Painter et al. 2007; Laaksonen et al. 2008) to Yakutia (now Republic of Sakha) (Iablokoff-Khnzorian 1985). A few localities were mentioned, for example, in Sergeeva and Stolbov (2020) and Yuferev (1986). *Pytho abieticola* also occurs in northern China (Painter et al. 2007).

In the Fennoscandinavian countries, the species is widespread in Sweden (SLU Artdatabanken 2022) and Finland (Rassi et al. 2015, and laji.fi), while it is rare in Norway, where its distribution is restricted to the easternmost part near the Swedish border.

In the Baltic States, its presence was recently confirmed in Estonia using flight interception traps in old-growth forests (Roosileht U., pers. comm.; unpublished data). The species is not known in Latvia or Lithuania and its occurrence is considered unlikely (Telnov D., pers. comm.).

In Central Europe, the species has a relict distribution in isolated populations, often occurring in mountains (Iablokoff-Khnzorian 1985). In Poland, Kubisz et al. (2014) give a few localities and state that it is a rare species with a scattered distribution, a situation identical to that in the Czech Republic (Horion 1956; Heyrovský 1960; Streček 1988; Vávra and Stanovský 2013; Horák 2017). In Slovakia, the only known record is mentioned by Švec (1984). In Austria, only a few old records are known (Reitter 1892; Franz 1974), the last from 1909. In Germany, the only known record dates to 1959 (“Kreuzlinger Forst bei München von M. Hüther” in Horion 1960). However, this observation is considered doubtful, as it is not supported by a specimen in the Hüther collection in the Zoologische Staatssammlung München (Hendrich L., pers. comm.). Furthermore, it purportedly comes from an unsuitable forest site where the congeneric species *P. depressus* occurs (Bussler H. and Fuchs H., pers. comm.).

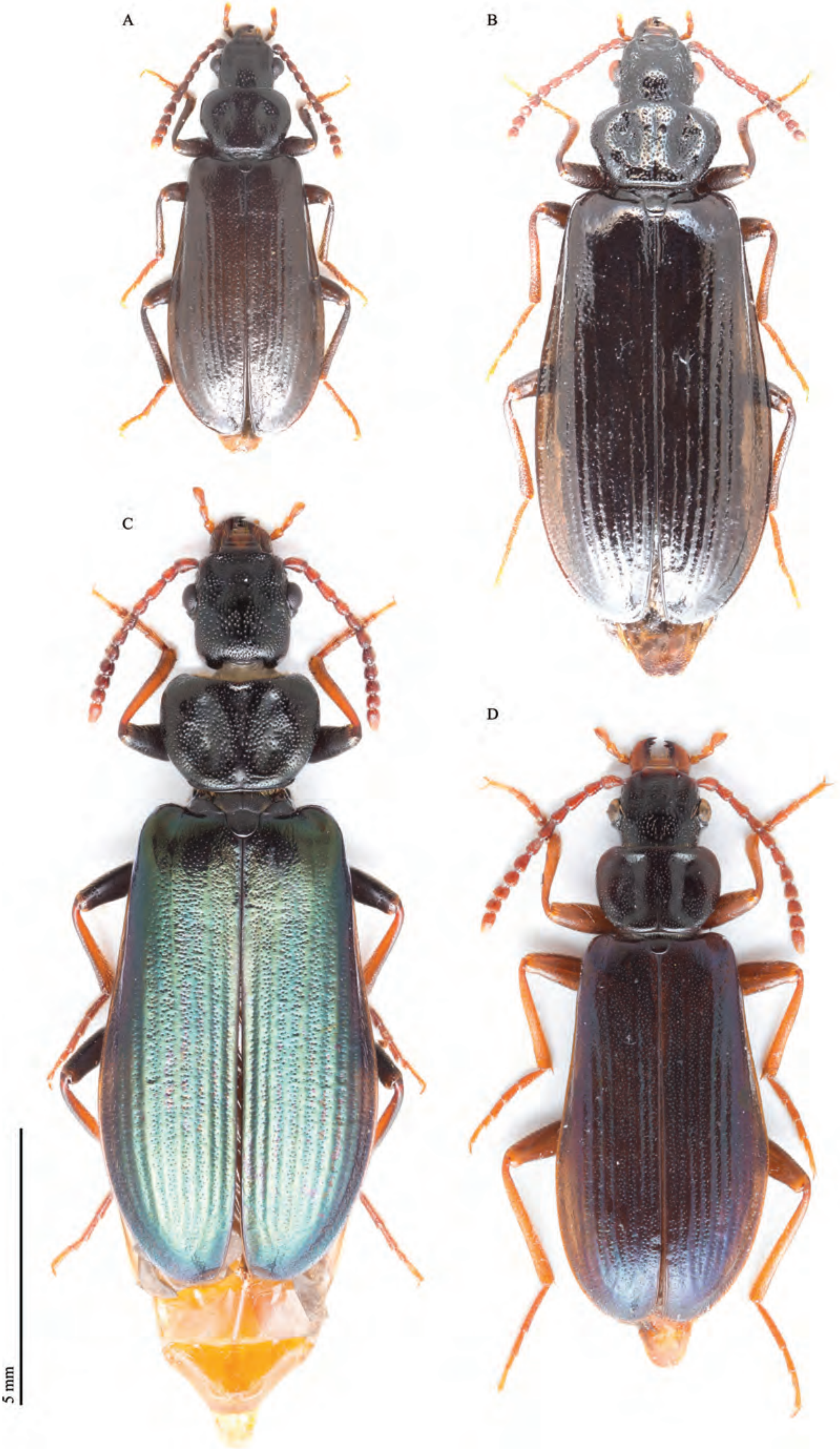


Figure 5. Habitus of **A.** *P. abieticola* male (Ponts-de-Martel Valley); **B.** *P. abieticola* female (Swiss National Park); **C.** *P. depressus* female (Ponts-de-Martel Valley); **D.** *P. depressus* male (Ponts-de-Martel Valley). (Photos: A. Sanchez).

Figure 6. Male genitalia in ventral view of **A.** *P.abieticola* and **B.** *P.depressus*. Last segment of maxillary palpi of **C.** *P.abieticola* and **D.** *P.depressus*. (Photos: A. Szallies and A. Sanchez)

The discovery of *P. abieticola* in Switzerland significantly extends the limit of its range westward (Fig. 8). The Swiss records are also among the few recent (post-2000) known from Central Europe.

Ecology

While the ecological requirements of the at least partially sympatric species *P. kolwensis* are relatively well known (see e.g. Burakowski 1962; Siitonen and Saaristo 2000), those of *P. abieticola* are still incomplete and some information in the literature is even contradictory.

Pytho abieticola is associated with spruce forests, often in primeval forest areas (Burakowski et al. 1987; Horák 2017), and usually inhabits swampy sites (Saalas 1917, 1923). According to Saalas (1917, 1923) and Pollock (1991), *P. abieticola* is exclusively a spruce-associated beetle, but data on *Pinus* and *Abies* are also reported (Koch 1989), although the accuracy of these data is unknown. With its flattened and flexible body perfectly adapted to subcortical life (Burakowski 1976), the larva develops under the bark of fallen trees of medium or small size (7–18 cm diameter according to Saalas 1923 and Burakowski et al. 1987, 6–25 cm according to Saalas 1917), that are freshly dead (within the last few years). According to Pollock (1991), the logs used by the different *Pytho* species are probably only suitable for 4–10 years. *Pytho abieticola* often lives in older and drier trees than the other two European *Pytho* species, although all three species are sometimes found on the same tree (Siitonen J., pers. comm.). Fallen trees favourable to *P. abieticola* lie horizontally (Saalas 1917) and ideally are not in direct contact with the ground (Saalas 1923; Burakowski et al. 1987; Siitonen J., pers. comm.). This happens, for example, when trees are broken or uprooted by the wind (Burakowski 1976) and are then supported by their branches. Saalas (1923) stated that he was not aware of any findings of the species on standing dead trees, which is generally also true for other *Pytho* species (Pollock 1991). Favourable logs are not in dense forest but in semi-shaded or open places (Siitonen J., pers. comm). Generally, the dry bark has already partially loosened and is easily detached in pieces (Siitonen J., pers. comm).

Like other species of the genus, *P. abieticola*, according to Saalas (1923), uses trees previously colonised by bark beetles (Curculionidae, Scolytinae), especially *Pityogenes chalcographus* (Linnaeus, 1760), *Polygraphus* spp. and *Hylastes* spp. The larvae likely feed principally on the decaying cambial-phloem layer that remains after the other insects have left the layer. Although some literature sources (e.g. Koch 1989) classify *P. abieticola* as zoophagous, it is indeed more likely that its larvae feed primarily on decaying wood and fungi, as has been shown for *P. depressus* (Andersen and Nilssen 1978; Smith and Sears 1982; Watt 1987; Pollock 1991; Vázquez 1993). However, they are probably also opportunistic and cases of cannibalism between *P. abieticola* larvae have been reported (Sahlberg 1875; Saalas 1923). They can easily be reared following the recommendations of Andersen and Nilssen (1978) and Pollock (1988).

Larval development probably takes several years (at least three, according to Burakowski et al. 1987), and larvae of various size can be found throughout the year (Saalas 1923). Pupation takes place between the second half of July and the first half of September (Burakowski et al. 1987). The pupal stage lasts about two weeks (Sahlberg 1875). The adults overwinter in pupal cells under bark. They are most easily found during this period, before emerging in spring, primarily in April and May.

Figure 7. Larvae of **A.** *P. abieticola* (from Swiss National Park) and **B.** *P. depressus* (from Ponts-de-Martel Valley). Dorsal view (**C**, **D**) and lateral view (**E**, **F**) of tergite 9 of the same larvae. (Photos: A. Sanchez).

Our catches fit well into this general framework, as our sites in the Jura mountains were in spruce forests bordering peat bogs. The specimens were found in relatively open forest areas where some logs had been mechanically felled in previous years and were lying above the ground. In the Swiss National Park, most of the specimens were also found in particularly humid environments, especially on the steep slope to the Spöl stream. All larvae were found on trees lying horizontally just above the ground. Although most of our subcortical findings of larvae and adults of *P. abieticola* were made on spruce, as reported in the literature, we were also able to confirm the use of Swiss mountain pine as a host species, at least occasionally. In our three Swiss localities, we could also find the more widespread *P. depressus* in more or less close proximity to *P. abieticola* (in the Saignelégier region, they were even found on the same log). Both species are thus sympatric in the study area, a coexistence that has already been reported, e.g. in the primeval forest of Białowieża (Kubisz et al. 2014).

Status and threats

Pytho abieticola is in severe decline in Fennoscandia and even more so in Central Europe. With the exception of Finland, where it is only considered 'Near Threatened NT' (Malmberg et al. 2019), it is thus threatened (or regionally extinct) in all European countries where it occurs (respectively occured). It is considered 'Vulnerable VU' in Sweden (SLU Artdatabanken 2020), 'Endangered EN' in Poland (Pawłowski et al. 2002), 'Critically Endangered CR' in the Czech Republic (Horák 2017) and in Norway (Ødegaard et al. 2021), and 'Regionally Extinct RE' in Austria (Jäch et al. 1994) and in Germany (Schmidl et al. 2021), even though its occurrence in Germany is questionable. While it was not possible to find information on its threat status in Russia, the species is not mentioned in the Slovakian Red List (Holecová and Franc 2001). At the global scale, the species is considered 'Least concern LC' by Pettersson et al. (2010), probably assuming that its situation is better in Western Russia, where a large part of *P. abieticola* populations certainly occur. This assumption seems to be confirmed by the results obtained by Laaksonen et al. (2008), who showed that Karelian forests in Russia, where forest management was very limited until recently, were better preserved (and less fragmented), and therefore harboured more populations of *P. abieticola* (and even more of *P. kolwensis*) than forests in neighbouring Finland. However, the global status of *P. abieticola* is under revision and the species will certainly be classified as threatened in the next European Red List (Dodelin B., pers. comm.).

Degradation and destruction of natural forests through intensive logging and the resulting fragmentation of habitat represent the greatest threat to the species. Like all other species of the genus, *P. abieticola* occurs only in old-growth forest areas and requires continuous spatial and temporal availability of large amounts of dead wood, which qualifies it as a typical "Primeval forest relict" species (Eckelt et al. 2017). In the case of *P. abieticola*,

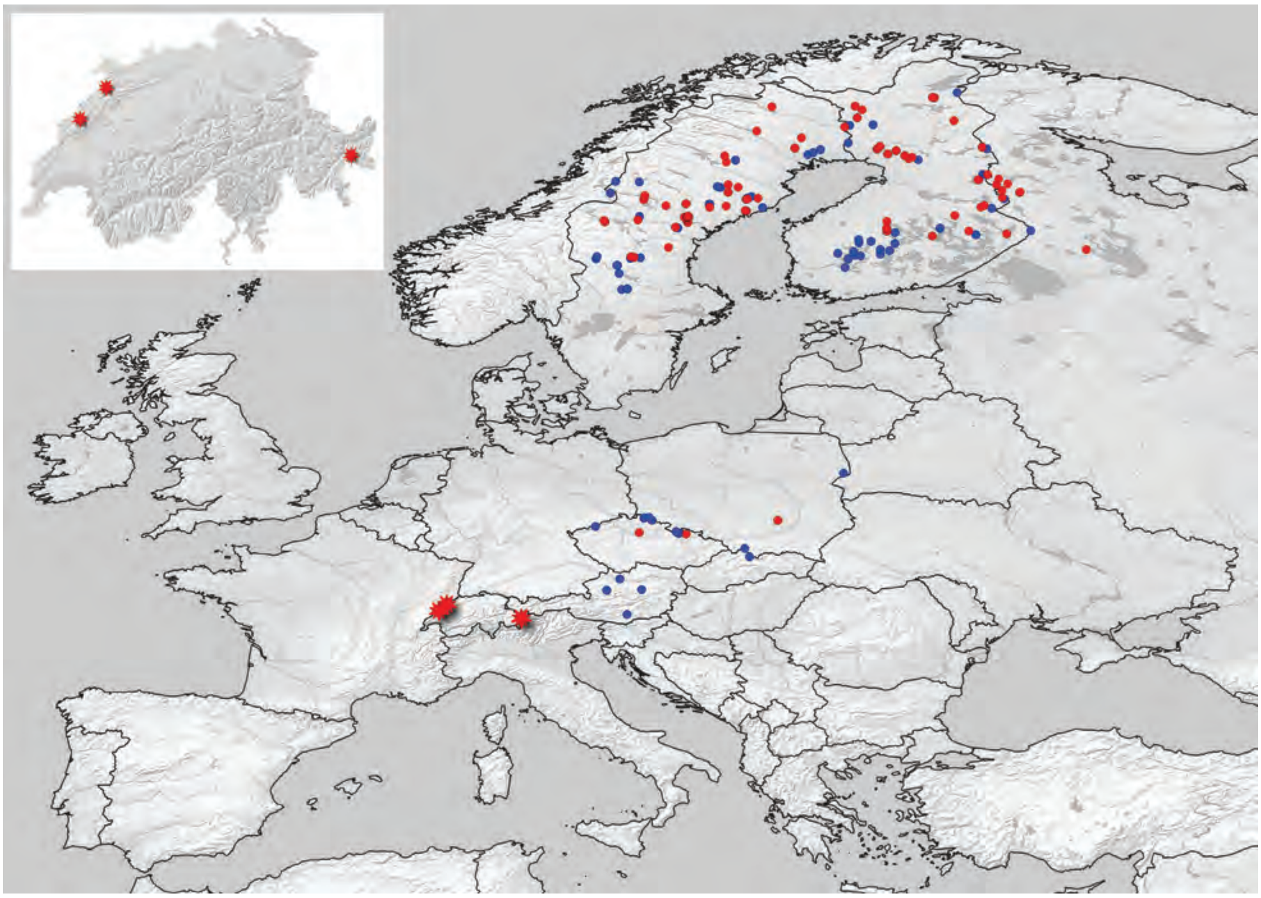


Figure 8. Distribution of *Pytho abieticola* in Europe, with a close-up of Switzerland (in blue: observations before 2000; in red: observations since 2000). Swiss localities are indicated by stars. The species is also widespread in Russia and reaches northern China, but data are scarce. (Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com).

the required resources are very specific: small to medium-sized spruce logs, with already partially loosened dry bark, that are elevated off the ground in semi-shaded or open spaces. Moreover, they quickly (after only a few years) become unsuitable for the species, for example when the bark becomes too loose, or the trunks reach a more advanced stage of decay. Thus, these resources must be regularly "renewed" and constantly available. Since the species can also colonise trees felled mechanically, effective measures to promote *P. abieticola* can simply be established even if favourable dead wood (i.e. naturally fallen) is lacking. Following our observations, cantonal authorities and site managers should take local measures to ensure the conservation of this species.

Conclusion

The knowledge on the distribution of *P. abieticola* has improved since Horion (1960), who mentioned only four records in Central Europe. However, its situation remains extremely critical, as only very few populations remain (Fig. 8). The discovery of new populations of this patrimonial species, wherever they may be located, is therefore very encouraging from a conservation point of view. Surveys in other old-growth coniferous forests, especially at the edges of open peat bogs, should be carried out and may reveal further populations of *P. abieticola*. Swiss localities in the Jura mountains, within 10 km of the French border, indicate a very probable occurence in that country, particularly in peat bogs of the Jura. An occurrence in northern Italy also seems likely, as the Swiss national park borders Italy.

Acknowledgements

We would like to thank the Service de la Faune, des Forêts et de la Nature of the canton of Neuchâtel, and particularly Sébastien Tschanz, for financing the inventory of the Ponts-de-Martel Valley, as well as the sponsors of the research carried out in the Swiss National Park (ANU, AWN, FOEN, the Bündner Naturmuseum Chur and the Parrotia foundation). We also thank the regional authorities (Canton of Neuchâtel and of Jura, Swiss National Park) for the attribution of collection permits. We are grateful to Carl-Michael Andersson, Pablo Hebeisen, Beat Wermelinger, Nicolas Roth and Romain Angeleri for their support of the field work in the National Park and we would like to thank Abenis AG, and particularly Romano Costa, Remo Wild, and Barbara Huber for the good collaboration. Our thanks to Hervé Brustel, Heinz Bussler, Benoît Dodelin, Andreas Eckelt, Herbert Fuchs, Nicolas Gouix, Lars Hendrich, Erwin Holzer, Uwe Hornig, Ondřej Konvička, Frank Lange, Uno Roosileht, Juha Siitonen, and Dmitry Telnov for sharing their information on the species and European localities. Thanks to Michel Sartori for providing us with the photographic equipment, and to Christian Monnerat and Laurent Juillerat for various advice. Finally, we are grateful to Jessica Litman for checking and improving the English, and to Hervé Brustel and Darren Pollock for their valuable comments on the manuscript.

References

Andersen J, Nilssen AC (1978) The food selection of *Pytho depressus* L. (Coleoptera, Pythidae). Norwegian Journal of Entomology 25: 225–226.

Baur B, Scheurer T [Eds] (2014) Wissen schaffen: 100 Jahre Forschung im Schweizerischen Nationalpark. Nationalpark Forschung in der Schweiz 100/I. Haupt Verlag, Bern, 384 pp.

Brustel H (2012) Polytrap 2010: new “soft design” window flight trap for saproxylic beetles. In: Jurc M (Ed.) Saproxylic beetles in Europe: monitoring, biology and conservation. Ljubljana, Slovenian Forestry Institute, Silva Slovenica 137: 91–92.

Burakowski B (1962) Obserwacje biologiczno-morfologiczne nad *Pytho kolwensis* C. Sahlb. (Coleoptera, Pythidae) w Polsce. Fragmenta Faunistica 10: 173–204. https://doi.org/10.3161/00159301FF1962.10.12.173

Burakowski B (1976) Coleoptera: Pythidae-Lagriidae-Alleculidae. Zeszyt 88, Rozmiazgowate-Pythidae. In: Mikolajczyk W (Ed.) Klucze do oznaczania owadów Polski. Wroclawska Drukarnia Naukowa, Warsaw, 3–18.

Burakowski B, Mroczkowski M, Stefańska J (1987) Chrząszcze – Coleoptera. Cucujoidea, część 3. Katalog Fauny Polski 23(14): 309.

Chittaro Y, Sanchez A (2016) Liste commentée des Tenebrionoidea (Coleoptera) de Suisse. Partie 1: Aderidae, Anthicidae, (Boridae), Melandryidae, Meloidae, Mycetophagidae, Mycteridae, Prostomidae, Pyrochroidae, Pythidae, Ripiphoridae, Salpingidae, Tenebrionidae, Tetratomidae, Zopheridae. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 89: 183–235.

Eckelt A, Müller J, Bense U, Brustel H, Bussler H, Chittaro Y, Cizek L, Frei A, Holzer E, Kadej M, Kahlen M, Köhler F, Möller G, Mühle H, Sanchez A, Schaffrath U, Schmidl J, Smolis A, Szallies A, Németh T, Wurst C, Thorn S, Christensen RHB, Seibold S (2017) ”Primeval forest relict beetles” of Central Europe: A set of 168 umbrella species for the protection of primeval forest remnants. Journal of Insect Conservation 22: 15–28. https://doi.org/10.1007/s10841-017-0028-6

Franz H (1974) Die Nordost-Alpen im Spiegel ihrer Landtierwelt, Band IV. Universitätsverlag Wagner, Innsbruck-München, 707 pp.

GBIF.org (10 August 2022) GBIF Occurrence Download. https://doi.org/10.15468/dl.6wuhvj

Háva J, Zahradník P (2021) A contribution to the knowledge of the genus *Pytho* Latreille, 1796 (Coleoptera: Pythidae) from China, with the description of *Pytho sichuanicus* sp. n. Acta Zoologica Bulgarica 73(1): 27–30.

Heyrovský L (1960) K bionomii a zoogeografii druhů rodu *Pytho* F. v Československu (Col., Pythidae). Časopis Slezského muzea v Opavě, Series A, 9: 41–43.

Holecová M, Franc V (2001) Červený (ekosozoologický) zoznam chrobákov (Coleoptera) Slovenska. In: Baláž D, Marhold K, Urban P (Eds) Červený zoznam rastlín a živočíchov Slovenska. Ochrana Prírody, 20 (Suppl.): 111–128.

Horák J (2017) Pythidae. In: Hejda R, Farkač J, Chobot K (Eds) Červený seznam ohrožených druhů České republiky. Bezobratlí. Agentury ochrany přírody a krajiny ČR, Praha, 403–404.

Horion A (1956) Faunistik der mitteleuropäischen Käfer. Band V: Heteromera. Entomologische Arbeiten aus dem Museum G. Frey Tutzing bei München, Sonderband, 1–336.

Horion A (1960) Koleopterologische Neumeldungen für Deutschland. IV. Reihe. Nachtrag zum „Verzeichnis der mitteleuropäischen Käfer”. Mitteilungen der Münchner Entomologischen Gesellschaft 50: 119–162.

Iablokoff-Khnzorian SM (1985) Les Pythidae paléarctiques. Deutsche Entomologische Zeitschrift 32: 193–229. https://doi.org/10.1002/mmnd.19850320129

Jäch MA, Adlbauer K, Barries W, Cate PC, Franz H, Geiser E, Geiser R, Holzschuh C, Kirschenhofer E, Kreissl E, Novak G, Probst J, Reiser P, Schillhammer H, Schmid H, Schödl S, Suppantschitsch W, Zabransky P, Zelenka W (1994) Rote Liste der gefährdeten Käfer Österreichs (Coleoptera). Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie, Band 2: 107–200.

Kaszab Z (1969) 11. Fam. Pythidae. In: Freude H, Harde KW, Lohse GA (Eds) Die Käfer Mitteleuropas. Band 8: Teredilia, Heteromera, Lamellicornia. Goecke & Evers, Krefeld, 92–99.

Koch K (1989) Die Käfer Mitteleuropas. Ökologie, Band 2. Goecke & Evers, Krefeld, 382 pp.

Kubisz D, Iwan D, Tykarski P (2014) Tenebrionoidea: Tetratomidae, Melandryidae, Ripiphoridae, Prostomidae, Oedemeridae, Mycteridae, Pythidae, Aderidae, Scraptiidae. Critical checklist, distribution in Poland and meta-analysis. Coleoptera Poloniae 2. University of Warsaw – Faculty of Biology, Natura optima dux Foundation, Warszawa, 470 pp.

Laaksonen M, Peuhu E, Várkonyi G, Siitonen J (2008) Effects of habitat quality and landscape structure on saproxylic species dwelling in boreal spruce-swamp forests. Oikos 117: 1098–1110. https://doi.org/10.1111/j.0030-1299.2008.16620.x

Malmberg S, Mannerkoski I, Martikainen P, Clayhills T, Helve E, Hyvärinen E, Karjalainen S, Mattila J, Muona J, Rassi P (2019) Kovakuoriaiset – Beetles. In: Hyvärinen E, Juslén A, Kemppainen E, Uddström A, Liukko UM (Eds) Suomen lajien uhanalaisuus – Punainen kirja 2019. The 2019 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, 391–425.

Ødegaard F, Hanssen O, Laugsand AE, Olberg S (2021) Biller: Vurdering av granbarkflatbille *Pytho abieticola* for Norge. Rødlista for arter 2021. Artsdatabanken.

Painter JN, Siitonen J, Hanski I (2007) Phylogeographical patterns and genetic diversity in three species of Eurasian boreal forest beetles. Biological Journal of the Linnean Society 91(2): 267–279. https://doi.org/10.1111/j.1095-8312.2007.00797.x

Parolini JD (2012) Vom Kahlschlag zum Naturreservat. Geschichte der Waldnutzung im Gebiet des Schweizerischen Nationalparks. Haupt Verlag, 213 pp.

Pawłowski J, Kubisz D, Mazur M (2002) Coleoptera. In: Głowaciński Z (Ed.) Red-List of Extinct and Endangered Animals. Instytut Ochrony Przyrody PAN, Kraków, 88–110.

Pettersson R, Hyvärinen E, Munteanu N, Istrate P, Schlaghamersky J, Schmidl J (2010) *Pytho abieticola*. The IUCN Red List of Threatened Species 2010: e.T157801A5149331. [Accessed on 16 September 2022]

Pollock DA (1988) A technique for rearing subcortical Coleoptera larvae. The Coleopterists Bulletin 42: 311–312.

Pollock DA (1991) Natural history, classification, reconstructed phylogeny and geographic history of *Pytho* Latreille (Coleoptera, Pythidae). Memoirs of the Entomological Society of Canada 154: 1–104. https://doi.org/10.4039/entm123154fv

Pollock DA (2008) Pythidae. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea. Stenstrup: Apollo Books, 413–414.

Pollock DA (2020) Pythidae. In: Iwan D, Löbl I (Eds) Catalogue of Palaearctic Coleoptera. Vol. 5. Revised and Updated Second Edition. Tenebrionoidea. Leiden, Boston, E. J. Brill, 564–565.

Rassi P, Karjalainen S, Clayhills T, Helve E, Hyvärinen E, Laurinharju E, Malmberg S, Mannerkoski I, Martikainen P, Mattila JA, Muona JE, Pentinsaari M, Rutanen I, Salokannel J, Siitonen J, Silfverberg H (2015) Provincial list of Finnish Coleoptera 2015. Sahlbergia 21, Supplement 1.

Reitter E (1892) Coleopterologische Notizen. XLV. Wiener Entomologische Zeitung 11: 186–188. https://doi.org/10.5962/bhl.part.27706

Richard JL (1961) Les forêts acidophiles du Jura: étude phytosociologique et écologique. Matériaux pour le levé géobotanique de la Suisse 38, 164 pp.

Saalas U (1917) Die Fichtenkäfer Finnlands. Studien über die Entwicklungsstadien, Lebensweise, und geographische Verbreitung der an *Picea excelsa* Link. lebenden Coleopteren nebst einer Larvenbestimmungstabelle. I. Allgemeiner Teil und Spezieller Teil l. Suomalaisen Tiedeakatemian Justantama, Helsinki, 547 pp. https://doi.org/10.5962/bhl.title.38683

Saalas U (1923) Die Fichtenkäfer Finnlands. II. Studien über die Entwicklungsstadien, Lebensweise, und geographische Verbreitung der an *Picea excelsa* Link. lebenden Coleopteren nebst einer Larvenbetimmungstabelle. Annales Academiae Scientiarum Fennicae A 22, 746 pp.

Sahlberg J (1875) Ueber die Finnischen Arten der Käfer-Gattung *Pytho* und deren Larven. Deutsche Entomologische Zeitschrift 19(1): 219–224. https://doi.org/10.1002/mmnd.48018750118

Schmidl J, Bense U, Bussler H, Fuchs H, Lange F, Möller G (2021) Rote Liste und Gesamtartenliste der „Teredilia" und Heteromera (Coleoptera: Bostrichoidea: Lyctidae, Bostrichidae, Anobiidae, Ptinidae; Tenebrionoidea) Deutschlands. In: Ries M, Balzer S, Gruttke H, Haupt H, Hofbauer N, Ludwig G, Matzke-Hajek G (Eds) Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 5: Wirbellose Tiere (Teil. 3). Münster (Landwirtschaftsverlag). Naturschutz und Biologische Vielfalt 70(5): 165–186.

Sergeeva EV, Stolbov VA (2020) A review of Tenebrionoid beetle fauna (Coleoptera, Tenebrionoidea) of the Tyumen region. Amurian Zoological Journal 12(2): 224–242. https://doi.org/10.33910/2686-9519-2020-12-2-224-242

Siitonen J, Saaristo L (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. Biological Conservation 94: 211–220. https://doi.org/10.1016/S0006-3207(99)00174-3

SLU Artdatabanken (2020) Rödlistade arter i Sverige 2020. SLU, Uppsala, 242 pp.

SLU Artdatabanken (2022) *Pytho abieticola*. https://www.artportalen.se/search/map/taxon/101691

Smith DB, Sears MK (1982) Mandibular structure and feeding habits of three morphologically similar coleopterous larvae: *Cucujus clavipes* (Cucujidae), *Dendroides canadensis* (Pyrochroidae) and *Pytho depressus* (Salpingidae). The Canadian Entomologist 114(2): 173–175. https://doi.org/10.4039/Ent114173-2

Strečєk J (1988) Zajímavé nálezy brouků ze skupiny čeledí Heteromera a Clavicornia v ČSSR. Zprávy Československé společnosti entomologické při ČSAV 24 (3–4): 65–66.

Švec Z (1984) Faunistic records from Czechoslovakia. Pythidae. Acta Entomologica Bohemoslovaca 81: 398.

Vávra JC, Stanovský J (2013) Brouci (Coleoptera). In: Roháček J, Ševčík J, Vlk R (Eds) Příroda Slezska. Slezské zemské muzeum, Opava, 295–311.

Vázquez XA (1993) Fauna Iberica. Vol. 5. Coleoptera: Oedemeridae, Pyrochroidae, Pythidae, Mycteridae. Museo Nacional de Ciencias Naturales, Madrid, 181 pp.

Yuferev GI (1986) Ecological characteristics of terrestrial coleopterofauna of Svecha district of Kirov oblast. Ecology of animals of the Volga and Urals region, 25–32. [in Russian]

Alpine Entomology 7 2023, 13–20 | DOI 10.3897/alpento.7.96436

PENSOFT.

Alpine Entomology

Inventory and pattern of distribution of mayflies (Insecta, Ephemeroptera) in the Draa river basin, southern Morocco

Mokhtar Benlasri[1], Nils Kaczmarek[2], Majida El Alami[3], Mohamed Ghamizi[1], Elisabeth Berger[2]

1 *Museum of Natural History, University Cadi Ayyad, Faculty of Science Semlalia, Marrakech, Morocco*
2 *RPTU – University of Kaiserslautern-Landau, iES Institute for Environmental Sciences, Landau, Germany*
3 *University Abdelmalek Essâadi, Faculty of Science, Tetouan, Morocco*

https://zoobank.org/54964BE0-8299-44EA-8F01-7C895FE235C6

Corresponding author: Mokhtar Benlasri (benlasri@gmail.com)

Academic editor: Jean-Luc Gattolliat ♦ **Received** 17 October 2022 ♦ **Accepted** 9 February 2023 ♦ **Published** 13 March 2023

Abstract

The Draa river basin is located south of the High Atlas Mountain rangee in Morocco. The Ephemeroptera (mayflies) fauna of its three sub-basins: the High, Middle, and Lower Draa are poorly known. This study contributes to the knowledge of Ephemeroptera and its distribution in relation to environmental parameters in this area. The larvae of Ephemeropteran species were collected during six field campaigns in 17 sites using a Surber sampler. A total of thirteen species belonging to ten genera and five families were identified. among which seven taxa were recorded for the first time in the southern Atlas area: *Baetis maurus*, *Baetis rhodani*, *Cheleocloeon dimorphicum*, *Cloeon simile*, *Procloeon stagnicola*, *Labiobaetis neglectus* and *Oligoneuriopsis skhounate*. The limits of distribution of most species can be explained by the increase in water temperature and electrical conductivity especially at lower altitudes.

Key Words

Bioindicators, biodiversity, Draa watershed, High Atlas, mayflies, Morocco

Introduction

Mayflies (order Ephemeroptera) have a worldwide distribution. being absent only in Antarctica and some remote oceanic islands (Barber-James et al. 2008; Jacobus et al. 2019). This order encompasses approximately 3.700 species. 450 genera. and 42 families (Sartori and Brittain 2015; Salles et al. 2018; Jacobus et al. 2019). The Ephemeroptera's larvae live in a variety of freshwater/aquatic habitats. including lakes, wetlands, streams and rivers (Bouchard 2004).

The development cycle of mayflies depends essentially on water. The larvae. after hatching from the egg undergo, a series of molts during their growth (Barber-James et al. 2008). The adult stage (subimago and imago) are the only terrestrial stages with only a short life span: from a few hours to a few days (Brittain 1982). Because of their reliance on water this order is useful in ecological studies particularly in estimating the biological quality and biomonitoring of freshwaters (Bauernfeind and Moog 2000). They have a great bioindicative value with respect to the disturbances undergone by the watercourses, in fact among the Ephemeroptera there are a certain number of species with strict ecological requirements (Bebba et al. 2015). They also have a great importance in the energy flow as they participate massively in the transfer of energy and carbon in the aquatic ecosystem (Bottova et al. 2012) and between the aquatic and terrestrial ecosystems, where they may be consumed by many riparian species such as birds, bats, spiders and lizards (Jacobus et al. 2019).

Since the twentieth and early twenty-first centuries, many mayfly-related studies have been carried out in Algeria (Soldan and Thomas 1985; Gagneur and Thomas 1988; Bebba et al. 2015; Mebarki et al. 2017; Benhadji et al. 2020; Lounaci et al. 2020; Samraoui et al. 2020) and in Tunisia (Boumaiza and Thomas 1986; Yalles-Satha et al. 2021). These studies have allowed to establish a list of 50 Algerian and 25 Tunisian species (Lounaci et al. 2000;

Zrelli et al. 2016 respectively). In Morocco the first studies of mayflies date back to Lestage (1925) and Kimmins (1938). Since 1970 further studies were carried out over almost all of Morocco. In 1983, Dakki and El Agbani 1983) established a first list of 26 species that was subsequently enriched by other authors (Alba-Tercedor and El Alami 1999; El Alami et al. 2000; Berrahou et al. 2001; Himmi et al. 2009; Chahboune et al. 2014; Lamri et al. 2016; El Bazi et al. 2017; Mabrouki et al. 2017, 2019; Berger et al. 2021). Recently a list of 54 species of mayflies was drawn up for Morocco (El Alami et al. 2022). This list has been updated to 55 by the discovery of a new species: *Centroptilum* cf. *luteolum* Kaltenbach, Vuataz & Gattolliat, 2022 (Kaltenbach et al. 2022).

Despite all those studies concerning Morocco, the Draa's Ephemeroptera remain still almost unknown. The last study of a small part of this basin dates back to 1989 (Bouzidi 1989) followed by the study conducted by Berger in 2017 (Berger et al. 2021). This area is located in a transition zone between the southern Atlas Mountains and the Saharan desert region that is strongly affected by climate change. This area is isolated from other parts of Morocco by the High Atlas Mountain barrier, the humid fresh winds condense the precipitations on the northern slope which leaves the southern slope under the effect of the hot sirocco of the desert with scarcity of precipitations (Ajakane and Boumezough 1996).

The objectives of this study are to update the list of Ephemeroptera by covering a large study area including the Upper, the Middle and a part of the Lower Draa. For this purpose, we have established the list of Ephemeroptera colonizing this basin and complete the inventory of Ephemeroptera for Morocco by adding different streams of the hydrographic network south of the High Atlas. Furthermore, we studied the environmental factors that shape the distribution of Ephemeroptera in the Draa basin, we also aim to locate in the study area the regions that have a high Mayfly diversity.

Materials and methods

Study area

The geography of Morocco is characterized by the presence of four mountain ranges: the Rif in the north and the Atlas in the center, which is divided into three range: the High Atlas, the Middle Atlas and the Anti Atlas). The Draa basin, subject of this study is located in the south of the High Atlas that covers the reliefs of the southern part of the High Atlas until the south of the city of Zagora and extends to the Atlantic Ocean in the West (Fig. 1). This basin is characterized by a heterogeneous topographic configuration: a mountainous zone, a zone of semi-desert plains, desert plains, a zone of desert plateaus and a coastal zone (Agence du Bassin Hydrolique souss massa Drâa 2008). The Draa River basin is located in an arid climate characterized by harsh winter with temperatures below -1 °C and hot summers with average temperatures of 45 °C. The number of rainy days varies between 30 and 40 between September and May (ABH 2012). In the mountainous zone, the climate can be humid, with precipitation that can cross the tops of the mountains.

The Draa basin covers an area of 115 000 km^2 (Agence du Bassin Hydrolique souss massa Drâa 2008) and is subdivided into three sub-basins (Fig. 1): the sub-basin of the Upper Draa is upstream of the El Mansour Eddahbi dam (near the city of Ouarzazate). Several streams, both temporary and permanent drain the Atlas into this dam: Ounilla, Iriri, Fint, Imini, Dades and its tributary Mgoune**.**

The sub-basin of the Middle Draa covers the area downstream of the El Mansour Eddahbi dam to the south of Zagora and extends to Mhamid El Ghizlane. It includes the main watercourse of Draa, which is dry during a large part of the year and whose water flow depends essentially on water releases from the dam.

The sub-basin of the Lower Draa, extends from the area of Mhamid El Ghizlane to the mouth of the Draa river in the Atlantic Ocean.

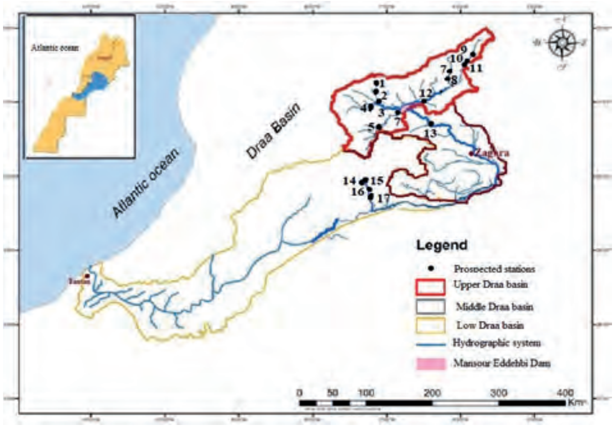


Figure 1. Location of the prospected sites in the sub-basins of the Draa river basin.

Seventeen sites were selected in the Draa basin (Table 1), twelve sites are located in the Upper Draa encompassing the mostly permanent streams that feed the El Mansour Eddahbi dam, three sites in Ounilla (St1-3), one in Iriri (St4), two in Fint (St5-6), two in Mgoune (St7-8) and four in Dades (St9-12). We originally selected four sites in the middle Draa, of which st13 and three others downstream between St13 and the city of Zagora in the Draa river. Unfortunately, the dryness of the river in this sub-basin did not allow us to make the sampling since 2020, except for the site at Tamnougalt (St13), which keeps a minimum of water with the releases of the dam. Furthermore, in the Lower Draa, the Draa river is completely dry, here we sampled in four sites that were located in a tributary of the Lower Draa: The Tissint stream (St14-17).

Table 1. List of the sites. UD: Upper Draa; MD: Middle Draa; LD: Lower Draa.

Basin	Site	Name	River	GPS Coordinates	Altitude (m.s.l.)	Sampling dates					
						Jun 19	Fe 20	Oct 20	Ap 21	May 21	Oct 21
UD	St1	Ounilla upstream	Ounilla	31°15.71'N, 7°9.24'W	1724		X	X	X	X	X
UD	St2	Ounilla middlestream	Ounilla	31°8.80'N, 7°8.43'W	1425		X	X	X	X	X
UD	St3	El mellah	Oued El maleh	31°0.69'N, 7°6.01'W	1228	X	X	X	X	X	
UD	St4	Iriri	Iriri	30°56.27'N, 7°12.60'W	1261		X	X	X	X	X
UD	St5	Ait douchene	Fint (up stream)	30°39.46'N, 7°05.56'W	1336		X	X	X	X	X
UD	St6	Tarmigt	Fint	30°51.91'N, 6°50.79'W	1114	X	X	X	X	X	X
UD	St7	Dades upstream	Dades	31°35.61'N, 5°52.36'W	1814		X	X		X	
UD	St8	Gorges de Dades	Dades	31°33.37'N, 5°54.51'W	1753	X	X	X		X	X
UD	St9	Middle Dades	Dades	31°30.28'N, 5°56.72'W	1656		X	X		X	X
UD	St10	Dades downstream	Dades	31°0.72'N, 6°29.61'W	1190		X	X		X	X
UD	St11	Mgoune upstream	Mgoune	31°21.83'N, 6°10.27'W	1545		X	X		X	X
UD	St12	Mgoune downstream	Mgoune	31°20.07'N, 6°10.82'W	1508		X	X		X	X
MD	St13	Tamnougalt	Draa	30°40.40'N, 6°24.36'W	919	X	X	X			X
LD	St14	Akka nait sidi 1 (left)	Tissint	29°54.57'N, 7°19.87'W	584		X	X	X	X	X
LD	St15	Akka nait sidi 2 (right)	Tributary tissint	29°54.71'N, 7°19.87'W	582		X	X	X	X	X
LD	St16	Tissint near the road	Tissint	29°49.54'N, 7°11.92'W	486	X	X	X	X	X	X
LD	St17	Mghimima	Zguid	29°46.81'N, 7°10.10'W	483	X	X	X	X	X	X

Sampling and sorting

The sampling was conducted from June 2019 to October 2021. The first sample in June 2019 was done following a qualitative protocol to know which site we could use in the subsequent samplings. Later, quantitative samplings were carried out using a 0.20 m × 0.25 m Surber sampler with a net mesh size of 500 µm. Twenty spots per site were sampled to cover all microhabitats over a length about ten times the width of the riverbed.

Samples were stored in airtight bottles with 70 % ethanol. Specimens were sorted preliminarily *in situ* to remove sediment and vegetation as much as possible. The final sorting was done in the laboratory under a binocular magnifying glass to separate the specimens to species level using morphological criteria. The identification of the larvae was made using various keys and original descriptions (Müller-Liebenau 1969; Soldan and Thomas 1985; Elliott et al. 1988; El Alami et al. 2000; Tachet et al. 2000; Bouchard 2004; Gattolliat and Sartori 2008).

Water temperature, electrical conductivity and pH.were measured using a multiparameter device (WTW Multiliner Multi 3510 IDS) (Table 2).

Data analysis

The correlations between water temperature, electrical conductivity, pH and species richness were studied using the Pearson correlation coefficient.

We used a cluster analysis (single linkage agglomerative clustering) using Euclidean distance to cluster sites with similar species composition.

A Correspondence Analysis (CA) based on species presence/absence data (frequencies) from all sampling periods combined was used to visualize differences in species composition between sites. Subsequently environmental variables from the respective sites were fitted to the CA plot, the mean number of specimens over time was used.per each locality. RStudio (version 1.2.5019) and the packages “Vegan” (Oksanen et al. 2019), “car” (Fox and Weisberg 2018) and “ggpubr” (Kassambara 2020) were used for statistical analysis.

Table 2. Physicochemical parameters measured during the sampling periods.

Sites	Temperature (C)		Conductivity (µS)		pH	
	Mean	SD	Mean	SD	Mean	SD
St1	20	4	1921	441	7.31	0.35
St2	19	4	2669	1074	7.45	0.34
St3	22	4	8999	2600	7.31	0.09
St4	20	2	602	34	7.68	0.20
St5	20	4	885	129	7.39	0.10
St6	26	1	1234	129	7.54	0.10
St7	15	5	754	67	7.58	0.50
St8	16	3	829	208	7.56	0.39
St9	16	3	1022	666	7.39	0.27
St10	18	5	1441	1291	7.48	0.26
St11	16	3	1120	614	7.67	0.38
St12	19	2	1126	217	7.40	0.18
St13	25	1	2167	386	7.35	0.07
St14	26	2	8986	2417	7.30	0.08
St15	25	4	6431	3542	7.32	0.15
St16	25	3	13098	5095	7.46	0.31
St17	25	5	13199	938	7.42	0.06

Results

Physicochemical parameters

Temperature was negatively correlated with altitude and pH (Table 2, Fig. 2A, B). Electrical conductivity was negatively correlated with altitude and positively correlated with water temperature (Fig. 2C, D). No correlation was found between pH and water temperature and electrical conductivity.

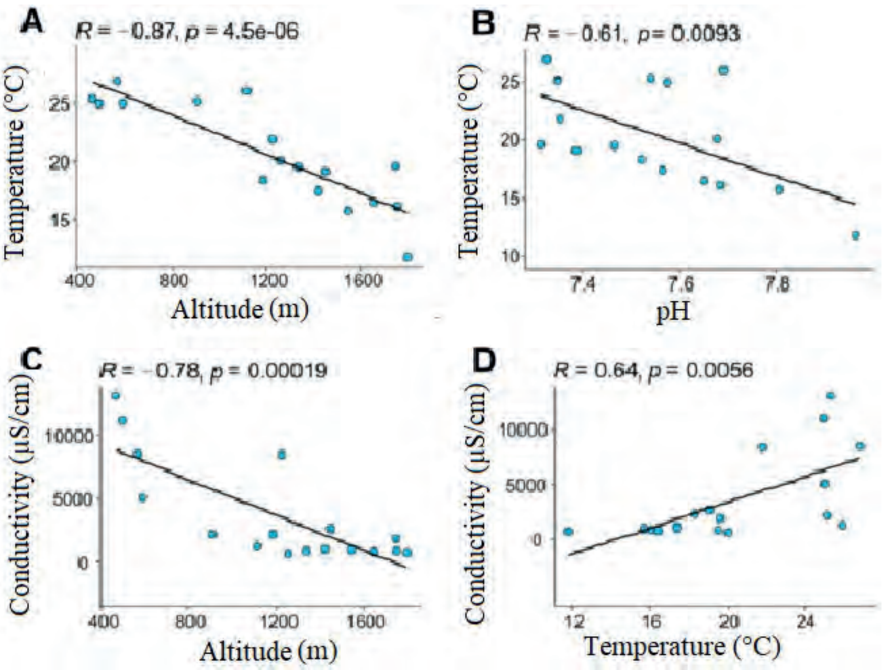


Figure 2. Significant correlation between environmental parameters. **A.** Water temperature/altitude; **B.** Water temperature/pH; **C.** Electrical conductivity/altitude; **D.** Electrical conductivity/water temperature.

Distribution of species

Thirteen species of Ephemeroptera belonging to ten genera and five families were identified in the basin during the samplings (Table 3), Per site we found from two to eleven species, with one species being present in all sites these (Table 3; Suppl. materal 1).

Concerning the number of species of Ephemeroptera by sub-basin (Fig. 3; Suppl. materal 1): The Upper Draa is the richest with 13 species collected (all species of the basin are present), the Middle Draa is less diversified with six species, the Lower Draa is the poorest with only two species.

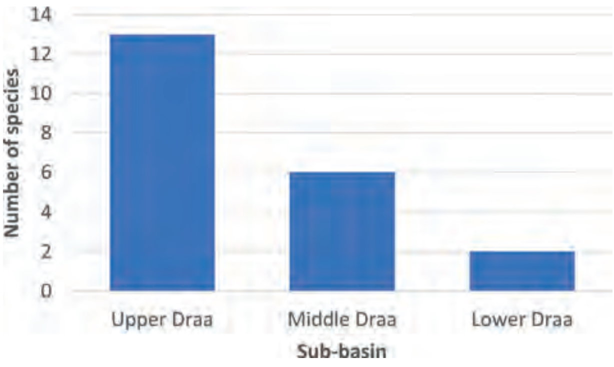


Figure 3. Number of species per sub-basin.

The family of Baetidae was the most diverse, with seven species, *Baetis pavidus* and *Caenis luctuosa* were the most widespread species, with a frequency (the number of sites where the species was found compared to the total number of sites surveyed) of 100% and 88.2% respectively (Table 3). The number of individuals collected varied from one sampling event to another (Suppl. materal 1). However, the presence of the species in each site did not vary (Suppl. materal 1) except for *Oligoneuriopsis skhounate*, which was collected only once in St10.

The number of species richness was negatively correlated with conductivity (Fig. 4A), and the water temperature was negatively correlated with altitude (Fig. 4B), Temperature does not predict species richness in this basin. (Fig. 4C). No correlation was found between pH and the number of species.

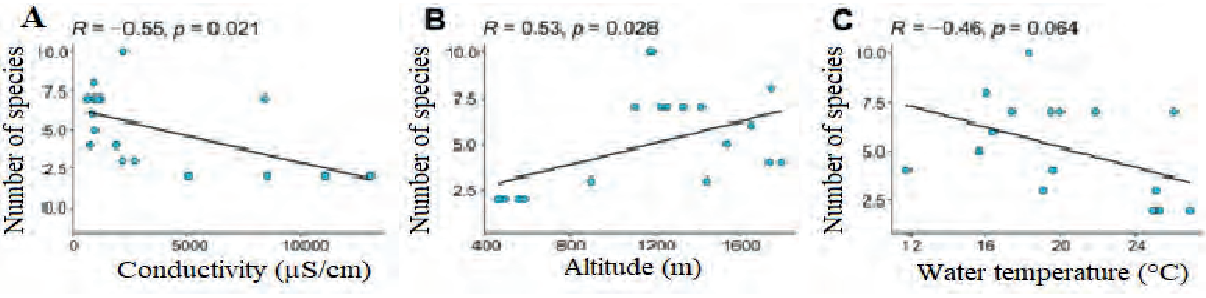


Figure 4. Number of species according to environmental parameters with correlations. **A.** Number of species/electrical conductivity; **B.** Number of species/altitudes; **C.** Number of species/water temperature.

Table 3. Distribution of Ephemeroptera in Draa basin.

Species\ Sites	***Caenis pusilla***	***Caenis luctuosa***	***Choroterpes atlas***	***Baetis maurus***	***Baetis rhodani***	***Baetis pavidus***	***Labiobaetis neglectus***	***Procloeon stagnicola***	***Cheleocloeon dimorphicum***	***Cloeon similie***	***Oligoneuriopsis skhounate***	***Ecdyonurus rhothchildi***	***Rhithrogena* sp.**	**Species richness**
St1	+	+			+	+								4
St2		+				+								2
St3		+				+	+		+	+				5
St4		+	+			+		+	+	+				6
St5		+			+	+	+	+	+	+				7
St6		+	+			+	+	+	+	+				7
St7	+			+	+	+						+		5
St8	+	+			+	+	+					+	+	7
St9	+	+			+	+						+		5
St10	+	+	+		+	+	+			+	+	+	+	10
St11	+			+	+	+						+	+	6
St12	+	+		+		+						+	+	6
St13		+	+		+	+								4
St14		+				+								2
St15		+				+								2
St16		+				+								2
St17		+				+								2
Frequency	41.2	88.2	23.5	17.6	47.1	100	29.4	17.6	23.5	29.4	5.9	35.3	23.5	

The first two axes of the CA explained 47.2% of the total variation (Fig. 5). According to the CA plot, *Caenis luctuosa* and *Baetis pavidus* are present in almost all areas, even those with higher conductivity and higher water temperature (St314-17). One cluster of sites is associated with the correlated variables of lower altitude and higher temperature (Fig. 2A) and contains species like *Cheleocloeon dimorphicum* and *Cloeon similie*. The cluster of St10 is associated with the presence of *Oligoneuriopsis skhounate*, Sites St1, St2, St7, St9, St11 and St12 can be clustered by their altitudes, with the presence of species adapted to these altitudes, such as *Ecdyonurus rotschildi*, *Rhithrogena* sp. and *Caenis pusilla*.

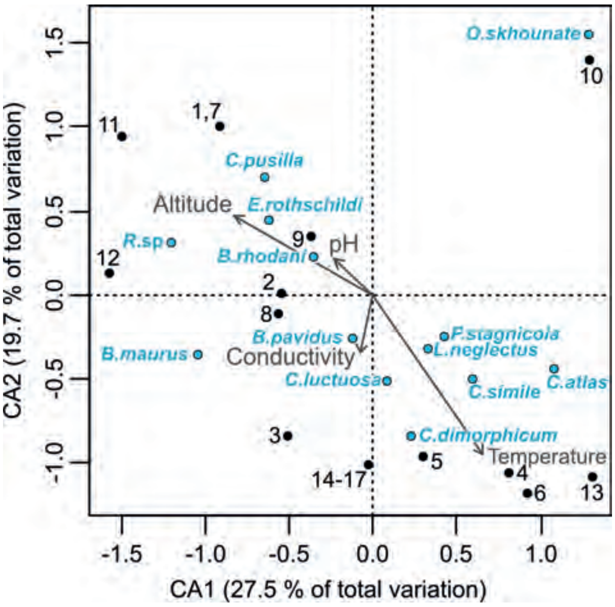


Figure 5. CA ordination plot (Scaling 2) with the relationship between environmental variables and Ephemeropteran species.

Discussion

Among the thirteen species found in this area. seven species were recorded for the first time in the Upper Draa sub-basin: *Baetis maurus*, *Baetis rhodani*, *Cheleocloeon dimorphicum*, *Cloeon simile*, *Labiobaetis neglectus*, *Procloeon stagnicola* and *Oligoneuriopsis skhounate*, but no new species were recorded for the whole basin. We found four Maghrebian endemic species: *Cheleocloeon dimorphicum*, *Procloeon stagnicola*, *Ecdyonurus rotschildi*, *Choroterpes atlas*; three Iberian-Maghrebian endemic species: *Baetis maurus*, *Labiobaetis neglectus*, *Oligoneuriopsis skhounate*; three Palearctic species: *Baetis rhodani*, *Cloeon similie*, *Caenis luctuosa*; one Atlanto-Mediterranean species: *Baetis pavidus*; and one European-Mediterranean species: *Caenis pusilla*, *Rhithrogena* sp. was not identified to species level as only imagos can be identified specific level.

High Atlas endemic species that have been reported on the northern slopes of this mountain range~~e~~, mainly *Alainites oukaimeden* and *Baetis berberus* (El Alami et al. 2022) were not found in the south slope of the Draa basin. A species of Heptageniidae *Ecdyonurus rothschildi* cited by Bouzidi in 1989, in the river of Ounilla in the west of the Upper Draa basin was no longer found in that river but was collected further east in the rivers of Dades and Mgoune. The same author found *Oligoneuriella skoura* in the Mgoune and Dades Rivers in 1989, but these two species were not found in the entire area in this study. Some species with wide distribution in other regions, such as *Ecdyonurus rothschildi* (El Alami et al. 2022) are confined to high altitudes in the Draa Basin. *Oligoneuriopsis skhounate* which has a wide distribution in Morocco (Mabrouki et al. 2017), was only found in one site in a low altitude with low conductivity.

According to topographic and climatic conditions, the Draa basin is divided into three zones: a zone at high altitude in the reliefs of the southern slopes of the High Atlas where three rivers with strong current with low conductivity and low water temperature flow (Ounilla, Mgoune and Dades), this zone is characterized by cold water species such as *Ecdyonurus rothschildi*, *Rhithrogena* sp., *Baetis rhodani*, *Caenis pusilla* and *Baetis maurus*. A second intermediate zone located in the valley of the Ouarzazate basin which is part of the South Atlas furrow where the climate is less cold than the high mountain zones (Iriri Fint and Ait Douchene) and where the conductivity is not very high, we find the species *Cheleocloeon dimorphicum*, *Cloeon simile*, *Procloeon stagnicola*, *Labiobaetis neglectus* and *Choroterpes atlas* in addition to the species of wide ecological range: *Caenis luctuosa* and *Baetis pavidus*. Finally in a third Saharan zone with high conductivity and high summer temperature (Tissint, Mghimima and Akka nait sidi) we find the resistant euryhaline species *Caenis luctuosa* and *Baetis pavidus*.

The absence of larvae of *Oligoneuriopsis skhounate* during all the samples collected from September 2020 to April 2021 can be explained by the phenomenon of diapause caused by the low winter temperatures (Zrelli et al. 2010).

Ephemeroptera in this area are affected by physicochemical parameters, the irregularity of the Draa rivers caused by climatic factors such as periods of summer drought, autumnal floods, or periods of high flow after snow melt (as was the case in the spring of the year 2021). Human factors also highly impact the Ephemeroptera diversity, in peculiar in relation to the intake of water from the rivers for agricultural activities, this intake is accentuated during the dry seasons which can completely dry up the river during years of severe drought. These flow fluctuations directly impact the community of aquatic macroinvertebrates whose life cycles are intimately linked to the aquatic environment.

In the Middle Draa, rainfall scarcity and repeated droughts have impacted the river's flow, which now relies almost solely on releases from the El Mansour Eddahbi dam. The excessive use of water in agriculture further exacerbates the situation, leading to a lack of permanent water flow in the river. This has resulted in drying up of several sites which we found to be rich in macroinvertebrates in 2019. After falling dry since February 2020, we were only able to sample a small puddle that remained from dam releases and showed low macroinvertebrate richness

In our study, the distribution of Ephemeroptera was limited by conductivity with fewer species found in high saline sites, furthermore, we found a nearly significant negative correlation of species richness and water temperature. With increasing temperatures and salinity levels in the future (Williams 1999) we can assume a loss of some additional stenotherm species (Kaczmarek et al. 2021).

Acknowledgements

Thanks to the professors Jean-Luc Gattolliat and Michel Sartori for their precious help in the identification of the species.

We also thank Khawla Lazrak for her help in measuring the physicochemical parameters in the field Funding is provided by the Museum d'Histoire naturelle de Marrakech. Cadi Ayyad University and the German Federal Ministry of Education and Research (BMBF) is funding the project SaliDraa جوج within the framework of the Strategy. Research for Sustainability (FONA) www.fona.de/en as part of its Social-Ecological Research funding priority. funding no 01UU1906 project Salidraa جوج (https://salidraajuj.uni-landau.de/).

Responsibility for the content of this publication lies with the author.

References

Agence du Bassin Hydrolique souss massa Drâa (2008) Etude D'actualisation Du Plan Directeur D'amenagement Integre Des Ressources En Eau (Pdaire). Agence du Bassin Hydrolique Souss Massa: e57.

Agence du Bassin hydrolique Souss massa Drâa D (2012) Bassin de Draa. https://www.fichier-pdf.fr/2012/05/20/bassin-de-draa/ [November 18, 2021]

Ajakane A, Boumezough (1996) Ecological characteristics of the benthic macro-invertebrate of high altitude streams (Morocco). Water quality and limnological issues.

Alba-Tercedor J, El El Alami M (1999) Description of the Nymphs and Eggs of *Acentrella almohades* sp. n. from Morocco and Southern Spain (Ephemeroptera: Baetidae). Aquatic Insects (Vol. 21) (1999). Aquatic Insects 21(4): 241–247. https://doi.org/10.1076/aqin.21.4.241.4509

Barber-James HM, Gattolliat J-L, Sartori M, Hubbard MD (2008) Global diversity of mayflies (Ephemeroptera, Insecta) in freshwater. Hydrobiologia 595: 339–350. https://doi.org/10.1007/s10750-007-9028-y

Bauernfeind E, Moog O (2000) Mayflies (Insecta: Ephemeroptera) and the assessment of ecological integrity: a methodological approach. In: Jungwirth M, Muhar S, Schmutz S (Eds) Assessing the Ecological Integrity of Running Waters: 71–83. https://doi.org/10.1007/978-94-011-4164-2_6

Bebba N, El alami M, Arigue SF, Arab A (2015) Etude mésologique et Biotypologique du peuplement des Ephéméroptères de l'oued Abdi (Algerie). Journal of Materials and Environmental Science 6(4): 1164–1177. [ISSN: 2028-2508 CODEN: JMESCN: 14.]

Benhadji N, Sartori M, Abdellaoui-Hassaïne K, Gattolliat J-L (2020) Reports of Baetidae (Ephemeroptera) species from Tafna Basin, Algeria and biogeographic affinities revealed by DNA barcoding. Biodiversity Data Journal 8: 1–23. https://doi.org/10.3897/BDJ.8.e55596

Berger E, Bossenbroek L, Beermann ArneJ, Schäfer Ralph B, Znari M, Riethmüller S, Sidhu N, Kaczmarek N, Benaissa H, Ghamizi M, Plicht S, Ben salem S, El Qorchi F, Naimi M (2021) Social-ecological interactions in the Draa River Basin, southern Morocco: Towards nature conservation and human well-being using the IPBES framework. Science of the Total Environment 769: e144492. https://doi.org/10.1016/j.scitotenv.2020.144492

Berrahou A, Cellot B, Richoux P (2001) Distribution longitudinale des macroinvertébrés benthiques de la Moulouya et de ses principaux affluents (Maroc). Annales de Limnologie – International Journal of Limnology 37: 223–235. https://doi.org/10.1051/limn/2001020

Bottova K, Derka T, Svitok M (2012) Life history and secondary production of Mayflies (Ephemeroptera) indicate disturbance in two small carpathian streams. International review of hydrobiology 97(2): 100–116. https://doi.org/10.1002/iroh.201111364

Bouchard Jr RW (2004) Chapter 4 Ephemeroptera (Mayflies). Guide to aquatic invertebrates of the upper Midwest. Water ressorces center, University of Minnesota, St.Paul, 208 pp.

Boumaiza M, Thomas AGB (1986) Répartition et écologie des Ephéméroptères de Tunisie (1ère partie) (Insecta, Ephemeroptera). Archives institut Pasteur Tunis 63(4): 567–599.

Bouzidi A (1989) Recherches hydrobiologiques sur les cours d'eau des massifs du Haut-Atlas (Maroc): bio-écologie des macroinvertébrés et distribution spatiale des peuplements. These de doctorat. Aix-Marseille 3. https://www.theses.fr/1989AIX30022 [November 18, 2021]

Brittain JE (1982) Biology of Mayflies. Annual Review of Entomology 27(1): 119–147. https://doi.org/10.1146/annurev.en.27.010182.001003

Chahboune M, Chahlaoui A, Zaid A (2014) Contribution to comparative study of the physico-chemical quality of waters of Moulouya and Ansegmir rivers in upstream of Hassan II dam (Province of Midelt, Morocco). Journal of Biodiversity and Environmental Sciences 4(2): 278–288.

Dakki M, El Agbani A (1983) Ephéméroptères d'Afrique du nord, 3 elements pour la connaissance de la faune Marocaine. Bulletin de l'institut scientifique, Rabat, 115–126. http://www.israbat.ac.ma/wp-content/uploads/2015/01/BIS_7_115-126.pdf [November 7, 2021]

El Alami M, El Yaagoubi S, Gattolliat J-L, Sartori M, Dakki M (2022) Diversity and distribution of mayflies from Morocco (Ephemeroptera, Insecta). Diversity 14: e498. https://doi.org/10.3390/d14060498

El Alami M, Dakki M, Errami M, Alba-Tercedor (2000) Nouvelles données sur les Baetidae du Maroc (Insecta: Ephemeroptera). Zoologica baetica 11: 105–113.

El Bazi RE, El Alami M, Khadri O, Errochdi S, Slimani M, Bennas N (2017) Contribution a látude de la biodiversite aquatique des aires protegées du Maroc. Les macroinvertebres aquatiques du projet du Parc Naturel de Bouhachem (nord-ouest du Maroc) II: Ephemeroptera, Plecoptera, Trichoptera. Boletín de la Sociedad Entomologica Aragonesa, 55–66.

Elliott JM, Humpesch UH, Macan TT (1988) Larvae of the British ephemeroptera: A key with ecological notes. Freshwater Biological Association.

Fox J, Weisberg S (2018) An R companion to applied regression (3rd edn.). Sage publication. https://toc.library.ethz.ch/objects/pdf03/z01_978-1-5443-3647-3_01.pdf [December 8, 2021]

Gagneur J, Thomas AGB (1988) Contribution à la connaissance des Ephéméroptères d'Algérie I. Répartition et écologie (1ère partie) (Insecta, Ephemeroptera). Bulletin de la Société d'histoire naturelle de Toulouse 1241988: 213–223.

Gattolliat J-L, Sartori M (2008) What is *Baetis rhodani* (Pictet, 1843) (Insecta, Ephemeroptera, Baetidae)? Designation of a neotype and redescription of the species from its original area. Zootaxa 1957: 69–80. https://doi.org/10.11646/zootaxa.1957.1.3

Himmi O, El Alami M, Bennas N, Belqat B, Kettani K (2009) Évaluation de la biodiversité des macroinvertebres aquatiques de tahaddart au maroc: interêt pour la conservation et la gestion rationnelle des ressources hydriques. Sustainable management of Mediterranean coastal fresh and transitional water bodies: a socio-economic and environmental analysis of changes and trends to enhance and sustain stakeholder benefits, Firenze University Press, 17 pp.

Jacobus LM, Macadam CR, Sartori M (2019) Mayflies (Ephemeroptera) and Their Contributions to Ecosystem Services. Insects 10: e170. https://doi.org/10.3390/insects10060170

Kaczmarek N, Schäfer RB, Berger E (2021) Environmental change threatens freshwater insect communities in Northwest Africa: A meta-analysis. Frontiers in Environmental Science 9: e671715. https://doi.org/10.3389/fenvs.2021.671715

Kaltenbach T, Vuataz L, Samraoui B, Yaagoubi SE, El Alami M, Gattolliat J-L (2022) Two new species of Centroptilum Eaton, 1869 from North Africa (Ephemeroptera, Baetidae). ZooKeys 1131: 71–97. https://doi.org/10.3897/zookeys.1131.91017

Kassambara A (2020) ggpubr:"ggplot2" based publication ready plots.

Kimmins DE (1938) A new moroccan Ephemeroptera. Annals and Magazine of Natural History 1: 302–305. https://doi.org/10.1080/00222933808526771

Lamri D, Hassouni T, Loukili A, Belghyti D (2016) Structure and macroinvertebrate diversity in the Moulouya river basin, Morocco. Journal of Entomology and Zoology Studies 4(4): 1116–1121.

Lestage JA (1925) Contribution à l'étude des Ephéméroptères.pdf. Extrait des Annales de Biologie Lacustre TOME XIII, FASC. 3, 4 1924 Série III. Le Groupe Ephémérellidien: e77.

Lounaci A, Brosse S, Thomas A, Lek S (2020) Abundance, diversity and community structure of macroinvertebrates in an Algerian stream: The Sébaou wadi. Annales De Limnologie-International Journal of Limnology 36(2): 123–133. https://doi.org/10.1051/limn/2000008

Mabrouki Y, Taybi AF, El Alami M, Berrahou A (2017) New and interesting data on distribution and ecology of Mayflies from Eastern Morocco (Ephemeroptera). Journal of Materials and Environmental Sciences 8(8): 2839–2859.

Mabrouki Y, Taybi AF, El Alami M, Berrahou A (2019) Biotypology of stream macroinvertebrates from North African and semi arid catchment: Oued Za (Morocco). Journal of Materials and Environmental Science 420: 17. [1–11] https://doi.org/10.1051/kmae/2019009 [02 April 2019]

Mebarki M, Taleb A, Arab A (2017) Environmental factors influencing the composition and distribution of mayfly larvae in northern Algerian wadis (regional scale). Revue d'Ecologie, Terre et Vie 72: 303–313. https://doi.org/10.3406/revec.2017.1893

Müller-Liebenau I (1969) Revision der europäishen arten der Gattung Baetis Leach, 1815 (Insecta Ephemeroptera). Gewass Abwass 48: 1–214.

Oksanen J, Guillaume Blanchet F, Friendly M (2019) Vegan: Com-munity Ecology Package. R package version 2.5-6.

Pihan JC, Mohati A (1985) Les peuplements benthiques du reseau permanent de l'Oued Ourika, Haut Atlas de Marrakech; qualité des eaux. SIL Proceedings, 1922–2010 22(4): 2110–2113. https://doi.org/10.1080/03680770.1983.11897631

Salles FF, Domínguez E, Molineri C, Boldrini R, Nieto C, Dias LG (2018) Order Ephemeroptera. In: Thorp JH, Rogers DC (Eds) Thorp and Covich's Freshwater Invertebrates, Elsevier, 61–117. https://doi.org/10.1016/B978-0-12-804223-6.00003-2

Samraoui B, Márquez-Rodríguez J, Ferreras-Romero M, El-Serehy A, Samraoui F, Sartori M, Gattolliat JL (2020) Biogeography, ecology, and conservation of mayfly communities of relict mountain streams, north-eastern Algeria. Aquatic Conservation: Marine and Freshwater Ecosystems 31(12): 1–13. https://doi.org/10.1002/aqc.3719 [December 19, 2021]

Sartori M, Brittain JE (2015) Order Ephemeroptera. In: Thorp JH, Rogers DC (Eds) Thorp and Covich's Freshwater Invertebrates, Elsevier, 873–891. https://doi.org/10.1016/B978-0-12-385026-3.00034-6

Soldan T, Thomas AGB (1985) Centroptilum dimorphicum sp. n., a new species of mayfly (Ephemeroptera, Baetidae) from Algeria. Acta Entomologica Bohemoslovaca 82(3): 180–186. [ISSN 0001-5601] http://www.ephemeroptera-galactica.com/pubs/pub_s/pubsoldant1985p180.pdf [November 22, 2021]

Tachet H, Richoux P, Bournaud M, Usseglio-Polatera P (2000) Invertébrés d'eau douce: systématique, biologie, écologie. Nouvelle édition. CNRS éditions. https://bibliotheques.mnhn.fr/medias/detailstatic.aspx?INSTANCE=exploitation&RSC_BASE=HORIZON&RSC_DOCID=440952 [November 17, 2021]

Williams VD (1999) Salinisation: A major threat to water resources in the arid and semi-arid regions of the world. Lakes & Reservoirs: Science, Policy and Management for Sustainable Use 4(3–4): 85–91. https://doi.org/10.1046/j.1440-1770.1999.00089.x

Yalles-Satha A, El Alami M, Kechemir L hanane, Desvilettes C, Chenchouni H (2021) Diversity, phenology and distribution of mayfly larvae (Ephemeroptera) along an altitudinal gradient in two permanent Wadis of Algeria. Oriental Insects 56(1): 14–46. https://doi.org/10.1080/00305316.2021.1904022

Zrelli S, Boumaiza M, Bejaoui M, Gattolliat J-L, Sartori M (2016) New data and revision of the Ephemeroptera of Tunisia. Inland Water Biology Supplement 3: 99–106.

Zrelli S, Bejaoui M, Touyalia S, Korbaa M, Boulaaba S, Boumaiza M (2010) Cycle de vie d'Oligoneuriopsis skhounate Dakki et Giudicelli, 1980 (Insecta, Ephemeroptera) dans l'oued Joumine (Ichkeul, Tunisie Septentrionale). Actes de la CIFE VI, Travaux de l'Institut Scientifique, Série Zoologie, Rabat, 2010, N° 47, Tome I, 97–99.

Supplementary material 1

Inventory of species of Draa basin collected in all trips

Authors: Mokhtar Benlasri
Data type: List of the species sampled in the Draa basin
Explanation note: The list with the number of each species in each sample during the study period.

Link: https://doi.org/10.3897/alpento.7.96436.suppl1

Supplementary material 2

Parameters mesured during the samples

Authors: Mokhtar Benlasri
Data type: Database of the measured physico-chemical parameters
Explanation note: The database of the measured physico-chemical parameters in every site during all the field trips.

Link: https://doi.org/10.3897/alpento.7.96436.suppl2

Alpine Entomology 7 2023, 21–35 | DOI 10.3897/alpento.7.102639

The hidden diet – examination of crop content reveals distinct patterns of pollen host use by Central European bees of the genus *Hylaeus* (Hymenoptera, Colletidae)

Andreas Müller[1]

1 *ETH Zurich, Institute of Agricultural Sciences, Biocommunication and Entomology, Schmelzbergstrasse 9/LFO, 8092 Zurich, Switzerland*

https://zoobank.org/8003C76B-473D-480B-8C45-1D2E6AAB0731

Corresponding author: Andreas Müller (andreas.mueller@usys.ethz.ch)

Academic editor: Jessica Litman ♦ **Received** 24 February 2023 ♦ **Accepted** 7 April 2023 ♦ **Published** 20 April 2023

Abstract

Masked or yellow-faced bees of the genus *Hylaeus* (Colletidae) differ in their mode of pollen transportation from most other bees in that they ingest the pollen directly on the flowers and carry it back to the nest inside the crop located in the anterior half of the metasoma. Due to this hidden mode of pollen transportation, the examination of pollen collected by *Hylaeus* females requires the dissection of the metasoma. Although this method has never been applied in Europe, the great majority of the Central European *Hylaeus* species were supposed to be pollen generalists based on observations of flower visits. The microscopical analysis of pollen removed from 30 crops each of 36 Central European *Hylaeus* species revealed that the proportion of species exhibiting an exclusive or strong preference for pollen from a single plant taxon is much higher than hitherto assumed and that the current assumption of the genus *Hylaeus* to largely consist of pollen generalists is wrong. Nineteen of the 36 species examined are strictly or largely dependent on a single plant taxon for collecting pollen, such as Apiaceae (n = 11 species), Rosaceae (n = 3), *Reseda* (Resedaceae) (n = 2), *Allium* (Amaryllidaceae) (n = 1), Asteraceae (n = 1) and *Melilotus* (Fabaceae) (n = 1). The 36 *Hylaeus* species examined collected pollen from the flowers of 31 plant families, of which the Apiaceae and Rosaceae (particularly *Potentilla* and *Rubus*) were by far the most important contributing almost 60% to the pollen host spectrum of the entire genus. The comparison between pollen host spectrum and flower visiting records showed that the pollen generalists use the flowers of the Asteraceae as nectar rather than pollen sources, corroborating earlier findings that the digestion of Asteraceae pollen requires physiological adaptations to cope with its unfavourable or protective properties. In summary, the patterns of pollen host use by bees of the genus *Hylaeus* do not substantially differ from those of other Palaearctic bee taxa despite the masked bees' unusual habit to ingest the pollen directly on the flowers and to transport it inside their body back to the nest.

Key Words

Anthophila, Apiformes, Asteraceae paradox, Asteroideae, Carduoideae, oligolecty, polylecty

Introduction

Bees are vegetarian wasps, whose larvae usually develop on a mixture of pollen and nectar within the brood cells of the nests built by the mother bees (Westrich 1989; Michener 2007). In most species, nesting females carry pollen collected on flowers back to the nest on the hind legs and/or on the underside of the metasoma (Westrich 1989; Michener 2007). Due to this external mode of pollen transportation, pollen is easily accessible for examination. In fact, extensive pollen analytical work starting with the seminal publications by Chambers (1968); Raw (1974); Westrich and Schmidt (1986, 1987) and Westrich (1989) and followed by numerous further investigations for example by Müller (1996, 2018); Michez et al. (2008); Müller and Kuhlmann (2008); Sedivy et al. (2008, 2013); Haider et al. (2014); Wood et al. (2016) or Wood and Roberts (2017) led to a fairly good knowledge of the pollen host preferences of large parts of the Central European bee fauna.

Bees of the genus *Hylaeus* – a cosmopolitan taxon of colletid bees comprising several hundred species worldwide (Ascher and Pickering 2020) – differ in their mode of pollen transportation from most other bees in that they ingest the pollen directly on the flowers and carry it back inside the metasomal crop to the nest, where it is regurgitated into the brood cells (Westrich 1989; Michener 2007). Due to this hidden mode of pollen transportation, pollen is accessible for examination only after dissection of the metasoma, a method that has never been applied for European species of this genus.

Based on field observations, all Central European *Hylaeus* species are currently assumed to be pollen generalists (“polylectic”) except for three species, which are most probably pollen specialists (“oligolectic”) on *Allium* (Amaryllidaceae), *Reseda* (Reseda) and Asteraceae, respectively (Scheuchl and Willner 2016; Westrich 2018; Wiesbauer 2020). However, reliable identification of *Hylaeus* in the field down to species level is strongly hampered by the small size and the uniform morphology of most Central European species, casting doubt on the field-based assumption that the vast majority of species is polylectic. Furthermore, as the spectrum of flowers exploited for nectar is often much wider than for pollen, observations of flower visits without careful differentiation between pollen and nectar uptake poorly reflect pollen host preferences and often conceal pollen specializations (Westrich and Schmidt 1987). In fact, the analysis of pollen remains in larval faeces of three North American *Hylaeus* species revealed that all three species collected pollen almost exclusively on Rosaceae in spite of long lists of flower visitation records comprising taxa belonging to numerous different plant families (Scott 1996).

In the present study, the pollen host preferences of 36 Central European *Hylaeus* species including four species restricted in their distribution to higher elevations in the Alps were analysed by microscopical analysis of pollen removed from the crops of collected females. Specifically, the following questions were addressed: i) What are the pollen host spectra of the Central European species? ii) Which plant taxa serve as the most important pollen hosts for the genus in Central Europe? iii) Are there differences between the pollen host spectrum of the genus as assessed in the present study and records of flower visits in the field?

Material and methods

Bee species

Masked or yellow-faced bees of the genus *Hylaeus* Fabricius (Colletidae) are distributed on all continents except for Antarctica (Michener 2007). Currently, about 760 species are known, of which 47 occur in Central Europe belonging to ten subgenera (Dathe et al. 2016; Ascher and Pickering 2020). The Central European representatives of *Hylaeus* are small, black, nearly hairless bees usually ranging in length from 3.5 mm to 7 mm. Most species are characterised by the presence of white or yellow markings on the face. The proboscis of all species is very short, limiting nectar uptake to flowers with easily reachable nectar, which is either exposed or – if secreted at the base of the flowers – accessible thanks to the small body size of the bees. The Central European species nest in preexisting cavities such as insect borings in dead wood, hollow stems, soil fissures, abandoned above and below ground nests of aculeate Hymenoptera, abandoned *Lipara* reed galls or between stones; more rarely, they excavate the nests in the pith of plant stems (Westrich 2018). The brood cell walls are constructed with glandular secretions, which solidify after application by the specialised bilobed tongue to a transparent and cellophane-like waterproof membrane (Batra 1980; Almeida 2008).

For the present study, 36 Central European *Hylaeus* species were selected representing about 80% of *Hylaeus* species diversity in Switzerland, Germany and Austria (Dathe et al. 2016). The species identification was based on Amiet et al. (2014) and Dathe et al. (2016). In addition, the publications by Doczkal and Schmid-Egger (1992) and Straka and Bogusch (2011) were used for the proper identification of the two very similar species *Hylaeus pictipes* and *H. taeniolatus* and the three species of the *Hylaeus gibbus* group, respectively.

Pollen host spectrum

To assess the pollen host spectra of the 36 *Hylaeus* species, the crop content of a total of 1027 pinned females from museum and private collections captured between the middle of the 20th century and 2022 was analysed by light microscopy. For each species, 30 pollen-containing crops were dissected originating from females collected at 30 different localities within the study area, which encompassed Switzerland, Baden-Württemberg (Germany) as well as Vorarlberg and Tirol (Austria). Localities were defined as different if the data on the collection labels differed with respect to collection site and/or collection date. For the four rare species *Hylaeus crassanus*, *H. glacialis*, *H. incongruus* and *H. moricei*, the targeted number of 30 different crop contents from 30 different localities was not attained and part of the females originated from outside the study area (see Table 1).

To remove pollen from the crop, which is located in the anterior half of the metasoma, the female was stripped off from the insect pin to a polystyrene underlay and her metasoma was opened in dry state under a stereomicroscope between the second and third tergal segment with a scalpel. This procedure tore open the very thin crop walls, revealing the pollen masses that were located between the base of the metasoma and the proventriculus. The pollen was removed from the crop with a pair of tweezers and its amount was assigned to four classes, ranging from 4/4 (full crop) to 1/4 (crop filled to one fourth), before it was transferred to a microscopical slide and embedded

Table 1. Pollen host spectrum of 36 Central European bee species of the genus *Hylaeus* (Colletidae). Subgeneric classification according to Dathe et al. (2016). n = total number of pollen loads, N = number of pollen loads from different localities. Countries: A = Austria (Vorarlberg, Tirol), CH = Switzerland, D = Germany (Baden-Württemberg), E = Spain, F = France, FL = Liechtenstein, IT = Italy, SK = Slovakia. Plant families: ADO = Adoxaceae, AMA = Amaryllidaceae, API = Apiaceae, ARA = Araliaceae, AST = Asteraceae, BOR = Boraginaceae, BRA = Brassicaceae, CAM = Campanulaceae), CAR = Caryophyllaceae, CIS = Cistaceae, CRA = Crassulaceae, ERI = Ericaceae, EUP = Euphorbiaceae, FAB = Fabaceae, FAG = Fagaceae, GEN = Gentianaceae, HYP = Hypericaceae, LAM = Lamiaceae, LYT = Lythraceae, ORO = Orobanchaceae, PLA = Plantaginaceae, POL = Polygonaceae, RAN = Ranunculaceae, RES = Resedaceae, RHA = Rhamnaceae, ROS = Rosaceae, RUB = Rubiaceae, SAX = Saxifragaceae, SCR = Scrophulariaceae, TIL = Tiliaceae, VIT = Vitaceae; ORO/PLA = indeterminable pollen grains belonging either to *Euphrasia*, *Rhinanthus* (both Orobanchacee) or *Veronica* (Plantaginaceae). Definitions of bee pollen host ranges after Müller and Kuhlmann (2008).

Bee species	n	N	Origin (total number/ number of cantons) of pollen loads	% pollen grain volume (number of loads)	Preferred host	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Pollen host range in Central Europe
Subgenus *Abrupta*									
Hylaeus cornutus Curtis, 1831	30	30	CH (26/10), D (4)	API 94.2% (30), AST (Asteroideae) 2.7% (7), BRA 1.8% (1), EUP (*Euphorbia*) 1.3% (1)	Apiaceae	94.2	70.0	100	Polylectic with strong preference for Apiaceae
Subgenus *Dentigera*									
Hylaeus brevicornis Nylander, 1852	30	30	CH (30/12)	API 59.4% (19), ROS (*Rubus*) 15.5% (5), ROS (*Potentilla*) 13.8% (6), ROS (other) 0.4% (1), EUP (*Euphorbia*) 3.5% (1), CRA 3.2% (2), AST (Asteroideae) 0.4% (3), HYP (*Hypericum*) 0.2% (), unknown 3.6% (1)	–	–	–	–	Polylectic (6 plant families)
Hylaeus glacialis Morawitz, 1872	18	17	CH (15/2), F (2), IT (1)	API 68.0% (13), CIS (*Helianthemum*) 8.8% (2), CRA 7.6% (3), SAX (*Saxifraga*) 6.6% (3), ROS (*Rubus*) 3.2% (1), LAM (Nepetoideae) 2.8% (1), BRA 1.5% (2), CAR 1.5% (2)	–	–	–	–	Polylectic (8 plant families)
Hylaeus gredleri Förster, 1871	30	30	CH (29/12), FL (1)	API 91.8% (28), ROS (*Potentilla*) 6.2% (1), EUP (*Euphorbia*) 1.8% (2), AST (Asteroideae) 0.2% (1)	Apiaceae	91.8	86.7	93.3	Polylectic with strong preference for Apiaceae
Hylaeus kahri Förster, 1871	30	30	CH (30/7)	API 93.0% (28), CRA 5.1% (3), FAG (*Castanea*) 1.8% (3), AST (Asteroideae) 0.1% (1),	Apiaceae	93.0	76.7	93.3	Polylectic with strong preference for Apiaceae
Hylaeus pilosulus (Pérez, 1903)	30	12	CH (21/1), E (6), F (3)	RES (*Reseda*) 100% (30)	*Reseda* (Resedaceae)	100	100	100	Narrowly oligolectic on *Reseda* (Resedaceae)
Subgenus *Hylaeus*									
Hylaeus angustatus (Schenck, 1861)	30	30	CH (30/7)	ROS (*Rubus*) 16.8% (6), ROS (*Potentilla*) 15.5% (5), BOR (*Echium*) 13.9% (8), CAM (*Campanula*) 7.8% (3), CAM (*Jasione*) 6.1% (3), LAM (Nepetoideae) 6.9% (5), FAB (*Melilotus*) 6.1% (2), BRA 5.8% (1), RES (*Reseda*) 5.8% (2), AMA (*Allium*) 3.5% (2), CIS (*Helianthemum*) 3.5% (2), CRA 2.8% (1), ORO/PLA 1.6% (2), PLA (*Linaria*) 1.1% (1), API 1.5% (1), AST (Asteroideae) 0.8% (3), RUB 0.4% (1), unknown 0.1% (1)	–	–	–	–	Polylectic (14 plant families)
Hylaeus annulatus (Linnaeus, 1758)	30	30	CH (26/7), FL (4)	ROS (*Potentilla*) 23.2% (13), ROS (*Rubus*) 10.8% (5), ROS (*Rosa*) 1.2% (1), CAM 13.4% (8), ORO/PLA 11.7% (10), CIS (*Helianthemum*) 10.3% (6), API 7.5% (5), LAM (Nepetoideae) 6.8% (5), LAM (Lamioideae) 1.6% (2), AMA (*Allium*) 6.8% (4), RAN (*Trollius*) 3.0% (2), RAN (*Ranunculus*) 0.5% (2), ERI 1.5% (3), CRA 0.8% (2), CAR 0.4% (1), AST (Asteroideae) 0.2% (1), BRA 0.2% (1), ORO (*Melampyrum*) 0.1% (1)	–	–	–	–	Polylectic (13 plant families)
Hylaeus communis Nylander, 1852	30	30	CH (30/10)	API 30.6% (14), ROS (*Rubus*) 16.9% (5), CAM 8.6% (4), PLA (*Plantago*) 7.8% (4), PLA (*Linaria*) 1.0% (2), CRA 6.6% (2), RES (*Reseda*) 5.0% (1), FAB (*Melilotus*) 4.6% (4), AST (Asteroideae) 4.3% (7), CAR 3.5% (2), POL (*Fallopia*) 3.3% (1), BOR (*Echium*) 2.6% (1), LAM (Nepetoideae) 2.5% (2), BRA 1.3% (1), RHA (*Frangula*) 0.5% (1), RUB 0.5% (2), HYP (*Hypericum*) 0.4% (1)	–	–	–	–	Polylectic (16 plant families)
Hylaeus leptocephalus (Morawitz, 1871)	30	30	CH (18/5), D (12)	FAB (*Melilotus)* 74.7% (22), BRA 9.4% (4), ROS (*Rubus*) 3.7% (2), ROS (*Potentilla*) 3.2% (1), RES (*Reseda*) 2.7% (1), LAM (Nepetoideae) 1.6% (1), TIL (*Tilia*) 1.6% (1), API 1.3% (1), AST (Asteroideae) 0.8% (3), AST (Cichorioideae) 0.3% (1), EUP (*Euphorbia*) 0.3% (1), HYP (*Hypericum*) 0.1% (1), unknown 0.3% (1)	*Melilotus* (Fabaceae)	74.7	63.3	80.0	Polylectic with strong preference for *Melilotus* (Fabaceae)

Bee species	**n**	**N**	**Origin (total number/ number of cantons) of pollen loads**	**% pollen grain volume (number of loads)**	**Preferred host**	**% pollen grain volume of preferred host**	**% pure loads of preferred host**	**% loads with preferred host**	**Pollen host range in Central Europe**
Hylaeus moricei (Friese, 1898)	18	16	D (8), A (7), CH (3/2)	BRA 29.1% (5), ROS (*Rubus*) 23.3% (5), ROS (*Potentilla*) 0.4% (1), ROS (*Filipendula*) 0.1% (1), LAM (Lamioideae) 12.8% (4), API 9.0% (4), AMA (*Allium*) 6.7% (1), FAB (*Melilotus*) 6.4% (2), LYT (*Lythrum*) 3.3% (1), SCR 2.7% (1), PLA (*Linaria*) 2.4% (1), BOR (*Echium*) 1.6% (1), BOR (*Phacelia*) 1.3% (1), AST (Asteroideae) 0.5% (3), RHA (*Frangula*) 0.4% (3)	–	–	–	–	Polylectic (12 plant families)
Hylaeus nigritus (Fabricius, 1798)	30	30	CH (30/9)	AST (Carduoideae) 77.4% (27), AST (Asteroideae) 18.9% (28), AMA (*Allium*) 2.1% (2), CAR 0.6% (1), API 0.2% (2), CAM 0.2% (1), CRA 0.1% (1), unknown 0.7% (2)	Carduoideae and Asteroideae (Asteraceae)	96.1	76.7	100	Broadly oligolectic on Carduoideae and Asteroideae (Asteraceae)
Hylaeus nivalis (Morawitz, 1867)	30	30	CH (30/7)	CAM 19.7% (11), CAR 15.6% (14), ORO/PLA 15.5% (7), PLA (Linaria) 1.1% (1), CRA 12.6% (10), ROS (*Potentilla*) 8.9% (7), ROS (*Rubus*) 0.3% (1), CIS (*Helianthemum*) 8.3% (6), LAM (Nepetoideae) 6.6% (8), LAM (Lamioideae) 5.1% (1), AST (Carduoideae) 1.4% (1), AST (Cichorioideae) 0.4% (2), EUP (*Euphorbia*) 1.5% (1), AMA (*Allium*) 0.8% (1), RUB 0.7% (3), API 0.3% (1), unknown 1.2% (3)	–	–	–	–	Polylectic (12 plant families)
Hylaeus paulus Bridwell, 1919	30	30	CH (28/8), D (1), FL (1)	ROS (*Rubus*) 58.3% (20), ROS (*Potentilla*) 25.3% (8), BRA 5.1% (2), AMA (*Allium*) 4.9% (2), API 3.3% (3), PLA (*Veronica*) 1.7% (1), HYP (*Hypericum*) 0.7%, (1), AST (Asteroideae) 0.4% (4), unknown 0.3% (1)	Rosaceae (*Potentilla, Rubus*)	83.6	60.0	83.3	Polylectic with strong preference for Rosaceae (*Potentilla, Rubus*)
Hylaeus tyrolensis Förster, 1871	30	30	CH (27/11), A (2), FL (1)	API 100% (30)	Apiaceae	100	100	100	Broadly oligolectic on Apiaceae
Subgenus *Koptogaster*									
Hylaeus punctulatissimus Smith, 1842	30	30	CH (29/9), D (1)	AMA (*Allium*) 96.0% (29), FAB (*Melilotus*) 2.2% (1), TIL (*Tilia*) 1.7% (1), CRA 0.1% (1)	*Allium* (Amaryllidaceae)	96.0	90	96.7	Narrowly oligolectic on *Allium* (Amaryllidaceae)
Subgenus *Lambdopsis*									
Hylaeus crassanus (Warncke, 1972)	13	10	CH (7/3), IT (4), F (2)	FAB (*Melilotus*) 60.3% (10), CAM (*Jasione*) 12.5% (1), API 11.8% (4), BOR (*Echium*) 11.2% (2), AST (Asteroideae) 4.2% (1)	–	–	–	–	Polylectic (5 plant families)
Hylaeus dilatatus (Kirby, 1802)	30	30	CH (30/8)	API 56.6% (22), AST (Carduoideae) 11.3% (7), AST (Asteroideae) 2.4% (8), ROS (*Rubus*) 5.4% (3), ROS (*Agrimonia*) 1.0% (1), ROS (*Potentilla*) 0.5% (1), CIS (*Helianthemum*) 5.8% (2), CAR 4.0% (4), CRA 3.0% (5), FAB (*Melilotus*) 2.4% (2), HYP (*Hypericum*) 2.4% (1), BOR (*Echium*) 2.0% (2), PLA (*Plantago*) 1.6% (2), RUB 1.2% (2), RAN (*Clematis*) 0.4% (2)	–	–	–	–	Polylectic (12 plant families)
Hylaeus pfankuchi (Alfken, 1919)	30	30	CH (23/9), D (7)	ROS (*Potentilla*) 62.7% (24), ROS (*Rubus*) 11.2% (5), ROS (*Filipendula*) 1.7% (1), API 20.3% (11), ORO/PLA 1.2% (1), BRA 0.8% (1), AST (Asteroideae) 0.3% (2), LAM (Nepetoideae) 0.3% (1), LYT (*Lythrum*) 0.2% (1), unknown 1.3% (2)	Rosaceae (*Potentilla, Rubus, Filipendula*)	75.7	53.3	80.0	Polylectic with strong preference for Rosaceae (*Potentilla, Rubus, Filipendula*)
Hylaeus rinki (Górski, 1852)	30	30	CH (27/10), D (2), FL (1)	ROS (*Potentilla*) 53.5% (21), ROS (*Rubus*) 18.9% (12), API 22.3% (10), EUP (*Euphorbia*) 3.4% (2), AST (Asteroideae) 0.9% (2), AMA (*Allium*) 0.7% (1), unknown 0.3% (1)	Rosaceae (*Potentilla, Rubus*)	72.4	53.3	86.7	Polylectic with strong preference for Rosaceae (*Potentilla, Rubus*)
Subgenus *Nesoprosopis*									
Hylaeus pectoralis Förster, 1871	30	30	CH (24/4), A (3), D (3)	ROS (*Filipendula*) 18.8% (11), ROS (*Rubus*) 16.0% (7), ROS (*Sanguisorba officinalis*) 9.7% (5), ROS (*Potentilla*) 8.8% (5), API 20.2% (17), LYT (*Lythrum*) 7.8% (4), RHA (*Frangula*) 6.6% (10), LAM (Nepetoideae) 3.3% (2), AMA (*Allium*) 3.1% (2), ORO/PLA 1.7% (1), RAN (*Ranunculus*) 1.7% (2), AST (Asteroideae) 1.5% (2), CAR 0.8% (1)	–	–	–	–	Polylectic (10 plant families)
Subgenus *Paraprosopis*									
Hylaeus clypearis (Schenck, 1853)	30	30	CH (27/13), D (3)	API 97.9% (29), CRA 1.8% (1), RES (*Reseda*) 0.3% (1)	Apiaceae	97.9	93.3	96.7	Broadly oligolectic on Apiaceae

Bee species	n	N	Origin (total number/ number of cantons) of pollen loads	% pollen grain volume (number of loads)	Preferred host	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Pollen host range in Central Europe
Hylaeus pictipes Nylander, 1852	30	30	CH (23/6), D (7)	RES (*Reseda*) 24.7% (9), API 22.2% (6), BRA 22.0% (8), BOR (*Echium*) 11.6% (6), CRA 9.8% (5), ROS (*Rubus*) 4.2% (3), ROS (*Potentilla*) 1.5% (1), ARA (*Hedera*) 1.3% (1), LAM (Nepetoideae) 1.1% (1), AST (Asteroideae) 0.5% (2), EUP (*Euphorbia*) 0.6% (1), LYT (*Lythrum*) 0.5% (1),	–	–	–	–	Polylectic (11 plant families)
Hylaeus sinuatus (Schenck, 1853)	30	30	CH (30/12)	API 98.6% (29), FAG (*Castanea*) 1.4% (1)	Apiaceae	98.6	96.7	96.7	Broadly oligolectic on Apiaceae
Hylaeus styriacus Förster, 1871	30	30	CH (30/10)	API 100% (30)	Apiaceae	100	100	100	Broadly oligolectic on Apiaceae
Hylaeus taeniolatus Förster, 1871	30	30	CH (30/12)	API 92.8% (29), ROS (*Rubus*) 3.9% (1), ARA (*Hedera*) 3.0% (1), AST (Asteroideae) 0.1% (1), unknown 0.2% (1)	Apiaceae	92.8	90.0	96.7	Broadly oligolectic on Apiaceae
Subgenus *Patagiata*									
Hylaeus difformis (Eversmann, 1852)	30	30	CH (30/13)	ROS (*Rubus*) 27.1% (8), FAB (*Melilotus*) 20.4% (7), CAM (*Campanula*) 15.4% (8), SCR (*Scrophularia*) 13.2% (7), BOR (*Echium*) 9.3% (3), LAM (Nepetoideae) 8.3% (4), PLA (*Linaria*) 1.5% (2), ORO/PLA 1.0% (2), HYP (*Hypericum*) 1.3% (2), LYT (*Lythrum*) 1.1% (1), RHA (*Frangula*) 1.1% (2), unknown 0.3% (1)	–	–	–	–	Polylectic (10 plant families)
Subgenus *Prosopis*									
Hylaeus confusus Nylander, 1852	30	30	CH (29/10), D (1)	ROS (*Potentilla*) 28.1% (15), ROS (*Rubus*) 25.2% (15), ROS (*Aruncus*) 0.1% (1), ROS (other) 1.4% (1), CAM 13.2% (6), API 9.2% (6), CIS (*Helianthemum*) 7.8% (5), PLA (*Linaria*) 5.0% (1), ORO/PLA 4.9% (2), PLA (*Plantago*) 1.5% (1), HYP (*Hypericum*) 2.6% (4), AST (Asteroideae) 0.6% (1), ORO (*Melampyrum*) 0.4% (1)	–	–	–	–	Polylectic (8 plant families)
Hylaeus duckei (Alfken, 1905)	30	29	CH (18/7), A (4), D (3), F (3), IT (1), SK (1)	API 97.3% (29), BRA 1.2% (1), ROS (*Rubus*) 0.2% (1), ROS (other) 1.2% (1), unknown 0.1% (1)	Apiaceae	97.3	93.3	96.7	Broadly oligolectic on Apiaceae
Hylaeus gibbus Saunders, 1850	30	30	CH (28/8), D (2)	ROS (*Rubus*) 39.9% (16), ROS (*Potentilla*) 4.1% (4), ROS (other) 0.4% (1), FAB (*Melilotus*) 16.0% (11), API 14.5% (9), CIS (*Helianthemum*) 9.5% (4), CAM (*Campanula*) 3.3% (1), CAM (*Jasione*) 1.1% (1), HYP (*Hypericum*) 3.8% (2), CRA (1.9%) (1), AST (Asteroideae) 1.1% (1), PLA (*Plantago*) 1.0% (2), RES (*Reseda*) 0.8% (1), ADO (*Sambucus*) 0.6% (1), RUB (0.6%) (1), BOR (*Echium*) 0.5% (1), LAM (Nepetoideae) 0.3% (1), RHA (*Frangula*) 0.2% (1), unknown 0.4% (2)	–	–	–	–	Polylectic (15 plant families)
Hylaeus incongruus Förster, 1871	18	18	CH (18/5)	ROS (*Rubus*) 28.3% (7), ROS (*Potentilla*) 2.1% (2), FAB (*Melilotus*) 22.8% (5), CRA 11.2% (4), CAM (*Jasione*) 6.1% (1), CAM (*Campanula*) 4.5% (1), BOR (*Echium*) 7.0% (3), CIS (*Helianthemum*) 5.3% (4), LAM (Nepetoideae) 3.7% (3), Hypericaceae (*Hypericum*) 3.3% (2), API 2.3% (3), RES (*Reseda*) 2.1% (1), BRA 0.4% (1), PLA (*Plantago*) 0.4% (1), VIT (*Vitis*) 0.4% (1), AST (Asteroideae) 0.1% (1),	–	–	–	–	Polylectic (14 plant families)
Hylaeus signatus (Panzer, 1798)	30	30	CH (30/11)	RES (*Reseda*) 100% (30)	*Reseda* (Resedaceae)	100	100	100	Narrowly oligolectic on *Reseda* (Resedaceae)
Hylaeus variegatus (Fabricius, 1798)	30	30	CH (30/5)	API 88.6% (29), EUP (*Euphorbia*) 4.6% (1), ROS (*Potentilla*) 2.3% (1), RES (*Reseda*) 1.4% (1), AST (Asteroideae) 0.8% (2), CRA 0.7% (2), CIS (*Helianthemum*) 0.6% (1), RUB 0.2% (2), unknown 0.8% (2)	Apiaceae	88.6	76.7	96.7	Polylectic with strong preference for Apiaceae
Subgenus *Spatulariella*									
Hylaeus alpinus (Morawitz, 1867)	30	30	CH (28/8), A (2)	CIS (*Helianthemum*) 22.0% (12), ROS (*Potentilla*) 13.6% (10), ROS (*Rubus*) 0.7% (1), ROS (other) 2.8% (2), API 13.2% (7), CRA 11.4% (7), LAM (Nepetoideae) 9.2% (8), LAM (Lamioideae) 0.2% (1), ORO/PLA 9.0% (5), PLA (*Linaria*) 1.1% (2), SAX (*Saxifraga*) 5.4% (6), CAR 3.9% (5), RUB 3.2% (7), FAB (*Trifolium*) 1.0% (2), GEN (*Gentiana*) 0.8% (1), AST (Asteroideae) 0.7% (1), ERI 0.4% (1), unknown 1.4% (3)	–	–	–	–	Polylectic (13 plant families)

Bee species	**n**	**N**	**Origin (total number/ number of cantons) of pollen loads**	**% pollen grain volume (number of loads)**	**Preferred host**	**% pollen grain volume of preferred host**	**% pure loads of preferred host**	**% loads with preferred host**	**Pollen host range in Central Europe**
Hylaeus hyalinatus Smith, 1842	30	30	CH (30/10)	ROS (*Potentilla*) 13.8% (8), ROS (*Rubus*) 10.5% (6), API 21.6% (12), CAM (*Jasione*) 8.9% (3), HYP (*Hypericum*) 8.8% (3), LAM (Nepetoideae) 7.1% (5), CIS (*Helianthemum*) 6.4% (2), CRA 4.3% (4), RUB 3.4% (4), FAB (*Melilotus*) 3.3% (3), BRA 2.8% (1), RES (*Reseda*) 2.5% (1), BOR (*Echium*) 1.1% (2), PLA (*Plantago*) 1.1% (1), EUP (*Euphorbia*) 0.9% (1), CAR 0.2% (1), unknown 3.3% (3)	–	–	–	–	Polylectic (15 plant families)
Hylaeus punctatus (Brullé, 1832)	30	30	CH (30/11)	API 74.2% (26), RES (*Reseda*) 7.8% (2), HYP (*Hypericum*) 6.5% (3), ROS (*Rubus*) 5.5% (4), CRA 5.1% (1), LAM (Nepetoideae) 0.3% (1), BRA 0.2% (1), unknown 0.4% (2)	Apiaceae	74.2	56.7	86.7	Polylectic with strong preference for Apiaceae

in glycerol gelatine. When a crop contained more than one pollen type, the percentages of the different pollen types were estimated either by counting the grains along two entire transects chosen randomly across the cover slip (12 × 12 mm) at a magnification of 400× or, if the sample contained large numbers of pollen, by counting at least 500 grains on two partial transects. Pollen types represented by less than 5% of the counted grains were excluded to prevent a potential bias due to foreign pollen grains transported to the host flowers by other flower visitors or to pollen grains accidentally swallowed during mere nectar uptake. For crop contents consisting of two or more different pollen types, the proportion of the different types was corrected by their volume. For that purpose, the relative volume of all pollen types within the sample was estimated by eye and the counted numbers of each type multiplied by a factor that corresponded to its volume. After assigning different weights to crops according to their degree of filling (full crops were weighted four times more strongly than crops filled to only one fourth), the estimated percentages were summed up over all crop samples for each species.

The pollen grains were identified down to family or, if possible, to subfamily, tribal or genus level at a magnification of 400× or 1000× with the aid of the literature cited in Westrich and Schmidt (1986), Beug (2004) and a pollen reference collection. Difficult pollen types were identified by the palynologist Katharina Bieri (Biological Institute for Pollen Analysis, Kehrsatz, Switzerland). Pollen of the two closely related genera *Fragaria* and *Potentilla* (Rosaceae) could not be reliably separated by the method applied in the present study, both being subsumed under the “*Potentilla* type” in palynology (Beug 2004). Since Central European species of *Hylaeus* start to fly in early and mid-summer, when the spring flowering *Fragaria* is no longer in bloom, all pollen grains of the *Potentilla* type were assigned to the genus *Potentilla*, which is supported by observations in the field, where no visits to *Fragaria* flowers were recorded for *Hylaeus* bees (A. Müller unpublished data). The pollen grains of *Euphrasia*, *Rhinanthus* (both Orobanchacea) and *Veronica* (Plantaginaceae) are similar and morphologically merge into each other, so that it proved to be impossible to unambiguously separate the pollen of these three taxa; this undeterminable pollen is referred to as ORO/PLA in Table 1 and Figures 2–5. All pollen slides were deposited in the Entomological Collection of ETH Zurich. Information on nectar content and nectar availability of the pollen host flowers of *Hylaeus* was inferred from Kugler (1970) and Proctor and Yeo (1973).

Categories of pollen host range

To characterise the degree of host plant association, such as “narrow oligolecty”, “broad oligolecty”, “polylecty with strong preference” or “polylecty”, definitions proposed by Müller and Kuhlmann (2008) were followed. Two contrasting approaches were applied to infer oligolecty for a given species. The first approach averaged pollen host use across all individuals: a species was classified as oligolectic if 95% or more of the pollen grain volume belonged to the same plant family or genus. The second approach relied on the incidence of pure and mixed pollen loads: a species was classified as oligolectic if 90% or more of the females collected pure loads of one plant family or genus. In the present study, the two approaches differed only for one species, i.e. *Hylaeus taeniolatus*, which was classified as polylectic with strong preference for Apiaceae by the first approach and broadly oligolectic on Apiaceae by the second approach. As all crops except for one contained pollen of Apiaceae and most related species of the subgenus *Paraprosopis* proved to be Apiaceae specialists, *H. taeniolatus* was categorised as broadly oligolectic on Apiaceae.

Comparison between pollen host spectrum and flower visiting records

To clarify possible differences between pollen and nectar host use in the Central European *Hylaeus* species, the pollen host spectrum as assessed in the present study was compared with the flower records of females contained in the database of the Wildbienen-Kataster Baden-Württemberg. At the time of data retrieval in September 2021, the database comprised 3175 female flower records from 29 Central European *Hylaeus* species without differentiation between pollen and/or nectar uptake. These flower visiting observations were distributed all over Baden-Württemberg, recorded from 1916 to 2021 and provided mainly by H.R. Schwenninger, A. Schanowski, R. Prosi, M. Klemm, S. Krausch, M. Haider, H. Burger, R. Burger and V. von Königslöw. The pollen host spectra of the seven species not represented by flower visiting records in the Wildbienen-Kataster database, i.e. *Hylaeus alpinus*, *H. annulatus*, *H. crassanus*, *H. glacialis*, *H. nivalis*, *H. pilosulus* and *H. tyrolensis*, were removed and the comparison was limited to those 29 species, for which both pollen and flower visiting data were available.

Results

Pollen host spectrum at bee species level

Among the 36 Central European *Hylaeus* species, 19 (53%) exhibited an exclusive or strong preference for pollen from a single plant taxon (Table 1, Figs 1–3). Three species turned out to be narrowly oligolectic, i.e. *Hylaeus pilosulus* and *H. signatus* on *Reseda* (Resedaceae) and *H. punctulatissimus* on *Allium* (Amaryllidaceae). Seven species were found to be broadly oligolectic, i.e. *H. clypearis*, *H. duckei*, *H. sinuatus*, *H. styriacus*, *H. taeniolatus* and *H. tyrolensis* on Apiaceae and *H. nigritus* on Asteroideae and Carduoideae (Asteraceae). Nine species were classified as polylectic with strong preference, i.e. *H. cornutus*, *H. gredleri*, *H. kahri*, *H. punctatus* and *H. variegatus* with preference for Apiaceae, *H. paulus*, *H. pfankuchi* and *H. rinki* with preference for *Potentilla* and *Rubus* (Rosaceae) and *H. leptocephalus* with preference for *Melilotus* (Fabaceae). The remaining 17 species proved to be polylectic harvesting pollen on up to 16 plant families (Table 1, Fig. 4), i.e. *H. angustatus*, *H. brevicornis*, *H. communis*, *H. confusus*, *H. crassanus*, *H. difformis*, *H. dilatatus*, *H. gibbus*, *H. hyalinatus*, *H. incongruus*, *H. moricei*, *H. pectoralis*, *H. pictipes* as well as *H. alpinus*, *H. annulatus*, *H. glacialis* and *H. nivalis*, which are restricted in their distribution to the Alps.

Pollen host spectrum at bee genus level

The 36 Central European *Hylaeus* species collected pollen from the flowers of 31 plant families (Table 1, Fig. 5). However, only a few families were represented in high percentages in the pollen host spectrum of the genus as a whole. When summing the percentages of the plant families found in the host plant spectrum of each species across all species, the Apiaceae contributed 39.6% to the pollen host spectrum, followed by the Rosaceae with 18.7%, the Resedaceae with 7.0%, the Fabaceae with 6.1%, the Asteraceae with 3.7%, the Amaryllidaceae with 3.5% and the Campanulaceae with 3.4% (Figs 1, 5). These seven plant families accounted for more than 80% of the plants that the Central European *Hylaeus* species exploited for pollen, whereas the other 24 families were all represented by less than 3.0% in the genus' pollen host spectrum.

Pollen of Apiaceae was collected by all Central European *Hylaeus* species except for *Hylaeus difformis* and three oligolectic species specialised on Asteraceae or Resedaceae (Table 1, Figs 2–4). Based on field observations and the strongly differing morphology and size of the Apiaceae pollen grains recorded in the crop contents, all species including the oligolectic ones exploited several different genera among the Apiaceae. In contrast, almost 95% of all pollen of Rosaceae originated from the two genera *Potentilla* and *Rubus* (Fig. 5), pollen of Resedaceae and Amaryllidaceae exclusively came from the genera *Reseda* and *Allium*, respectively, over 99% of all pollen of Fabaceae was from the genus *Melilotus*, among the Asteraceae solely the two subfamilies Asteroideae and Carduoideae served as hosts and among the Campanulaceae only the two genera *Campanula* and *Jasione* were exploited.

About 89% of the pollen collected by the 36 *Hylaeus* species originated from herbs. Pollen of shrubs, such as *Clematis*, *Frangula*, *Hedera*, *Rosa*, *Rubus*, *Sambucus* and *Vitis*, was represented by slightly more than 10% with *Rubus* alone accounting for 9.6%. Pollen of trees, such as *Castanea* and *Tilia*, contributed only 0.2% to the host plant spectrum of the genus, while 0.4% of the pollen could not be attributed to one of the three vegetation layers.

About 93% of the pollen collected by the 36 *Hylaeus* species originated from flowers with easily accessible nectar, which is either exposed or secreted at the base of flowers that can be reached by the short-tongued *Hylaeus* bees thanks to their small body size. The remaining pollen came from flowers that either do not produce nectar or whose nectaries are not accessible due to their position at the base of narrow flower tubes. Pollen of nectarless flowers, such as *Agrimonia*, *Aruncus*, *Filipendula*, *Hypericum*, *Plantago*, *Sambucus*, *Sanguisorba* and *Rosa*, accounted for 2.3% of the flowers exploited for pollen. Pollen of flowers with inaccessible nectar, such as Carduoideae (Asteraceae) and *Trifolium*, was represented by 2.5% in the host plant spectrum of the genus, while 1.7% of the pollen could not be attributed to one of the three classes of nectar availability.

Comparison between pollen host spectrum and flower visiting records

The high importance of Apiaceae as host plants for the Central European *Hylaeus* species was also evident from the flower visiting records of 29 species from Baden-Württemberg. Out of 3175 flower visiting females observed, 1258 (39.6%) were recorded on Apiaceae, which is similar to the percentage of Apiaceae pollen in the crop contents of the same 29 species amounting to 42.4%. In striking contrast, with 838 (26.4%) flower visiting records the Asteraceae were the second most important plant family after the Apiaceae, whereas the percentage of Asteraceae pollen in the crop contents was only 4.3% across all 29 species. By excluding the Asteraceae specialist *Hylaeus nigritus*, this discrepancy

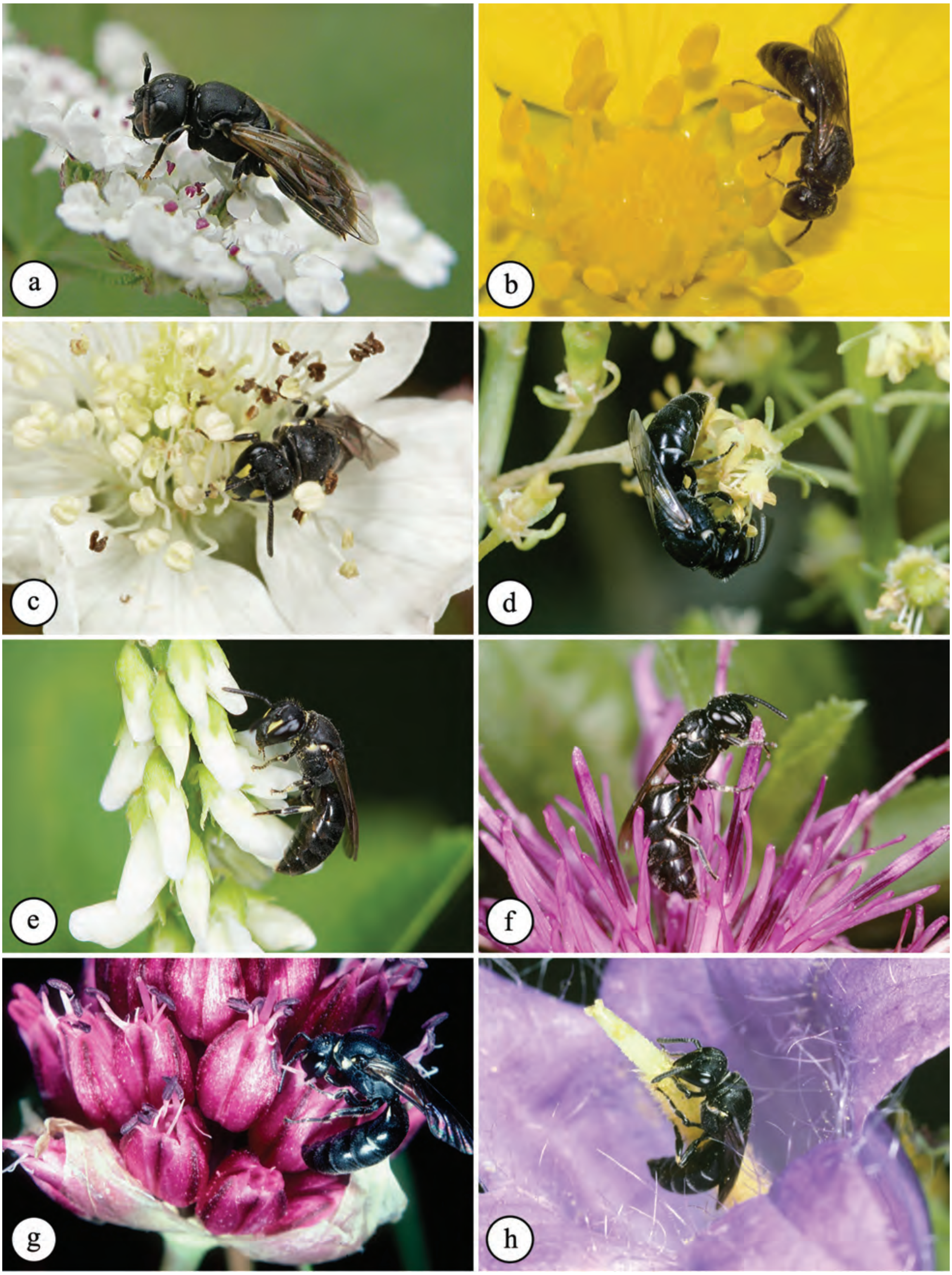
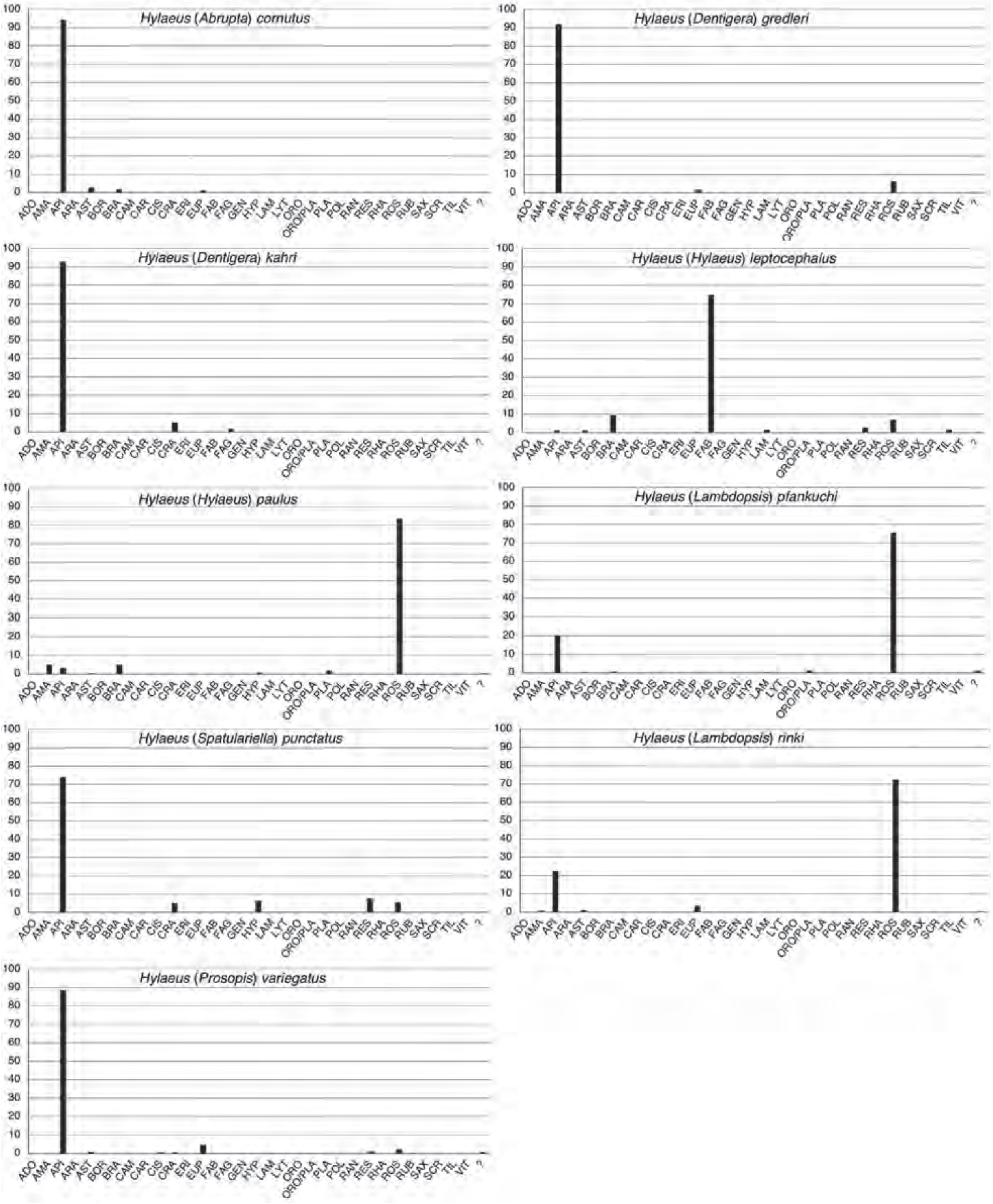


Figure 1. Important pollen hosts of Central European *Hylaeus* species. (**a**) *Daucus carota* (Apiaceae) and *Hylaeus cornutus* (photo S. Falk). (**b**) *Potentilla recta* (Rosaceae) and *Hylaeus brevicornis* (photo A. Haselböck). (**c**) *Rubus* spec. (Rosaceae) and *Hylaeus* spec. (photo B. Jacobi). (**d**) *Reseda lutea* (Resedaceae) and *Hylaeus signatus* (photo A. Krebs). (**e**) *Melilotus albus* (Fabaceae) and *Hylaeus* spec. (photo N. Vereecken). (**f**) *Centaurea scabiosae* (Asteraceae, Carduoideae) and *Hylaeus nigritus* (photo A. Krebs). (**g**) *Allium sphaerocephalon* (Amaryllidaceae) and *Hylaeus punctulatissimus* (photo A. Müller). (**h**) *Campanula trachelium* and *Hylaeus* spec. (photo A. Krebs).

Figure 2. Pollen host spectra of the ten Central European *Hylaeus* species classified as oligolectic. x-axis: Plant families: ADO = Adoxaceae, AMA = Amaryllidaceae, API = Apiaceae, ARA = Araliaceae, AST = Asteraceae, BOR = Boraginaceae, BRA = Brassicaceae, CAM = Campanulaceae), CAR = Caryophyllaceae, CIS = Cistaceae, CRA = Crassulaceae, ERI = Ericaceae, EUP = Euphorbiaceae, FAB = Fabaceae, FAG = Fagaceae, GEN = Gentianaceae, HYP = Hypericaceae, LAM = Lamiaceae, LYT = Lythraceae, ORO = Orobanchaceae, ORO/PLA = *Euphrasia*, *Rhinanthus* or *Veronica*, PLA = Plantaginaceae, POL = Polygonaceae, RAN = Ranunculaceae, RES = Resedaceae, RHA = Rhamnaceae, ROS = Rosaceae, RUB = Rubiaceae, SAX = Saxifragaceae, SCR = Scrophulariaceae, TIL = Tiliaceae, VIT = Vitaceae, ? = unknown pollen types. y-axis: Percentage of pollen volume contained in the female crops.


Hylaeus (*Abrupta*) *cornutus*

Hylaeus (*Dentigera*) *gredleri*

Hylaeus (*Dentigera*) *kahri*

Hylaeus (*Hylaeus*) *leptocephalus*

Hylaeus (*Hylaeus*) *paulus*

Hylaeus (*Lambdopsis*) *pfankuchi*

Hylaeus (*Spatulariella*) *punctatus*

Hylaeus (*Lambdopsis*) *rinki*

Hylaeus (*Prosopis*) *variegatus*

Figure 3. Pollen host spectra of the nine Central European *Hylaeus* species classified as polylectic with strong preference. Abbreviations as in Figure 2.

was even more pronounced with the percentage of female flower visits to the Asteraceae being 20.5% and the percentage of Asteraceae pollen in the crops being 1.1%. Although Asteraceae pollen was found in the crops of 22 out of the 26 polylectic *Hylaeus* species, its proportion was usually very small and ranged from 0.1–4.3% (mean 1.2%); the only exception was *H. dilatatus*, whose host plant spectrum included 13.7% Asteraceae pollen.

Discussion

The results of the present study show that the proportion of Central European *Hylaeus* species exhibiting an exclusive or strong preference for pollen from a single plant taxon is much higher than hitherto assumed and that the current assumption of the genus *Hylaeus* to largely consist of pollen generalists is wrong. Nineteen of the 36

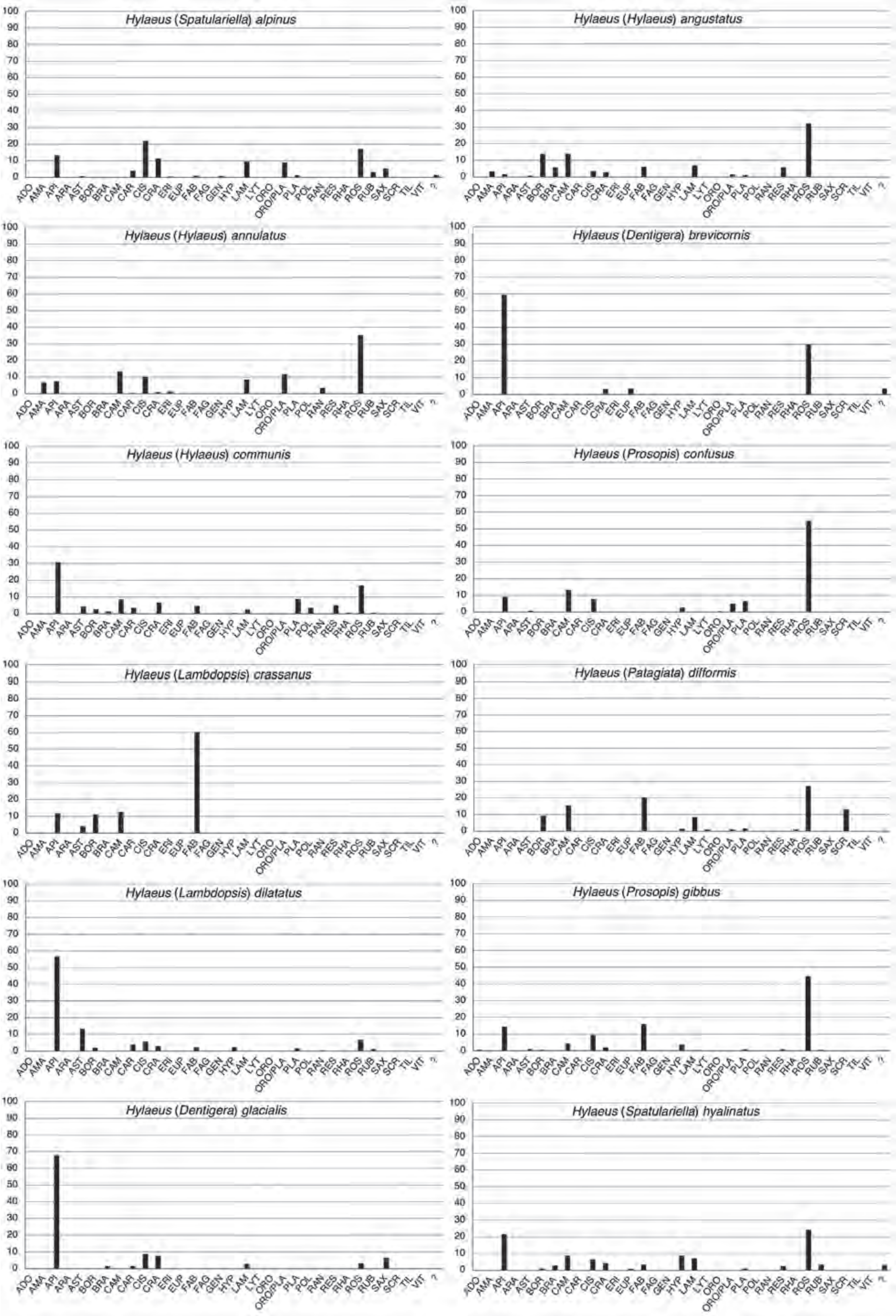


Figure 4. Pollen host spectra of the 17 Central European *Hylaeus* species classified as polylectic. Abbreviations as in Figure 2.

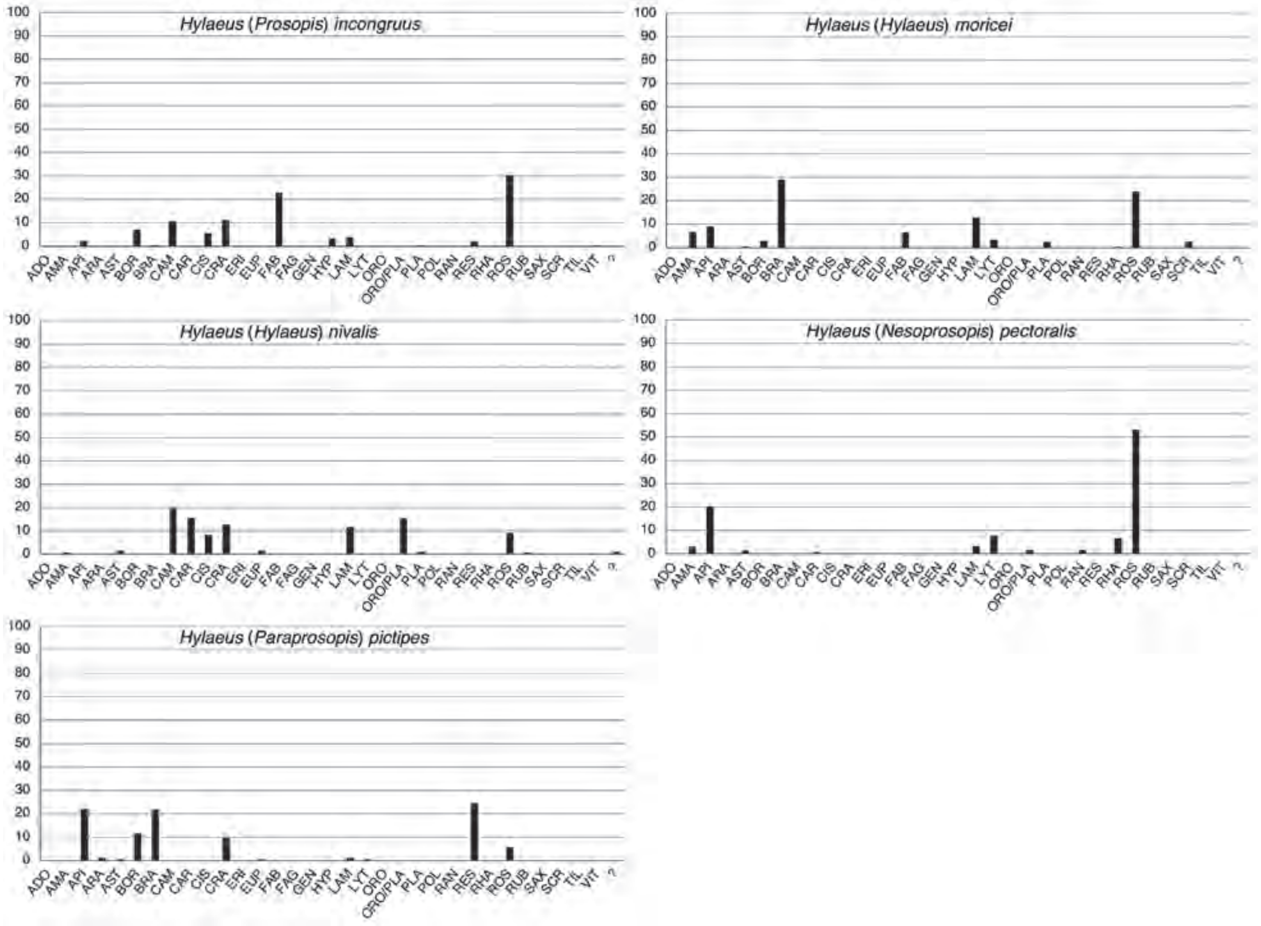


Figure 4. Continued.

Central European species examined are strictly or largely dependent on a single plant taxon for collecting pollen. For eleven of these species, flowers of the Apiaceae are the exclusive or strongly preferred hosts. The high significance of this plant family is also substantiated by the finding that the Apiaceae serve as pollen hosts for all Central European *Hylaeus* species with the exception of one polylectic species and three oligolectic species specialised on plant taxa other than the Apiaceae.

Phylogenetic inference is a powerful tool to reconstruct the evolution of pollen host preferences in bees (Müller 1996; Larkin et al. 2008; Sedivy et al. 2008, 2013; Haider et al. 2014). To date, no phylogeny of the genus *Hylaeus* including its Central European representatives is available, rendering any hypotheses on the evolution of pollen host use in this group of bees premature. Nevertheless, the results of the present study allow for some preliminary insights. First, species that show an exclusive or strong preference for Apiaceae occur in six out of the ten Central European subgenera; this finding suggests that the preference for Apiaceae might be an ancestral trait in the Palaearctic *Hylaeus* fauna or, alternatively, has independently evolved several times in the evolutionary history of the genus. Second, most species of the subgenus *Paraprosopis* are Apiaceae oligoleges, which suggests that the ancestor of the subgenus was specialised on Apiaceae. Third, the two morphologically similar and probably very closely related species *Hylaeus pfankuchi* and *H. rinki* (both belong to the subgenus *Lamdopsis*) have an almost identical pollen host spectrum with roughly 95% of the collected pollen originating from *Potentilla*, *Rosa* (both Rosaceae) and Apiaceae. Considering that these two *Hylaeus* species distinctly differ in their habitat choice with the former mainly occurring in wetlands with reed beds and the latter in forest clearings and along forest edges (Westrich 2018), the largely concordant pollen host choice likely has a genetic basis. The same might apply to two closely related species of the subgenus *Dentigera*, i.e. *H. gredleri* and *H. kahri*, which exhibit a strong preference for Apiaceae, as well as to the three species of the *Hylaeus gibbus* group, i.e. *H. confusus*, *H. gibbus*, *H. incongruus*, whose pollen host spectra are all dominated by Rosaceae and additionally include Apiaceae, Campanulaceae, Cistaceae, Hypericaceae and partly Fabaceae.

Flowers of 31 plant families serve as pollen hosts for the Central European *Hylaeus* species. With 33 families, the number of plant taxa exploited for pollen is similar in the western Palaearctic species of the related genus *Colletes* (Colletidae), and nearly 70% of the plant families used by the *Hylaeus* bees as pollen sources are also exploited by the *Colletes* bees (Müller and Kuhlmann 2008). Furthermore, there is no plant family in the pollen

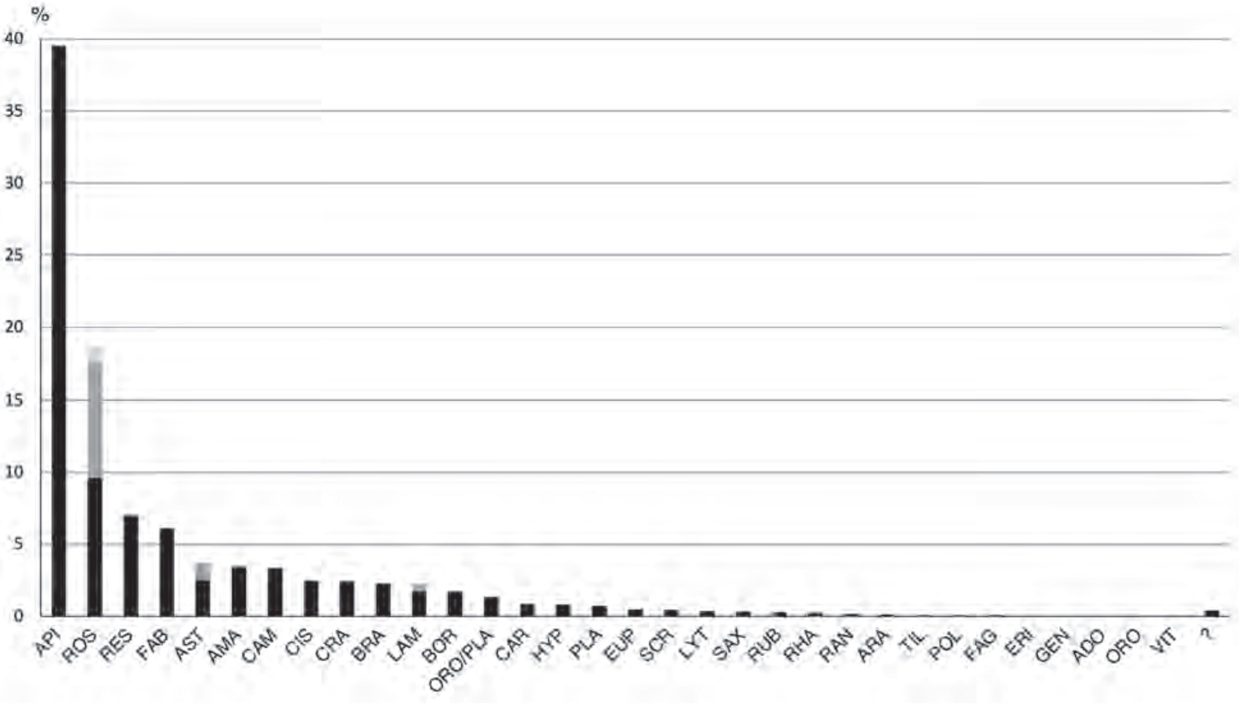


Figure 5. Pollen host spectrum of the genus *Hylaeus* in Central Europe (n = 36 species). Abbreviations as in Figure 2. ROS: black = *Rubus*, dark grey = *Potentilla*, light gray = other; AST: black = Carduoideae, dark grey = Asteroideae; LAM: black = Nepetoideae, dark grey = Lamioideae.

host spectrum of the genus *Hylaeus*, whose pollen is not collected by other short-tongued Central European bees, such as species of *Andrena* or *Lasioglossum* (Westrich 2018). Thus, the peculiar habit of *Hylaeus* bees to ingest the pollen directly on the flowers and to transport it back to the nest inside the crop does not translate into a pollen host spectrum different from other bee taxa.

The finding that 89% of the pollen collected by the Central European *Hylaeus* species originated from herbs and a further 9.6% from *Rubus*, which usually grows as a prostrate shrub, suggests that *Hylaeus* females restrict pollen harvesting mainly to the herbal layer. However, this finding might be biased since the females dissected for the present study were all netted by hand, which possibly resulted in an underrepresentation of specimens harvesting pollen in the shrub or tree layer. In fact, part of the pollen diet of *Hylaeus communis* in five European cities originated from trees (Casanelles-Abella et al. 2022).

About 93% of the plant taxa used by the Central European *Hylaeus* species as pollen hosts can also be exploited for nectar due to the easy access to the nectaries. In contrast, approximately 5% of the pollen hosts lack nectar or secrete nectar that is inaccessible to the *Hylaeus* bees. To compensate for this lack or inaccessibility of nectar, the females must visit other flowers to gain enough nectar for provisioning their brood cells, as is probably exemplified by the Asteraceae specialist *Hylaeus nigritus* and the pollen generalist *H. dilatatus*, for which flowers of Carduoideae (Asteraceae) are important pollen hosts. Although neither species is able to reach the nectaries at the base of the long-tubed Carduoideae flowers with their short proboscis, pollen of Carduoideae contributed 77.4% and 11.3% to the host plant spectra of *H. nigritus* and *H. dilatatus*, respectively. Interestingly, 25 out of 30 crop contents of *H. nigritus* contained a mixture of pollen from Carduoideae and Asteroideae, whereas only two contained solely Carduoideae pollen. Similarly, pollen of Carduoideae was recorded in 7 out of 30 crops in *H. dilatatus* but never constituted the only pollen type. This finding is likely explained by the necessity to combine mere pollen visits to the Carduoideae with visits to the Asteroideae or other plant taxa to obtain nectar.

The comparison between pollen host spectrum and flower visiting records revealed a striking discrepancy in the use of Asteraceae as host plants by the Central European *Hylaeus* species. After exclusion of the Asteraceae specialist *Hylaeus nigritus*, the percentage of Asteraceae pollen in the crop contents averaged only 1.1%, whereas more than 20% of all flower visiting females were observed on this plant family. The most likely explanation for this discrepancy is that the flowers of Asteraceae serve as nectar sources, but not or only marginally as pollen sources. This pattern of use of Asteraceae pollen by the *Hylaeus* bees supports recent findings that the pollen of this plant family possesses unfavourable or protective properties, which render its digestion difficult and necessitate physiological adaptations to successfully utilize it, resulting in a reduced ability to use alternative hosts (Müller and Kuhlmann 2008; Praz et al. 2008; Wood and Roberts 2018; Vanderplanck et al. 2020). This scenario –

known as the Asteraceae paradox – neatly applies to the polylectic *Hylaeus* species, which hardly exploit Asteraceae for pollen, and to *Hylaeus nigritus*, which is specialised on Asteraceae. However, it does not apply to *H. dilatatus*, which is the only polylectic *Hylaeus* species in Central Europe that collects pollen to a considerable degree on Asteraceae. This species might have inherited the ability to successfully utilise Asteraceae pollen from an ancestor specialised on this plant family, as is possibly the case in the *Colletes succinctus* group, which comprises both Asteraceae oligoleges and polyleges that partly exploit Asteraceae for pollen (Müller and Kuhlmann 2008).

Bee diversity and abundance have considerably declined in large parts of Europe during the last decades (Nieto et al. 2014; Powney et al. 2019). Species of the genus *Hylaeus* are no exception: thirteen of the 40 *Hylaeus* species recorded for Switzerland and six of the 31 species occurring in Baden-Württemberg are red-listed (Westrich et al. 2000; Müller and Praz in prep.). The results of the present study enable the targeted improvement of the food supply for these species at risk. Moreover, given the high importance of Apiaceae, Rosaceae, Resedaceae and Fabaceae as pollen hosts, the promotion of summer flowering Apiaceae (particularly *Daucus*), of *Potentilla* and *Rubus* (both Rosaceae), of *Reseda* (Resedaceae) and of *Melilotus* (Fabaceae), for example by including them into wildflower seed mixtures for pollinators, benefits a large part of the Central European *Hylaeus* species.

Conclusions

Although species of the genus *Hylaeus* differ from most other bees by their unusual habit to ingest the pollen directly on the flowers and to transport it internally back to the nest, their patterns of pollen host use are comparable to those of numerous other Palaearctic bee taxa in that i) the genus comprises species that cover the whole spectrum of host plant associations ranging from narrow oligolecty to broad polylecty, ii) a similar set of pollen hosts is used as in many other short-tongued bees, such as *Andrena*, *Colletes* or *Lasioglossum*, and iii) Asteraceae are hardly exploited for pollen by the polylectic species.

Acknowledgments

The present study would not have been possible without the many bee specialists and curators of entomological collections who generously provided *Hylaeus* specimens for dissection: G. Artmann, M. Aubert, H. Baur (Naturhistorisches Museum Bern), D. Bénon, M. Bur, R. Burger, A. Freitag (Muséum Cantonal des Sciences Naturelles Lausanne), S. Gerber (Musée de la Nature Sion), M. Greef (ETH Zurich), S. Gurten, M. Haider, P. Heller, M. Herrmann, S. Klopfstein (Naturhistorisches Museum Basel), T. Kopf, J. Litman (Muséum d'Histoire Naturelle de Neuchâtel), R. Neumeyer, C. Praz, R. Prosi, A. Rey, A. Schanowski, F. Schmid, H.R. Schwenninger, C. Sedivy, B. Steinemann, F. von Mentlen, R. Wenger and T. Wood. K. Bieri (Biologisches Institut für Pollenanalyse Kehrsatz) helped with the identification of difficult pollen types. The Wildbienenkataster Baden-Württemberg (H.R. Schwenninger, A. Schanowski, R. Prosi) generously provided an excerpt of flower visiting data of 29 *Hylaeus* species from Baden-Württemberg. V. Mauss provided information on the anatomy and morphology of the crop in aculeate Hymenoptera. The Fachstelle für Naturschutz Zürich permitted the collection of a small number of *Hylaeus* specimens within a protected area. S. Falk, A. Haselböck, B. Jacobi, A. Krebs and N. Vereecken provided photos of flower visiting *Hylaeus* females. A private foundation financed the present study as part of the project "Mehr als Bienen" led by the Tierpark Goldau. D. Buresch and A. Mäder (Tierpark Goldau) accompanied the study with advice and support since its beginning in 2020. Numerous helpful suggestions and comments were made by E. Almeida, H. Dathe and J. Litman, who reviewed the manuscript.

References

Almeida EAB (2008) Colletidae nesting biology (Hymenoptera: Apoidea). Apidologie 39: 16–29. https://doi.org/10.1051/apido:2007049

Amiet F, Müller A, Neumeyer R (2014) Apidae 2: *Colletes*, *Dufourea*, *Hylaeus*, *Nomia*, *Nomioides*, *Rhophitoides*, *Rophites*, *Sphecodes*, *Systropha*. Fauna Helvetica 4, 219 pp. [Centre Suisse de Cartographie de la Faune and Schweizerische Entomologische Gesellschaft]

Batra SWT (1980) Ecology, behavior, pheromones, parasites and management of the sympatric vernal bees *Colletes inaequalis*, *C. thoracicus* and *C. validus*. Journal of the Kansas Entomological Society 53: 509–538.

Beug HJ (2004) Leitfaden der Pollenbestimmung für Mitteleuropa and angrenzende Gebiete. Pfeil Verlag, München, 542 pp.

Ascher JS, Pickering J (2020) Discover life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species [accessed 10.2.2023]

Casanelles-Abella J, Müller S, Keller A, Aleixo C, Orti MA, Chiron F, Deguines N, Hallikma T, Laanisto L, Pinho P, Samson R, Tryjanowski P, Van Mensel A, Pellissier L, Moretti M (2022) How wild bees find a way in European cities: pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. Journal of Applied Ecology 59: 457–470. https://doi.org/10.1111/1365-2664.14063

Chambers VH (1968) Pollens collected by species of *Andrena* (Hymenoptera: Apidae). Proceedings of the Royal Entomological Society London (A)43: 155–160. https://doi.org/10.1111/j.1365-3032.1968.tb01018.x

Dathe HH, Scheuchl E, Ockermüller E (2016) Illustrierte Bestimmungstabellen für die Arten der Gattung *Hylaeus* F. (Maskenbienen) in Deutschland, Österreich und der Schweiz. Entomologica Austriaca, Supplement 1: 1–51.

Doczkal D, Schmid-Egger C (1992) Ergänzungen zur Wildbienenfauna Baden-Württembergs (Hymenoptera: Apoidea). Carolinea 50: 173–176.

Haider M, Dorn S, Sedivy C, Müller A (2014) Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees

(Megachilidae, Osmiini). Biological Journal of the Linnean Society 111: 78–91. https://doi.org/10.1111/bij.12186

Kugler H (1970) Blütenökologie. Gustav Fischer, Stuttgart, 345 pp.

Larkin LL, Neff JL, Simpson BB (2008) The evolution of a pollen diet: host choice and diet breadth of *Andrena* bees (Hymenoptera: Andrenidae). Apidologie 39: 133–145. https://doi.org/10.1051/apido:2007064

Michener CD (2007) The bees of the world, 2nd edn. Johns Hopkins University Press, Baltimore and London, 953 pp.

Michez D, Patiny S, Rasmont P, Timmermann K, Vereecken N (2008) Phylogeny and host-plant evolution in Melittidae s.l. (Hymenoptera, Apoidea). Apidologie 39: 146–162. https://doi.org/10.1051/apido:2007048

Müller A (1996) Host-plant specialization in western palearctic anthidiine bees (Hymenoptera: Apoidea: Megachilidae). Ecological Monographs 66: 235–257. https://doi.org/10.2307/2963476

Müller A (2018) Pollen host selection by predominantly alpine bee species of the genera *Andrena*, *Panurginus*, *Dufourea*, *Megachile*, *Hoplitis* and *Osmia* (Hymenoptera, Apoidea). Alpine Entomology 2: 101–113. https://doi.org/10.3897/alpento.2.29250

Müller A, Kuhlmann M (2008) Pollen hosts of western palaearctic bees of the genus *Colletes* (Colletidae) – the Asteraceae paradox. Biological Journal of the Linnean Society 95: 719–733. https://doi.org/10.1111/j.1095-8312.2008.01113.x

Müller A, Praz C (in preparation) Rote Liste der Bienen. Gefährdete Arten der Schweiz.

Nieto A, Roberts SPM, Kemp J, Rasmont P, Kuhlmann M, García Criado M, Biesmeijer JC, Bogusch P, Dathe HH, De la Rúa P, De Meulemeester T, Dehon M, Dewulf A, Ortiz-Sánchez FJ, Lhomme P, Pauly A, Potts SG, Praz C, Quaranta M, Radchenko VG, Scheuchl E, Smit J, Straka J, Terzo M, Tomozii B, Window J, Michez D (2014) European Red List of bees. Publication Office of the European Union, Luxembourg, 86 pp.

Powney GD, Carvell C, Edwards M, Morris R, Roy H, Woodcock B, Isaac N (2019) Widespread losses of pollinating insects in Britain. Nature communications 10: 1018. https://doi.org/10.1038/s41467-019-08974-9

Praz CJ, Müller A, Dorn S (2008) Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen? Ecology 89: 795–804. https://doi.org/10.1890/07-0751.1

Proctor M, Yeo P (1973) The pollination of flowers. Collins, London, 418 pp.

Raw A (1974) Pollen preferences of three *Osmia* species (Hymenoptera). Oikos 25: 54–60. https://doi.org/10.2307/3543545

Scheuchl E, Willner (2016) Taschenlexikon der Wildbienen Mitteleuropas. Quelle & Meyer, Wiebelsheim, 917 pp.

Scott V (1996) Pollen selection by three species of *Hylaeus* in Michigan (Hymenoptera: Colletidae). Journal of the Kansas Entomological Society 69: 195–200.

Sedivy C, Praz CJ, Müller A, Widmer A, Dorn S (2008) Patterns of host-plant choice in bees of the genus *Chelostoma*: the constraint hypothesis of host-range evolution in bees. Evolution 62: 2487–2507. https://doi.org/10.1111/j.1558-5646.2008.00465.x

Sedivy C, Dorn S, Widmer A, Müller A (2013) Host range evolution in a selected group of solitary bees: the Boraginaceae-Fabaceae paradox. Biological Journal of the Linnean Society 108: 35–54. https://doi.org/10.1111/j.1095-8312.2012.02013.x

Straka J, Bogusch P (2011) Contribution to the taxonomy of the *Hylaeus gibbus* species group in Europe (Hymenoptera, Apoidea and Colletidae). Zootaxa 2932: 51–67. https://doi.org/10.11646/zootaxa.2932.1.6

Vanderplanck M, Gilles H, Nonclercq D, Duez P, Gerbaux P (2020) Asteraceae paradox: chemical and mechanical protection of *Taraxacum* pollen. Insects 11, 304: 1–16. https://doi.org/10.3390/insects11050304

Westrich P (1989) Die Wildbienen Baden-Württembergs. Ulmer, Stuttgart, 972 pp.

Westrich P (2018) Die Wildbienen Deutschlands. Ulmer, Stuttgart, 824 pp.

Westrich P, Schmidt K (1986) Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera, Apoidea). Linzer biologische Beiträge 18: 341–360. https://doi.org/10.1051/apido:19870209

Westrich P, Schmidt K (1987) Pollenanalyse, ein Hilfsmittel beim Studium des Sammelverhaltens von Wildbienen (Hymenoptera, Apoidea). Apidologie 18: 199–214. https://doi.org/10.1051/apido:19870209

Westrich P, Schwenninger HR, Herrmann M, Klatt M, Klemm M, Prosi R, Schanowski A (2000): Rote Liste der Bienen Baden-Württembergs. Naturschutz-Praxis, Artenschutz 4, 56 pp.

Wiesbauer H (2020) Wilde Bienen, Biologie, Lebensraumdynamik und Gefährdung. Ulmer, Stuttgart, 480 pp.

Wood TJ, Holland JM, Goulson D (2016) Diet characterisation of solitary bees on farmland: dietary specialisation predicts rarity. Biodiversity and Conservation 25: 2655–2671. https://doi.org/10.1007/s10531-016-1191-x

Wood TJ, Roberts SPM (2017) An assessment of historical and contemporary diet breadth in polylectic *Andrena* bee species. Biological Conservation 215: 72–80. https://doi.org/10.1016/j.biocon.2017.09.009

Wood TJ, Roberts SPM (2018) Constrained patterns of pollen use in Nearctic Andrena (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts. Biological Journal of the Linnean Society 124: 732–746. https://doi.org/10.1093/biolinnean/bly080

Alpine Entomology 7 2023, 37–44 | DOI 10.3897/alpento.7.103981

Alpine
Entomology

The female of *Megacraspedus peslieri* Huemer & Karsholt, 2018 (Lepidoptera, Gelechiidae), a new case of brachyptery in alpine Lepidoptera

Peter Huemer[1]

1 *Naturwissenschaftliche Sammlung, Sammlungs- und Forschungszentrum, Tiroler Landesmuseen Betriebsges.m.b.H., A-6060 Hall in Tirol, Innsbruck, Austria*

https://zoobank.org/7D7AF4B4-6C57-4B67-8D7C-3162B34DE2A5

Corresponding author: Peter Huemer (p.huemer@tiroler-landesmuseen.at)

Academic editor: Bernard Landry ♦ **Received** 23 March 2023 ♦ **Accepted** 17 April 2023 ♦ **Published** 25 April 2023

Abstract

Megacraspedus peslieri was described from the Pyrenees in 2018 and subsequently also discovered at a few localities in the northern Cottian Alps (Italy). The hitherto unknown female was collected in these localities after a targeted search. As with some other representatives of the genus, the female is flightless and shows a strikingly strong reduction of the wings (brachyptery). Whereas the forewings are significantly shortened and narrowed, the hindwings are strongly reduced. Both the external morphology and the genitalia of the female are described and illustrated in detail, together with previously unpublished photographs of live adults of both sexes. The identification of specimens from the Alps as well as of the male and female were determined by means of a DNA barcode comparison with the holotype.

Key Words

Alps, brachyptery, DNA barcoding, female, *Megacraspedus peslieri*, wing reduction

Introduction

Wing reduction (brachyptery) or the complete loss of wings (aptery) are rare phenomena in Lepidoptera (Sattler 1991) and only reported for 35 families (Heppner 1991), with few recent additions i.e. for Notodontidae (Sattler and Wojtusiak 1999), Nymphalidae (Viloria et al. 2003) or Ethmiidae (Shovkoon 2008). Aptery is rarely a largely consistent group-specific trait, e.g. in the Psychidae and Heterogynidae (de Freina 2011; Arnscheid and Weidlich 2017). However, in most taxonomic groups with brachyptery there are different gradations of wing reduction, mainly of the hindwings and in the female, and the associated inability to fly (Huemer and Sattler 1989; Sattler 1991). Such tendencies are known in particular from climatically unfavourable areas such as subantarctic islands and mountain regions, but also from arid habitats, and in late autumn or winter-active species (Heppner 1991; Sattler 1991).

The gelechiid genus *Megacraspedus* is an example of widespread wing reduction, with the females of the majority of the 89 described species probably being brachypterous (Huemer and Karsholt 2018). Only in few closely related taxa such as the *M. fallax* species group do females seem to be normally winged (Huemer and Karsholt 2018; Huemer and Tokár 2021). Though more than half of the species are known exclusively from males, more or less pronounced reduction of wings, particularly hindwings, is widespread in species with described females, i.e. about 20 species. Here a hitherto unknown case of brachyptery is reported for *M. peslieri,* a species placed in a species group of its own.

Descriptive terminology follows Huemer and Karsholt (2018).

Material and methods

Sixteen males and two female specimens of *Megacraspedus peslieri* from France (holotype) and Italy have been examined. The material is preserved in the research collection of the Tiroler Landesmuseum Ferdinandeum (Hall, Austria) and kärnten.museum (Klagenfurt, Austria). The specimens were pinned and either spread or set. Initial species identification of males was based firstly on phenotypic characteristics (wing markings, colour, size), using the holotype of *M. peslieri* in the Tiroler Landesmuseum Ferdinandeum as a reference. This was confirmed by dissections and by DNA barcoding. Females were assigned to the species due to simultaneous occurrence with males and by the DNA barcode.

Tissue samples from a single hind leg of eight specimens were prepared according to prescribed standards to obtain the DNA barcode sequences of a 658 base-pair long segment of the mitochondrial COI gene (cytochrome c oxidase subunit 1). The tissue samples were 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). The only available barcode sequence of the nearest neighbor *Megacraspedus ibericus* Huemer & Karsholt, 2018 in BOLD was added to the analysis, whereas several already published sequences of *Megacraspedus* were not (Huemer and Karsholt 2018).

All sequences were submitted to GenBank and details including complete voucher data and images can be accessed in the public dataset "*Megacraspedus peslieri* [DS-MEGAPESL]" dx.doi.org/10.5883/DS-MEGAPESL 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 neighbor-joining tree was constructed under the Kimura two-parameter model in MEGA7 (Kumar et al. 2007). The photographs of live adults were taken with an Olympus OM-D Mark III camera and an Olympus 60 mm *f*/2.8 ED macro lens. The photographs of spread adults were taken with a Zeiss Stemi 508 KMAT stereo microscope, genitalia photographs with a Zeiss Axiolab 5 microscope, both adapted to an Olympus OM-D Mark III camera. Stacked photographs were edited using Helicon Focus 4.8 and Adobe Photoshop 6.0.

Results

Molecular analysis

Sequencing resulted in full length DNA barcodes of 658 bp for eight specimens of *M. peslieri*. The intraspecific p-distance was low with 0.32% on average and a maximum distance of 0.48%, mainly due to the slight deviation of the sequence of the holotype (Fig. 1), whereas the distance to the nearest neighbor *M. ibericus* was 7.37%. All specimens of *M. peslieri* clustered together and were assigned to the unique BIN:BOLD:ADM8362 (n = 9). Female specimens (specimen identifier TLMF_Lep_33721 and TLMF_Lep_3719) fully corresponded with males of the same cluster, thus strongly supporting the conspecifity of the males and females.

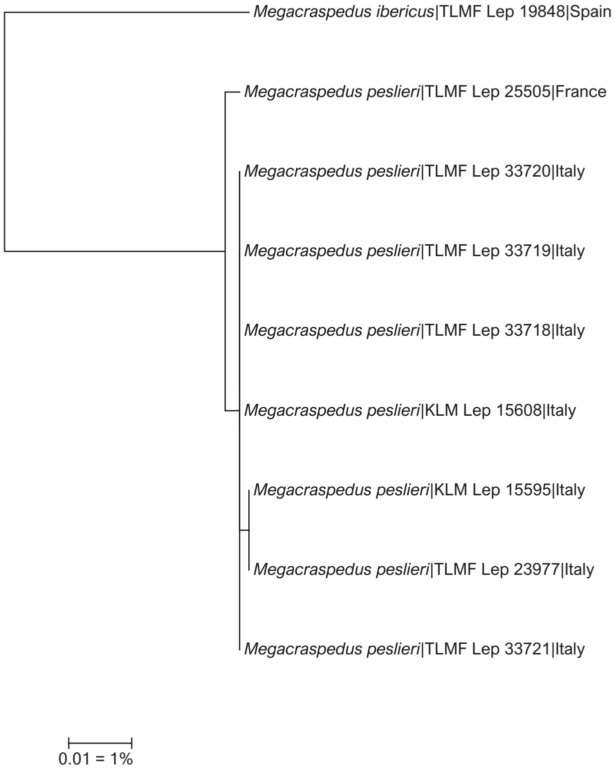


Figure 1. COI neighbor-noining tree of *Megacraspedus peslieri* and the nearest neighbor *M. ibericus*. Note: TLMF Lep 25505 represents the holotype.

Taxonomic part

Megacraspedus peslieri Huemer & Karsholt, 2018

Material examined. 24♂, 2♀: Italy, prov. Torino, PN Orsiera - Rocciavré, Fenestrelle, Forte Serre Marie, 1830 m a.s.l., 45°02'57"N, 07°03'03"E, 21.8.2022, leg. Huemer (DNA Barcodes TLMF Lep 33718-33721; gen. slide P. Huemer GEL 1351♀; 1♂: Italy, prov. Torino, PN Orsiera - Rocciavré, Villaretto, Gran Faetto, Colletto, 1445 m a.s.l., 45°00'28"N, 07°08'28"E, 21.9.2019, leg. Huemer (all coll. Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria).

Description (Figs 2–6). For a detailed description of the male including the male genitalia see Huemer and Karsholt (2018). Males (Figs 2, 4) are more variable in size than originally described, with a forewing length ranging from 7.2–9.0 mm; furthermore, the cream-coloured dorsum is clearly separated from the remaining and predominantly brownish mottled part of the forewing with mainly cream-coloured veins in fresh samples, and the third segment of the labial palpus is entirely cream-white.

Figure 2. *Megacraspedus peslieri*, male in natural resting position (Italy, Alpi Cozie).

Figure 3. *Megacraspedus peslieri*, female in natural resting position (Italy, Alpi Cozie).

Female (Figs 3, 5–6). Segment 2 of labial palpus with long scale brush, dark brown on outer and lower surface, cream-white mottled with brown on inner surface, cream-white on upper surface; segment 3 cream-white. Antennal scape without pecten; flagellum cream-white, annulated with light brown. Head and thorax cream-white with some light brown mottling, particularly on tegula. Forewing length 3.8–4.4 mm. Forewing distinctly reduced, shorter than abdomen, with strongly convex dorsal margin, cream-white ground colour intensely mottled with

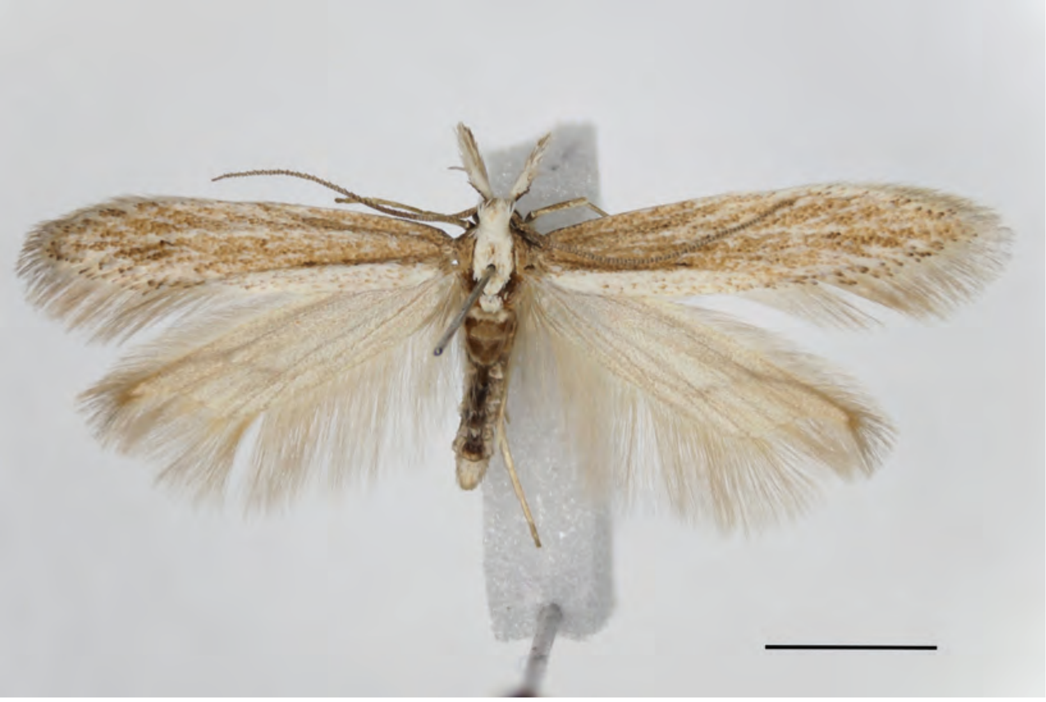


Figure 4. *Megacraspedus peslieri*, set male specimen (scale bar: 3 mm).

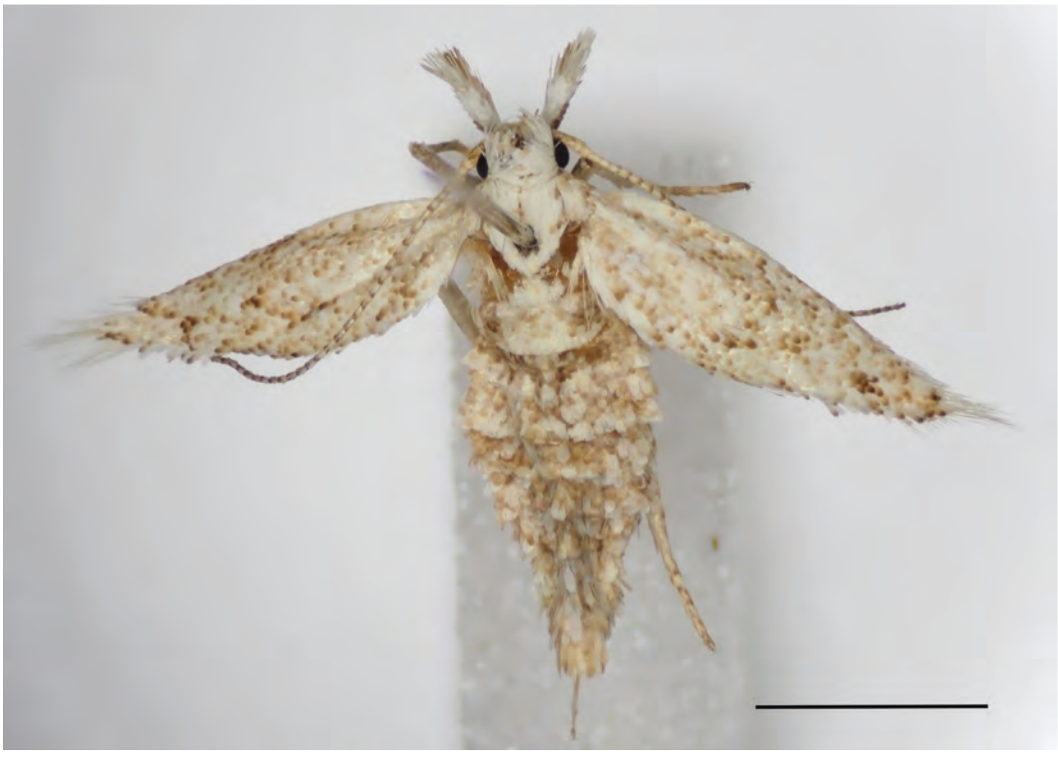


Figure 5. *Megacraspedus peslieri*, set female specimen (scale bar: 2 mm).

light brown; with few darker brown spots in middle and at apex; fringes reduced to group of very long, bristle-like hairs around apex. Hindwing reduced to minute sub-oval flap, with narrow long scales near apex, frenulum with one to two well-developed bristles.

The male and female are easily distinguished by the largely reduced wings of the female with an indistinct wing pattern compared to the male (Figs 2–5).

Female genitalia (Figs 7–8). Papilla analis large, weakly sclerotized, apically evenly rounded, slightly longer than segment VIII, lateral part with anteriorly widened sclerotized area; apophysis posterioris rod-like, short, about 1.65 mm long, apex slightly widened, rounded, anteriorly membranous intersegmental zone; segment VIII about 0.6 mm long, smooth, laterally sclerotized, medially membranous with microsculpture in anterior and posterior

Figure 6. *Megacraspedus peslieri*, details of female hindwing (marked with red arrow) (scale bar: 0.5 mm).

parts; subgenital plate without specialized sclerotizations, anterior edge with short sinusoid projection delimiting ostium bursae; apophysis anterioris rod-like, about as long as segment VIII; colliculum about 1/2 length of apophysis anterioris, wrinkled, with small sclerotization anteriorly; ductus bursae slender, about 1.5 mm long; corpus bursae clearly delimited, about as long as ductus bursae, slender; signum moderately small, laterally oblong spiny plate, with about two dozen small to strong spines.

Remarks. The female genitalia support the unique position of *M. peslieri* and clearly differ from all other species groups particularly by the simple structure of the subgenital plate without specialized sclerotizations in combination with the peculiar signum. Furthermore, the distally rounded papilla analis combined with a short apophysis posterioris is rarely observed in other species.

Biology. The species is on the wing late in the season, from late August to the last third of September and active even at low temperatures of ca 6 °C. Both males and females of *M. peslieri* were observed sitting on grass stems or on other herbaceous plants and detected by illumination with a headlamp in the first two to three hours of the night. Simultaneously, males were attracted to UV light in large numbers.

Distribution. Only known from few localities in the Pyrenees (France, Spain) and the Cottian Alps (Italy) (Huemer and Wieser 2020).

Habitat (Fig. 9). The habitat in the Cottian Alps is predominated by xeromontanous grassland intermixed with rock formations on siliceous soil, at montane elevations from approximately 1400 to 1800 m a.s.l. In the Pyrenees the species was collected at lower altitudes from ca 250 to 900 m a.s.l.

Discussion

Brachyptery is a relatively widespread morphological adaptation in alpine Lepidoptera, which is interpreted as an avoidance strategy against strong winds and the increased risk of wind drift. However, it is limited exclusively to the female sex, while in other regions such as subantarctic island faunas, for example, both sexes can be flightless in extreme cases (Sattler 1991). In a few genera restricted to the alpine and subnival altitudinal zones of the Alps and other European high mountains, brachyptery is a consistent phenomenon, including in particular the genera *Sattleria* (Gelechiidae) (Pitkin and Sattler 1991; Huemer and Hebert 2011; Huemer and Timossi 2014; Timossi and Ruzzier 2020; Timossi and Huemer 2022) and *Sphaleroptera* (Tortricidae) (Whitebread 2006; Timossi and Ruzzier 2023). In other genera such as *Kessleria* (Yponomeutidae) (Huemer and Mutanen 2015; Huemer and Tarmann 1992), *Oxypteryx* (Gelechiidae)

Figure 7. *Megacraspedus peslieri*, female genitalia (scale bar: 0.5 mm).

Figure 8. *Megacraspedus peslieri*, female corpus bursae with signum enlarged. (scale bar: 0.1 mm).

Figure 9. Habitat of *Megacraspedus peslieri* in the Cottian Alps, above Fenestrelle.

(Huemer et al. 2013), *Elophos* (Geometridae) (Müller et al. 2019) and *Agrotis* (Noctuidae) (Ronkay and Huemer 2018) there are different stages of brachyptery, from nearly fully winged to strongly pronounced wing reduction in high altitude taxa. Furthermore, brachyptery can also be restricted to few species within a genus, for example *Elachista brachypterella* (Elachistidae) (Klimesch 1990). In addition, the females of many fully winged species in mountain regions are generally not very active flyers.

The inability to fly, mostly manifested by wing reduction, is also found in some xeromontane groups of Lepidoptera in the Alps. A particularly striking example is the genus *Megacraspedus*. Representatives of this very diverse, palaearctic genus are found in many montane regions, with the Alps being highly important for species diversity. Despite extensive revisionary work by Huemer and Karsholt (2018), new species have been discovered or recognized in this region in the recent past, not least thanks to the increasing implementation of molecular methods (Huemer et al. 2020a, 2020b; Timossi and Huemer 2021). Though female brachyptery is widespread in *Megacraspedus*, the female remains unknown for about half of the species (Huemer and Karsholt 2018), despite some recent advances (Nel and Varenne 2019; Huemer and Tokár 2021). However, the inability to fly does not necessarily reflect an adaptation strategy to certain habitat conditions, but rather seems to be related to morphologically defined species groups (Huemer and Karsholt 2018). For example, in the Pannonic region of eastern Austria *M. podolicus* (Toll, 1942), a member of the *Megacraspedus fallax* species group, which is fully capable of flying can be found cohabiting with the strongly brachypterous species of the *Megacraspedus dolosellus* and *M. binotella* species groups. However, in the absence of any closely related species to the highly isolated *Megacraspedus peslieri* it has not been possible to predict the ability of the females to fly. Since the newly detected female strongly differs from the male by the much smaller size, shorter and relatively broader and pointed forewings, the largely reduced hindwings, and in the forewing colour and pattern, the question of conspecifity of the sexes arose, but it finally could be proved by a DNA barcode analysis.

The currently known and extremely disjunct distribution pattern (Pyrenees, southwestern Alps) of a species with such a pronounced brachyptery raises attention to further yet unresolved questions. Due to the very small and possibly irrelevant differences in the DNA barcodes between these populations, a (formerly) continuous distribution must be assumed, at least in post-glacial periods. Alternatively, however, the species might be much more widespread and simply overlooked in many places. However, this scenario seems unlikely due to the intensive collecting activities in southern France over a long period.

Acknowledgements

Paul D.N. Hebert and the entire team at the Canadian Centre for DNA Barcoding (Guelph, Canada) are acknowledged for continuous support with sequencing work. The author furthermore would like to express sincere thanks to the authorities of the Alpi Cozie Nature Park (Luca Marello and Michele Ottino) for issuing the necessary permits and to Christian Wieser (Klagenfurt, Austria) for help with field work. Subject editor and reviewers are acknowledged for careful work. Last but not least, Robert J. Heckford (Plympton, U.K.) and Stella Beavan (Zeal Monachorum, U.K.) are thanked for careful language proofreading with valuable comments.

References

Arnscheid WR, Weidlich M (2017) Psychidae. In: Karsholt O, Mutanen M, Nuss M (Eds) Microlepidoptera of Europe. Volume 8. Brill, Leiden & Boston, 423 pp. https://doi.org/10.1163/9789004340220

de Freina JJ (2011) Biologie, Verbreitung und Systematik des Komplexes von *Heterogynis paradoxa* Rambur, 1837 mit Beschreibung der *Heterogynis yerayi* sp. n. aus dem Kantabrischen Gebirge, Spanien (Lepidoptera: Zygaenoidea, Heterogynidae). Nachrichten des Entomologischen Vereins Apollo, Neue Folge 32(1/2): 9–24.

deWaard JR, Ivanova NV, Hajibabaei M, Hebert PDN (2008) Assembling DNA Barcodes: Analytical Protocols. In: Martin CC (Ed.) Methods in Molecular Biology: Environmental Genomics. Humana Press Inc., Totowa, USA, 275–293. [364 pp.] https://doi.org/10.1007/978-1-59745-548-0_15

Heppner JB (1991) Brachyptery and aptery in Lepidoptera. Tropical Lepidoptera 2(1): 11–40.

Huemer P, Elsner G, Karsholt O (2013) Review of the *Eulamprotes wilkella* species-group based on morphology and DNA barcodes, with descriptions of new taxa (Lepidoptera, Gelechiidae). Zootaxa 3746(1): 69–100. https://doi.org/10.11646/zootaxa.3746.1.3

Huemer P, Hebert PDN (2011) Cryptic diversity and phylogeography of high alpine *Sattleria*—a case study combining DNA barcodes and morphology (Lepidoptera: Gelechiidae). Zootaxa 2981(1): 1–22. https://doi.org/10.11646/zootaxa.2981.1.1

Huemer P, Karsholt O (2018) Revision of the genus *Megacraspedus* Zeller, 1839, a challenging taxonomic tightrope of species delimitation (Lepidoptera, Gelechiidae). ZooKeys 800: 1–278. https://doi.org/10.3897/zookeys.800.26292

Huemer P, Karsholt O, Aarvik L, Berggren K, Bidzilya O, Junnilainen J, Landry J-F, Mutanen M, Nupponen K, Segerer A, Šumpich J, Wieser C, Wiesmair B, Hebert PDN (2020a) DNA barcode library for European Gelechiidae (Lepidoptera) suggests greatly underestimated species diversity. ZooKeys 921: 141–157. https://doi.org/10.3897/zookeys.921.49199

Huemer P, Karsholt O, Wieser C (2020b) *Megacraspedus cottiensis* sp. nov. (Lepidoptera, Gelechiidae) from northern Italy - a case of taxonomic confusion. ZooKeys 963: 141–152. https://doi.org/10.3897/zookeys.963.54842

Huemer P, Mutanen M (2015) Alpha taxonomy of the genus *Kessleria* Nowicki, 1864, revisited in light of DNA-barcoding (Lepidoptera, Yponomeutidae). ZooKeys 503: 89–133. https://doi.org/10.3897/zookeys.503.9590

Huemer P, Sattler K (1989) Das brachyptere Weibchen von *Caryocolum laceratella* (Zeller, 1868) (Lepidoptera, Gelechiidae). Nota lepidopterologica 11: 256–264.

Huemer P, Tarmann G (1992) Westpaläarktische Gespinstmotten der Gattung *Kessleria* (Nowicki): Taxonomie, Ökologie, Verbreitung (Lepidoptera, Yponomeutidae). Mitteilungen der Münchner entomologischen Gesellschaft 81: 5–110.

Huemer P, Timossi G (2014) *Sattleria* revisited: unexpected cryptic diversity on the Balkan Peninsula and in the south-eastern Alps (Lepidoptera: Gelechiidae). Zootaxa 3780(2): 282–296. https://doi.org/10.11646/zootaxa.3780.2.4

Huemer P, Tokár Z (2021) Description of the female of *Megacraspedus podolicus* (Toll, 1942) (Lepidoptera: Gelechiidae). Zootaxa 5023(1): 147–150. https://doi.org/10.11646/zootaxa.5023.1.10

Huemer P, Wieser C (2020) Bemerkenswerte Neufunde von Schmetterlingen (Lepidoptera) für Italien (Cottische Alpen). Carinthia II 210/130: 457–470.

Klimesch J (1990) *Biselachista brachypterella* sp. n. (Lepidoptera, Elachistidae). Nota lepidopterologica 13(2–3): 137–146.

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. https://doi.org/10.1093/molbev/msw054

Müller B, Erlacher S, Hausmann A, Rajaei H, Sihvonen P, Skou P (2019) Ennomiinae II. In: Hausmann A, Sihvonen P, Rajaei H, Skou P (Eds) The Geometrid Moths of Europe. Volume 6. Brill, Leiden, 906 pp. https://doi.org/10.1163/9789004387485

Nel J, Varenne T (2019) A propos des femelles de cinq espèces françaises du genre *Megacraspedus* Zeller, 1839 (Lepidoptera, Gelechiidae). R.A.R.E. 27(2): 110–115.

Pitkin LM, Sattler K (1991) *Sattleria*: a European genus of brachypterous alpine moths (Lepidoptera: Gelechiidae). Bulletin of the British Museum (Natural History), Entomology 60: 205–241.

Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes 7: 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Ronkay L, Huemer P (2018) *Agrotis fatidica* (Hübner, 1824) species-group revisited, with description of two new species from the Alps and the Pyrenees (Lepidoptera, Noctuidae). Nota Lepidopterologica 41(1): 145–179. https://doi.org/10.3897/nl.41.23090

Sattler K (1991) A review of wing reduction in Lepidoptera. Bulletin of the British Museum (Natural History), Entomology 60: 243–288.

Sattler K, Wojtusiak J (1999) A new brachypterous *Xenomigia* species (Lepidoptera: Notodontidae) from Venezuela, Insect Systematics & Evolution 30(4): 435–442. https://doi.org/10.1163/187631200X00543

Shovkoon DF (2008) On the rediscovery of *Ethmia discrepitella* (Rebel, 1901) with remarks on brachyptery in females of *Ethmia* (Ethmiidae). Nota Lepidopterologica 31(2): 215–221.

Timossi G, Huemer P (2021) *Megacraspedus laseni* sp. nov. (Lepidoptera: Gelechiidae) from the Dolomites of north-eastern Italy. Zootaxa 4927(4): 559–566. https://doi.org/10.11646/zootaxa.4927.4.6

Timossi G, Huemer P (2022) *Sattleria enrosadira* sp. nov., a new cryptic, high alpine species from Northern Italy revealed by DNA barcodes and morphology (Lepidoptera, Gelechiidae). Zootaxa 5128(3): 435–443. https://doi.org/10.11646/zootaxa.5128.3.8

Timossi G, Ruzzier E (2020) Description of the female of *Sattleria sophiae* Timossi, 2014 (Lepidoptera: Gelechiidae). Zootaxa 4722(5): 491–494. https://doi.org/10.11646/zootaxa.4722.5.8

Timossi G, Ruzzier E (2023) Description of *Sphaleroptera orientana meridionalis* subs. n. (Lepidoptera: Tortricidae: Cnephasiini) from the Pale di San Martino Mountain plateau (Dolomites, NE Italy). Zootaxa 5249(1): 001–011. https://doi.org/10.11646/zootaxa.5249.1.1

Viloria AL, Pyrcz TW, Wojtusiak J, Ferrer-Paris JR, Beccaloni GW, Sattler K, Lees D (2003) A brachypterous butterfly? Proceedings of the Royal Society London, Biological Sciences 270: S21–S24. https://doi.org/10.1098/rsbl.2003.0015

Whitebread S (2006) *Sphaleroptera alpicolana* (Frölich, 1830) (Lepidoptera: Tortricidae, Cnephasiini): a species complex. Veröffentlichungen des Tiroler Landesmuseums Ferdinandeum 86: 177–204.

Alpine Entomology 7 2023, 45–55 | DOI 10.3897/alpento.7.103269

PENSOFT.

Alpine Entomology

Three alien bark and ambrosia beetles (Coleoptera, Curculionidae, Scolytinae) new to Switzerland

Andreas Sanchez[1], Yannick Chittaro[1], David Frey[2], Bärbel Koch[3], Doris Hölling[4], Eckehard G. Brockerhoff[5], Beat Ruffner[6], Miloš Knížek[7]

1 *info fauna, Avenue Bellevaux 51, CH-2000 Neuchâtel, Switzerland*
2 *Al Ciòs Consulenze Ambientali, Via Cantonale 79, CH-6818 Melano, Switzerland*
3 *Museo cantonale di storia naturale (MCSN), Via Carlo Cattaneo 4, CH-6901 Lugano, Switzerland*
4 *Swiss Federal Institute WSL, Swiss Forest Protection (WSS), Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*
5 *Swiss Federal Institute WSL, Forest Health and Biotic Interactions, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*
6 *Swiss Federal Institute WSL, Phytophathology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*
7 *Forestry and Game Management Research Institute, Strnady 136, CZ-252 02 Jíloviště, Czech Republic*

https://zoobank.org/5AD07389-A713-4656-B2B5-CDFAC1C01160

Corresponding author: Andreas Sanchez (andreas.sanchez@infofauna.ch)

Academic editor: Stève Breitenmoser ♦ **Received** 9 March 2023 ♦ **Accepted** 1 May 2023 ♦ **Published** 19 May 2023

Abstract

Identifying alien species is important to ensure the early detection of biological invasions and survey shifts in species distributions in the context of global change. Here, we report on three alien bark and ambrosia beetles newly detected in Switzerland: *Cyclorhipidion distinguendum* (Eggers, 1930), *C. pelliculosum* (Eichhoff, 1878), and *Hypothenemus eruditus* (Westwood, 1834). These species were recorded for the first time during a comprehensive survey of saproxylic beetles accross major forest types and along an altitudinal gradient during the entire growing season in the southern Alps, in the canton of Ticino. Their local abundance and number of occurrences accross different lowland forest habitats, including alluvial forests of national importance, indicates that all three species are already naturalized. Given their polyphagy, it is likely that all three species will become more extensively distributed across Switzerland, with a yet unknown environmental impact.

Key Words

Alien species, biological invasions, distribution, first record, faunistics, introduction, *Cyclorhipidion*, *Hypothenemus*

Introduction

The distributions of organisms are changing at fast rates worldwide (e.g., Pereira et al. 2010), a phenomenon amplified by globalization and the acceleration in trade, which increase the number of alien species across the world (Seebens et al. 2017). The correct identification of new arrivals is important to conduct risk assessments of potential pest organisms at an early stage of invasion and in general to elucidate shifts in species ranges in the context of global change (e.g., Blackburn et al. 2011; Simberloff et al. 2013; Hawkins et al. 2015).

Wood-boring insects are among the invasive species with the greatest ecological and economic impacts (Aukema et al. 2011) and their introduction pathways are generally well known (Essl et al. 2015): they are frequently introduced with wood packing materials used in international trade (Brockerhoff et al. 2006; Kirkendall and Faccoli 2010; Inward 2020), a trend that seems to be constantly increasing (Hulme et al. 2009; Lantschner et al. 2020). Moreover, since these species often come from warm regions, this increase is likely favoured by climate change (Pureswaran et al. 2022). In Europe, more than 30 species of exotic Scolytinae are currently known

(Kirkendall and Faccoli 2010; Sauvard et al. 2010; Barnouin et al. 2020; Marchioro et al. 2022) and these often originate from Asia (Kirkendall and Faccoli 2010; Roques et al. 2020; OFEV 2022).

Xyleborine ambrosia beetles (Coleoptera, Curculionidae, Scolytinae) are species depending on the presence of symbiotic fungi in the larval galleries of their host plants for larval and adult nutrition. The fungi are carried by adults females via their spores in adapted organs, the mycangia, and deposited in the larval galleries of their new hosts (Batra 1963; Beaver 1989; Mayers et al. 2022). The rapid colonization of new territories is facilitated by their high reproductive success: most ambrosia beetles are inbreeding, reproduce by sib-mating, and have a sex ratio strongly biased towards females (Kirkendall and Ødegaard 2007; Kirkendall and Faccoli 2010; Vega et al. 2015). Moreover, their marked host plant polyphagy favours a rapid adaptation to new environments. This is the case, for example, of *Xylosandrus germanus* (Blandford, 1894) and *Cyclorhipidion bodoanum* (Reitter, 1913), two species that have rapidly colonized numerous European countries following their introduction to the continent in 1950 and 1960, respectively (Kirkendall and Faccoli 2010; Galko et al. 2018; Fiala et al. 2021). Some bark beetles (including some *Hypothenemus* species), even if they are phloeophagous rather than obligate xylomycetophagous, share these characteristics of ecological plasticity, a broad host range, and a high reproductive success (inbreeding, sib-mating reproduction, and sex ratio biased toward females) which allow them to quickly colonize new territories (Mandelshtam et al. 2022).

In Switzerland, Scolytinae are represented by 112 species according to the recent checklist of Sanchez et al. (2020), of which seven species are considered invasive (OFEV 2022): *Cyclorhipidion bodoanum*, *Gnathotrichus materiarius* (Fitch, 1858), *Ips duplicatus* (C. R. Sahlberg, 1836), *Xyleborinus attenuatus* (Blandford, 1894), *Xyleborinus saxesenii* (Ratzeburg, 1837), *Xylosandrus crassiusculus* (Motschulsky, 1866), and *Xylosandrus germanus*. Since this publication, an additional alien species has been recorded in Switzerland: *Anisandrus maiche* (Kurentzov, 1941) (Ribeiro Correia et al. 2023, Preprint), with multiple specimens caught in the southern Alps, in the canton of Ticino. This region is particularly prone to the arrival of new alien species in Switzerland, as has already been shown for other organisms, in particular vascular plants (e.g., Mangili et al. 2016).

Here, we report on three new alien bark and ambrosia beetles species in Switzerland: the two xyleborine ambrosia beetles *Cyclorhipidion distinguendum* (Eggers, 1930), *C. pelliculosum* (Eichhoff, 1878), and *Hypothenemus eruditus* (Westwood, 1834). They were recorded for the first time in 2022 during a comprehensive survey of saproxylic beetles in all major forest typologies and along an altitudinal gradient in the southern Alps, in the canton of Ticino. We discuss the introduction mode, naturalization status, and invasion potential of each species.

Materials and methods

Sampling sites and methods

Saproxylic beetles were sampled at 57 forest sites (study plots) along an altitudinal gradient (195–1,971 m a.s.l.) in the canton of Ticino in the southern Alps, Switzerland, with 114 unbaited Polytrap™ interception traps (Brustel 2012) (Fig. 1). Two traps freely suspended 2 m above the forest floor were placed in each study plot, keeping an intertrap distance of 20–30 m. A saturated salt solution with neutral detergent was used as preserving fluid. The trap contents were collected every two weeks, between early March and the end of September 2022. In addition, one specimen of *Hypothenemus eruditus* was actively captured during a field campaign conducted by the first author in the extreme south of the canton of Ticino, in a wetland forest largely composed of poplars (Fig. 8).

Voucher specimens are deposited at the Museo cantonale di storia naturale (MCSN), at the Swiss Federal Research Institute WSL, and in the personal collections of A. Sanchez and M. Knížek. The data have been deposited in the national database info fauna (www.infofauna.ch).

All specimens were identified morphologically by A. Sanchez and M. Knížek. The identification of *Cyclorhipidion* species was based on criteria provided by Hoebeke et al. (2018) and Smith et al. (2020). Information on the taxonomic status of *Hypothenemus eruditus* was obtained from Kambestad et al. (2017). In addition, two specimens of each species were molecularly identified. The total genomic DNA was extracted from adults using the NucleoSpin Tissue XS Kit (Macherey-Nagel, Düren, Germany) according to the manufacturer's instruction. The COI-Barcode region was amplified and sequenced with standard primers LCO1490 and HCO2198 (Folmer et al. 1994).

To place our Swiss observations within a European context, we considered the distributions proposed by Alonso-Zarazaga et al. (2017, 2023) and the data deposited on the GBIF.org portal (2023), and complemented them with the following publications and the information provided by various European specialists: Great Britain (Turner and Beaver 2015), France (Noblecourt 2004; Dodelin 2018; Barnouin et al. 2020; B. Dodelin pers. comm.), Germany (Gebhardt 2014; H. Gebhardt pers. comm.), Greece (B. Dodelin pers. comm.), Italy (Masutti 1968), Malta (Mifsud and Knížek 2009), Portugal (Marchioro et al. 2022), Russia (Mandelshtam et al. 2018), Spain (López Romero et al. 2007), and Turkey (Tuncer et al. 2017).

Results

Among the more than 28,000 beetles trapped in 2022, 366 specimens were found to belong to three ambrosia and bark beetle species recorded for the first time in Switzerland: 187 females of *C. distinguendum*, 142 females

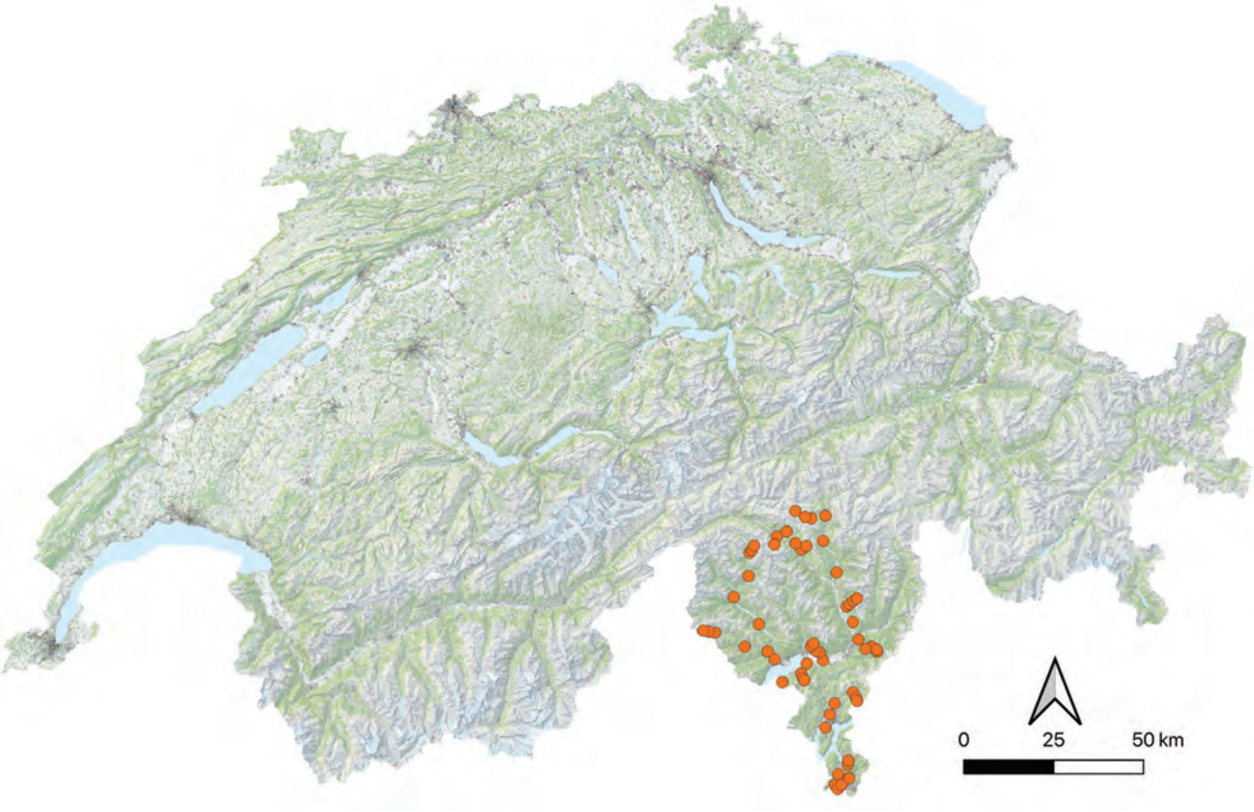


Figure 1. Location of the 114 interception traps (orange dots) in 2022 in the southern Alps, canton of Ticino. (Vector and raster map data swisstopo.ch).

of *C. pelliculosum*, and 37 specimens of *H. eruditus*. The details of the recorded specimens are shown below. If not specified otherwise, the collector (leg.) was the project coordinator D. Frey.

Cyclorhipidion distinguendum (Eggers, 1930)

Figs 2, 3

Switzerland • 1 ♀; Arbedo-Castione, El Gag; 2724273, 1119188 (46.212669245, 9.049077111); 328 m a.s.l.; 10 Apr.–2 May 2022; MCSN. • 2 ♀; Bellinzona, Ruderi del Castello di Claro; 2722751, 1124011 (46.256325540, 9.030627382); 437 m a.s.l.; 14 Jun.–14 Aug. 2022; MCSN. • 49 ♀; Capriasca, Solorónch; 2717643, 1101393 (46.053814854, 8.958714310); 620 m a.s.l.; 2717651, 1101409 (46.053957360, 8.958821658); 626 m a.s.l.; 31 Mar.–5 Sep. 2022; Sanchez A., Knížek M. coll. and MCSN. • 2 ♀; Cadenazzo; Ciossa Antognini; 2714516, 1113409 (8,921253831, 46,162423843); 201 m a.s.l.; 14 Mar.–14 Apr.; MCSN. • 1 ♀; Castel San Pietro, Al Ronco; 2721737, 1080586 (45.865958663, 9.006227205); 510 m a.s.l.; 3–17 May 2022; MCSN. • 1 ♀; Cevio, Ospedale; 2689580, 1130931 (46.323805242, 8.601830413); 426 m a.s.l.; 11–26 Apr. 2022; MCSN. • 13 ♀; Collina d'Oro, Al Lago di Muzzano; 2715093, 1094661 (45.993707761, 8.924126664); 339 m a.s.l.; 2715063, 1094662 (45.993721864, 8.923739798); 339 m a.s.l.; 31 Mar.–12 Aug. 2022; Sanchez A. coll. and MCSN. • 1 ♀; Locarno, Bolette; 2709941, 1112476 (46.154794646, 8.861816697); 195 m a.s.l.; 14–26 Jul. 2022; MCSN. • 11 ♀; Lugano, Ponte Curtina; 2722793, 1104469 (46.080562140, 9.026044051); 676 m a.s.l.; 2722772, 1104459 (46.080476025, 9.025770034); 676 m a.s.l.; 2 May–5 Sep. 2022; Sanchez A. coll. and MCSN. • 7 ♀; Mendrisio, Monte Cristo; 2718662, 1081690 (45.876433372, 8.966918208); 425 m a.s.l.; 2718653, 1081707 (45.876587841, 8.966806589); 438 m a.s.l.; 10 Mar.–17 May 2022; Knížek M. coll. and MCSN. • 2 ♀; Novazzano, In Gall; 2719654, 1078647 (45.848891375, 8.978921620); 293 m a.s.l.; 1 Jun.–12 Jul. 2022; MCSN. • 31 ♀; Novazzano, La Valéta; 2718486, 1077592 (45.839608442, 8.963626081); 445 m a.s.l.; 2718533, 1077578 (45.839474311, 8.964227340); 450 m a.s.l.; 31 Mar.–12 Jul. 2022; MCSN and WSL. • 62 ♀; Vezia, S. Martino; 2716328/1098298 (46.026206809, 8.940961559); 431 m a.s.l.; 2716354, 1098287 (46.026103397, 8.941294533); 414 m a.s.l.; 31 Mar.–3 Oct. 2022; Knížek M. coll., MCSN and WSL.

The morphological identification of *C. distinguendum* was confirmed by the genetic analysis of two specimens (the sequences were deposited on GenBank: accession numbers OQ872230 and OQ872233). A sequence comparison of the COI-Barcode region of 650 and 589 bp to accessions on the nucleotide database of the National Center for Biotechnology Information (NCBI) confirmed the two sequenced specimens as *C. distinguendum*. Both sequences displayed a 100% similarity with a voucher specimen sequence of *C. distinguendum* (accession number: MN183038.1).

Cyclorhipidion pelliculosum **(Eichhoff, 1878)**
Figs 4, 5

Switzerland • 1 ♀; Capriasca, Solorónch; 2717643, 1101393 (46.053814854, 8.958714310); 620 m a.s.l.; 14 Apr.–2 May 2022; MCSN. • 12 ♀; Castel San Pietro, Al Ronco; 2721737, 1080586 (45.865958663, 9.006227205); 510 m a.s.l.; 25 Apr.–1 Jun. 2022; MCSN and WSL. • 3 ♀; Collina d'Oro, Al Lago di Muzzano; 2715093, 1094661 (45.993707761, 8.924126664); 339 m a.s.l.; 10 Mar.–14 Apr. 2022; Sanchez A. coll. and MCSN. • 1 ♀; Gambarogno, Quinta; 2703119, 1107291 (46.109238055, 8.772383402); 311 m a.s.l.; 11 Apr.–2 May 2022; MCSN. • 14 ♀; Mendrisio, Monte Cristo; 2718662, 1081690 (45.876433372, 8.966918208); 425 m a.s.l.; 2718653, 1081707 (45.876587841, 8.966806589); 438 m a.s.l.; 31 Mar.–17 May 2022; Knížek M. coll., MCSN and WSL. • 13 ♀; Novazzano, In Gall; 2719654, 1078647 (45.848891375, 8.978921620); 293 m a.s.l.; 2719618, 1078694 (45.849320430, 8.978470196); 291 m a.s.l.; 11 Mar.–25 Apr. 2022; MCSN. • 86 ♀; Novazzano, La Valéta; 2718533, 1077578 (45.839474311, 8.964227340); 450 m a.s.l.; 2718486, 1077592 (45.839608442, 8.963626081); 445 m a.s.l.; 10 Mar.–1 Jun. 2022; Sanchez A., Knížek M. coll. and MCSN. • 8 ♀; Stabio, Colombera; 2717648, 1078757 (45.850232009, 8.953132727); 345 m a.s.l.; 31 Mar.–17 May 2022; MCSN. • 4 ♀; Vezia, S. Martino; 2716354, 1098287 (46.026103397, 8.941294533); 414 m a.s.l.; 31 Mar.–2 May 2022; MCSN.

The morphological identification of *C. pelliculosum* was confirmed by the genetic analysis of two specimens (the sequences were deposited on GenBank: accession numbers OQ872231, OQ872232). According to a fragment of 559 and 577 bp, the BLAST searches confirmed the two sequenced specimens as *C. pelliculosum*. The nucleotide sequences showed a 99.6% identity to the oxidase subunit I (COI) gene from *C. pelliculosum* (accession number: GU808702.1).

Hypothenemus eruditus **(Westwood, 1834)**
Figs 6, 7

Switzerland • 1 ex.; Stabio; Boschi; 715367, 076920 (45.834090180, 8.923328978); 416 m a.s.l.; 18 May 2022; Sanchez A. leg. and coll. • 3 ex.; Collina d'Oro, Al Lago di Muzzano; 2715063, 1094662 (45.993721864, 8.923739798); 339 m a.s.l.; 16 May–1 Jun. 2022; Sanchez A. coll. and MCSN. • 34 ex.; Locarno, Bolette; 2709941, 1112476 (46.154794646, 8.861816697); 195 m a.s.l.; 2709912, 1112488 (46.154907307, 8.861444194); 195 m a.s.l.; 11 Apr.–14 Jul. 2022; Sanchez A., Knížek M. coll., MCSN and WSL.

Despite several attempts on specimens morphologically identified as *H. eruditus*, genetic analyses yielded no results, probably due to insufficient DNA available in such a small specimen or by the deterioration of the DNA by the trap preservation fluid.

Discussion

The use of interception traps for saproxylic beetle surveys often allows the detection of cryptic species. This has, for example, enabled the discovery of several rare species in Switzerland (Sanchez et al. 2021; Chittaro et al. 2023). On the other hand, they can sometimes also allow the detection of new alien species, as has already been the case in Switzerland (Breitenmoser et al. 2022), in France (Dodelin 2018; Barnouin et al. 2020), or in Italy (Marchioro et al. 2022).

The important monitoring (using 114 traps) (Fig. 1) carried out in the canton of Ticino during the summer of 2022 (and reported here) led to the discovery of three new alien species in Switzerland occurring in great abundances, since 366 specimens of these species were captured.

Their ecology, their known distribution in neighbouring countries to date, and the possible threats to the environment associated with their presence are synthesised below.

Cyclorhipidion distinguendum

Cyclorhipidion distinguendum (Fig. 2) is an ambrosia beetle native to Asia, occurring orginally in China (Fujian), India (Uttar Pradesh), Japan, Nepal, Taiwan and Thailand (Chiang Mai) (Hoebeke et al. 2018). In Europe, it was first detected in France in 2013 using interception traps (Dodelin 2018). According to Barnouin et al. (2020) and the new data provided by Dodelin (2018; pers. comm.), it is now established in the country in a small geographical area (Fig. 3), with several specimens having been captured in the last years. However, the circumstances of its introduction remain unknown. It has not yet been reported in other neighbouring countries such as Germany (H. Gebhardt pers. comm.), Austria, or Italy (E. Ruzzier pers. comm.). Despite the monitoring campaigns carried out for many years in northern Italy to detect new alien species (Marchioro et al. 2022; Ruzzier et al. 2022), *C. distinguendum* has curiously not yet been found, even though it is now established in France and Switzerland, particularly close to the Italian borders (Fig. 3). Nevertheless, given that 62 specimens were trapped in 2022 in the extreme south of Ticino, less than 200 meters from the Italian border (latitude/longitude 45.839474311, 8.964227340 and 45.839608442, 8.963626081), the species is almost certainly already present in northern Italy and may soon be detected there as well.

Although its ecology is still poorly known, it seems to preferentially develop on several Fagaceae, Dipterocarpaceae and Pinaceae species, including *Castanea* sp. and *Quercus* sp. (Beaver et al. 2014; Hoebeke et al. 2018; Ruzzier et al. 2023). In France, it was captured «in moist alder mixed forest at low altitude and in beech-fir forests growing at low altitude» (Barnouin et

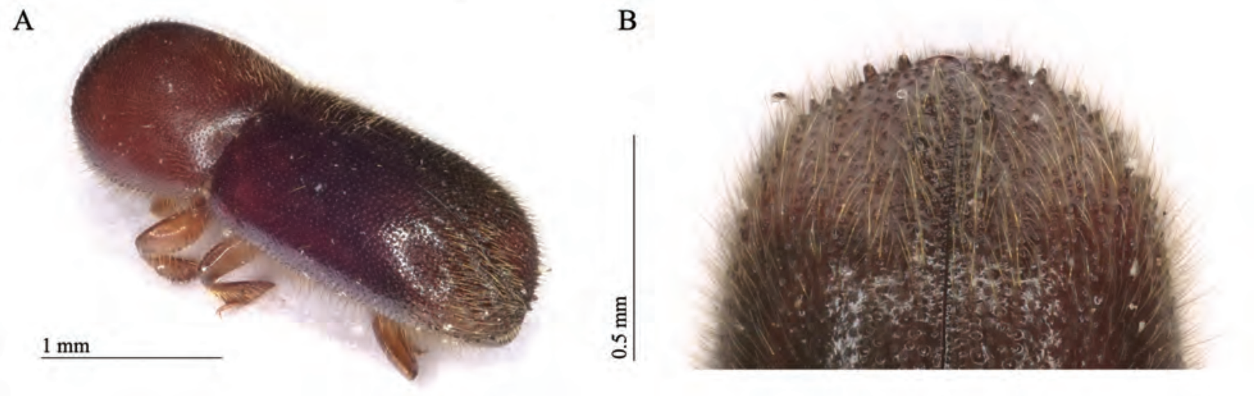


Figure 2. *Cyclorhipidion distinguendum*. **A**. Habitus; **B**. Elytral declivity. (Photos: A. Sanchez).

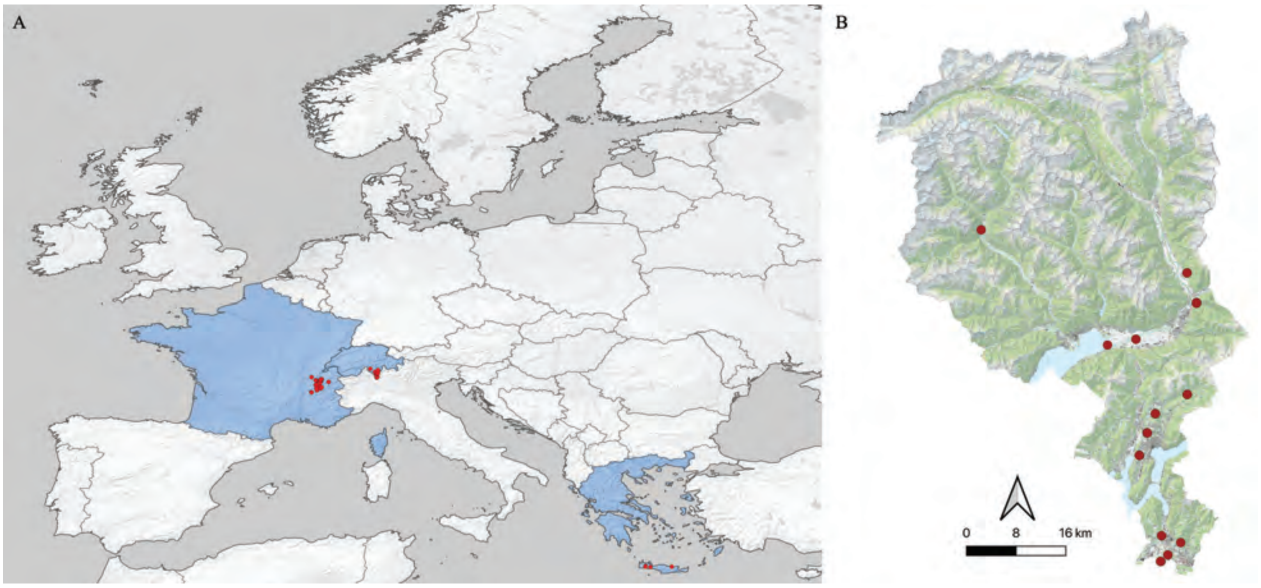


Figure 3. Actual known distribution of *Cyclorhipidion distinguendum* in **A**. Europe (the colonized countries are indicated in blue, and the red dots represent the exact locations of observations) and **B**. Ticino (Switzerland). (Vector and raster map data swisstopo.ch, naturalearthdata.com).

al. 2020). In Switzerland, the species also seems to be restricted to low elevations, with all specimens having been captured in deciduous forests located between 195 and 676 m a.s.l. Since all of these were caught by interception traps, no additional information on the host plants is available. As it has been discovered in multiple locations, the introduction source or locality cannot be reconstructed.

During the summer of 2022, *C. distinguendum* was regularly caught with traps between the 10th of March and the 10th of October, but more than 70% of the specimens were trapped between April and June. Thus, it seems that their peak activity is in spring. This hypothesis has been corroborated by French occurrences (Dodelin 2018; Barnouin et al. 2020).

Until now, no phytosanitary issues have been reported in relation to *C. distinguendum* in France or in the United States (Hoebeke et al. 2018; Barnouin et al. 2020), and this also appears to be the case in Switzerland.

Cyclorhipidion pelliculosum

Cyclorhipidion pelliculosum (Fig. 4) is also native to Asia and is known to occur in China (Fujian), India (Uttarakhand), Nepal and Taiwan (Alonso-Zarazaga et al. 2017, 2023). In Europe, it was first detected in 2013 in the Karlsruhe region in Germany (Gebhardt 2014). Since this first record, it has been found regularly in Germany (in 2017, 2018, 2022) (H. Gebhardt pers. comm.), but it still remains unknown in other countries neighbouring Switzerland. Nevertheless, since 214 specimens of *C. pelliculosum* were trapped in 2022 in the south of Ticino, less than 1 kilometre from the Italian border, it is almost certainly also present in Italy. Its future discovery in France is also very likely, given its presence in Germany near the Franco-German border (Fig. 5).

The first specimen discovered in Europe was found on a poplar (*Populus* sp.) trunk (Gebhardt 2014), while the following German specimens were collected under the bark of a dead standing European beech (*Fagus sylvactica* L.) and

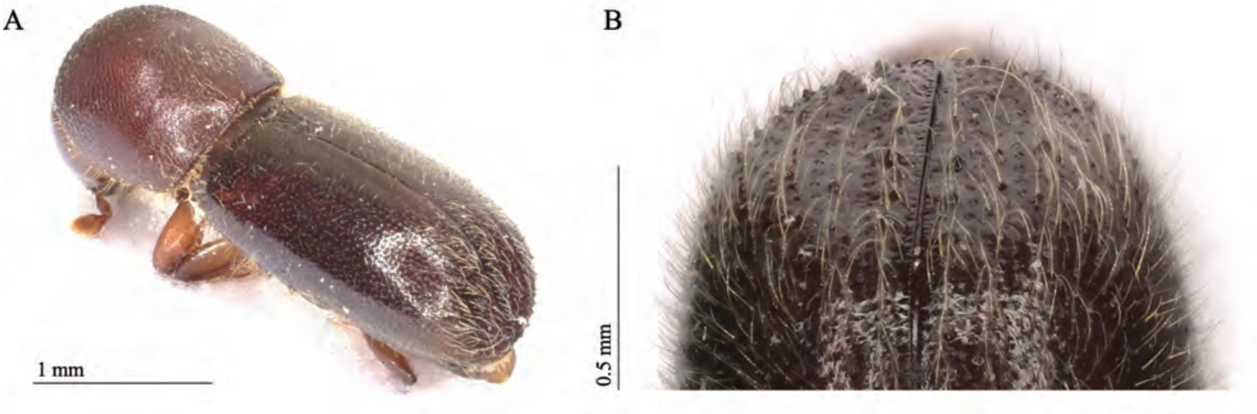


Figure 4. *Cyclorhipidion pelliculosum*. **A**. Habitus; **B**. Elytral declivity. (Photos: A. Sanchez).

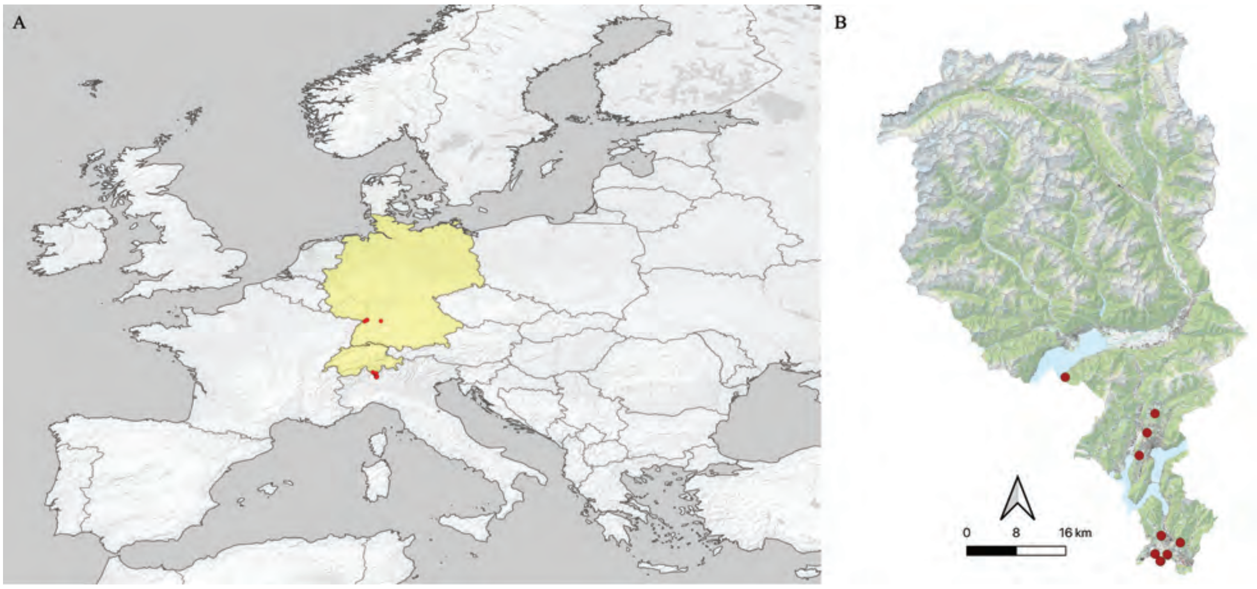


Figure 5. Actual known distribution of *Cyclorhipidion pelliculosum* in **A**. Europe (the colonized countries are indicated in yellow, and the red dots represent the exact locations of observations) and **B**. Ticino (Switzerland). (Vector and raster map data swisstopo.ch, naturalearthdata.com).

on oak (*Quercus* sp.) trunks (H. Gebhardt pers. comm.). Several other host species, including *Acer* sp., *Alnus* sp., *Betula* sp., *Castanea* sp., *Castanopsis* sp., *Juglans* sp. and *Quercus* sp., have been reported in the literature (e.g., in Wood and Bright 1992; Mandelshtam et al. 2018; Smith et al. 2020; Ruzzier et al. 2023). Like *C. distinguendum*, *C. pelliculosum* appears to have a maximum activity in spring and occurs only at low altitudes, a situation also observed in Germany (H. Gebhardt pers. comm.). In Switzerland, the 142 Swiss specimens were all caught between the 10th of March and the 1st of June in deciduous forests located between 291 and 620 m a.s.l. For the moment, no phytosanitary issues attributable to this specis have been noticed in Germany or Switzerland.

Hypothenemus eruditus

Hypothenemus eruditus (Fig. 6) belongs to one of the most diverse scolytine genera in the world, with more than 220 species currently described (Wood 2007; Vega et al. 2015; Huang et al. 2016; Johnson et al. 2020). With more than 70 recognized synonyms (Vega et al. 2015), *H. eruditus* likely represent a complex of several closely related species whose morphological identification is extremely difficult. Extensive genetic studies have shown that several synonyms may be resurrected to valid species in the future (Kambestad et al. 2017). Nevertheless, here we refer to *H. eruditus sensu lato*.

Originally present in tropical and subtropical regions, it is now sub-cosmopolitan and also present in many temperate regions (Vega et al. 2015; Huang et al. 2016). According to several authors, it may even be the most widespread and abundant Scolytinae in the world (Wood 2007; Kambestad et al. 2017). Occurring in Italy since at least 1924 (Ragusa 1924; Kirkendall and Faccoli 2010), it is now established in numerous European coutries (Fig. 7) including Croatia, France, Georgia, Italy, Malta, Portugal (including Azores), Russia, Spain (including Canary Islands), Turkey, and Ukraine (Alonso-Zarazaga et al. 2017, 2023; Marchioro et al. 2022). It was also detected in Britain in 2011 in a «tropical humid biome» with controlled conditions, but the species does not survive there in the wild (Turner and Beaver 2015).

Figure 6. Habitus of *Hypothenemus eruditus*. (Photo: A. Sanchez).

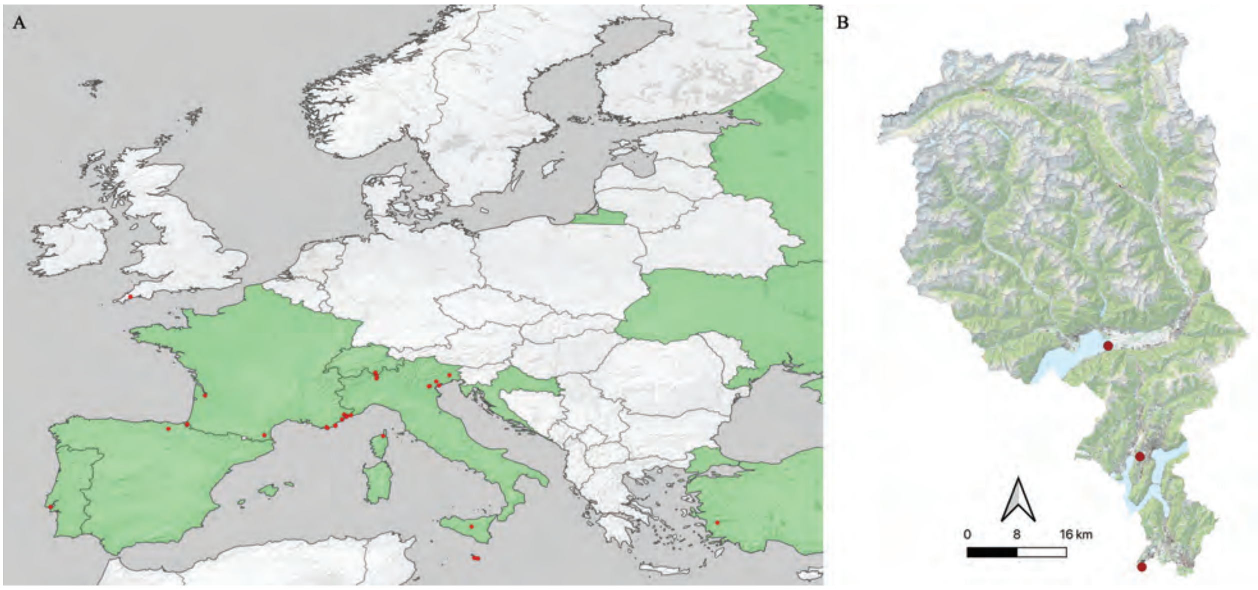


Figure 7. Actual known distribution of *Hypothenemus eruditus* in **A**. Europe (the colonized countries are indicated in green, and the red dots represent the exact locations of observations) and **B**. Ticino (Switzerland). (Vector and raster map data swisstopo.ch, naturalearthdata.com).

Hypothenemus eruditus is an extremely polyphagous species that develops in small branches, but also in the bark of trunks or branches, in flowers, grasses, seeds, leaf petioles, and twigs (Wood 1977; EPPO 2020) of plants (herbaceous, deciduous, and coniferous) belonging to several dozen genera worldwide (Atkinson 2022), as well as in manufactured products (Vega et al. 2015). In Europe, it has been regularly found together with *Hypoborus ficus* Erichson, 1836 (Balachowsky 1949; Noblecourt 2004) on fig trees (*Ficus* sp.) in France (Barnouin et al. 2020), and on mulberry (*Morus alba* L.) in Italy (Masutti 1968). In Switzerland, the first specimen was found in a wetland forest in the extreme south of the canton of Ticino, under the bark of a poplar (*Populus nigra* L.) (Fig. 8). The remaining specimens were all caught by interception traps placed in wetland forests also largely dominated by poplars, a very probable host plant in the region. The 37 Swiss specimens were caught between the 11th of April and the 14th of July, suggesting a period of stronger activity in spring. In France, the species was regularly caught in mid-summer (July-August) (data from GBIF.org), and in Malta, the species was even found in October and in January (one specimen in a dead branch of *Capparis* sp.) (Mifsud and Knížek 2009).

Due to the variety of substrates in which the species can develop, it is difficult to speculate about how it was

Figure 8. The wetland forest in which the first specimen of *H. eruditus* was captured. (Photo: A. Sanchez).

introduced into Switzerland. It is highly likely that the species is already naturalized in Switzerland, given that many individuals have been found in three localities several tens of kilometres apart. The European and Mediterranean Plant Protection Organization (EPPO) drew up a non-exhaustive list of means of transport of the species, including their entry with wood (round or sawn, with bark, including firewood), barks, wood chips, hogwood, wood processing residues (except sawdust and shavings), wood packaging material if not treated, processed wood material (e.g., plywood, veneer), plants for planting, or cut branches of host plants (EPPO 2020).

Despite its highly polyphagous diet, the species does not appear to cause phytosanitary problems in Europe (Huang et al. 2016), even if some authors consider the species to be of potential economic importance (López Romero et al. 2007), in particular as a citrus pest (Mandelshtam et al. 2022).

Occurrence and establishment in Switzerland

These three species were all discovered in Switzerland in 2022, but their already wide known distribution (Figs 3B, 5B, 7B) suggests that they have already been present in the country for several years. Based on the information available to us, these species appear to currently be restricted to the canton of Ticino, the region with the highest number of records of exotic species in the country. The southern part of the canton is certainly their gateway, as has been the case for many invasive species in Switzerland, like other insect species (Derron et al. 2005; Forster et al. 2009; Flacio et al. 2016; EPPO 2017), plants (Schönenberger et al. 2014; Mangili et al. 2016), or fungi (Prospero and Rigling 2012; Beenken et al. 2020). This trend can probably be explained by several factors: on the one hand, this region is a major transit route between northern and southern Europe, with important industrial areas through which many types of merchandise transit and, on the other hand, the mild insubric climate which may facilitate establishment and acclimatization of new species (Mangili et al. 2016). Moreover, this region borders Italy, the country with the highest number of exotic beetles in Europe (Marchioro et al. 2022). Difficult to detect and very polyphagous, these three bark and ambrosia beetle species will probably spread (or be introduced accidentally) in northern Switzerland in the coming years, a situation that has already happened previously with *Cyclorhipidion bodoanum*.

These three new species add to the list of alien Scolytinae that are already widely distributed in Switzerland (list of the invasive species provided in the introduction). Even if the majority of these species are now widely distributed in Switzerland, they do not seem to pose any phytosanitary problems for the moment, at least according to our current knowledge, which is often (very) incomplete (OFEV 2022). Nevertheless, national and cantonal institutions have been informed about the presence of these species in the country, and they will take the necessary measures to monitor the expansion of the species in the canton and the country.

In the last two years, four new alien Scolytinae species (including *A. maiche* (Ribeiro Correia et al. 2023, Preprint)) have been discovered in Switzerland, and new others will certainly be found in coming years. For example, *Xylosandrus compactus* (Chapuis & Eichhoff, 1875) is a potential invader. This species was found for the first time in Europe in Italy in 2011 (Garonna et al. 2012) and is now also present in France (Barnouin et al. 2020). However, in these two countries, it currently remains confined to the Mediterranean region, but global climate change may help this species to expand its distribution, as predicted by some distribution models (e.g., Urvois et al. 2021). *Xyloterinus politus* (Say, 1826) is another species that could become established in Switzerland in the future: it is already present in the Seine-Maritime department in northwestern France (Dodelin and Saurat 2017; Barnouin et al. 2020) and in Bavaria, Germany (Gebhardt and Doerfler 2018). Although these two species have been recorded in neighbouring countries at significant distances from Switzerland, the rapid colonization abilities of these species could lead them to reach the country in the coming years. Fortunately, not all alien species become established in Switzerland. For example, *Coccotrypes dactyliperda* (Fabricius, 1801), *Dactylotrypes longicollis* (Wollaston, 1864), or *Pagiocerus frontalis* (Fabricius, 1801) were accidentally introduced into Switzerland, but there is currently no evidence that these species have reproduced in the wild (Sanchez et al. 2020).

The intensive monitoring campaigns carried out in 2022 revealed new alien and potentially invasive species in Switzerland. This shows the importance of such campaigns, especially in Ticino, for quickly detecting the presence of new species in the territory, and thus allowing necessary measures to be taken to eradicate their expansion, if necessary and if possible. Concerning bark and ambrosia beetles, the monitoring campaigns should ideally be conducted in important transit areas of goods, ideally near the borders and in the airports, as is currently done in France and which has allowed the detection of *Xyloterinus politus* (Dodelin and Saurat 2017), or in cities or suburban areas, where most alien species are detected (Branco et al. 2019). Moreover, to evaluate the progression of these three species in Switzerland, monitoring campaigns should be carried out in other regions of the country.

Acknowledgments

We would like to thank Stève Breitenmoser, Heiko Gebhardt and Enrico Ruzzier for their valuable comments on the manuscript. We also thank them, and Benoît Dodelin, for sharing their information on the species and their distribution in different European localities. We are also grateful to Stefano Brignoli, Ivan Candolfi, Lisa Elzi, Giorgio Musso, Lucia Pollini Paltrinieri and Davide Prati for their support during the field work. We finally acknowledge Michel Sartori and Nadir Alvarez for providing us with the photographic equipment. The part of study conducted by Miloš Knížek was supported by the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0118.

References

Alonso-Zarazaga MA, Barrios H, Borovec R, Bouchard P, Caldara R, Colonnelli E, Gültekin L, Hlaváč P, Korotyaev B, Lyal CHC, Machado A, Meregalli M, Pierotti H, Ren L, Sánchez-Ruiz M, Sforzi A, Silfverberg H, Skuhrovec J, Trýzna M, Velázquez de Castro AJ, Yunakov NN (2017) Cooperative Catalogue of Palaearctic Coleoptera Curculionoidea. Sociedad Entomológica Aragonesa S.E.A. Monografías electrónicas SEA, Vol. 8, 729 pp. https://www.biotaxa.org/mesea/article/view/34195/30253

Alonso-Zarazaga MA, Barrios H, Borovec R, Bouchard P, Caldara R, Colonnelli E, Gültekin L, Hlaváč P, Korotyaev B, Lyal CHC, Machado A, Meregalli M, Pierotti H, Ren L, Sánchez-Ruiz M, Sforzi A, Silfverberg H, Skuhrovec J, Trýzna M, Velázquez de Castro AJ, Yunakov NN (2023) Cooperative catalogue of palaearctic Coleoptera Curculionoidea, 2nd edn. Sociedad Entomológica Aragonesa S.E.A. Monografías electrónicas SEA, Vol. 14, 780 pp. https://zoobank.org/References/911EF526-33F0-4970-8EC2-A7F5AC1E1D3D

Atkinson TH (2022) Bark and ambrosia beetles of the Americas. https://www.barkbeetles.info/index.php [accessed on 1st December 2022]

Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG, Von Holle B (2011) Economic impacts of non-native forest insects in the continental United States. PLoS ONE 6(9): e24587. https://doi.org/10.1371/journal.pone.0024587

Balachowsky A (1949) Coléoptères Scolytides. Faune de France 50. Librairie de la Faculté des Sciences, Paris, 320 pp.

Barnouin T, Soldati F, Roques A, Faccoli M, Kirkendall L, Mouttet R, Daubree J, Noblecourt T (2020) Bark beetles and pinhole borers recently or newly introduced to France (Coleoptera: Curculionidae, Scolytinae and Platypodinae). Zootaxa 4877(1): 51–74. https://doi.org/10.11646/zootaxa.4877.1.2

Batra LR (1963) Ecology of ambrosia fungi and their dissemination by beetles. Transactions of the Kansas Acadamy of Science 66: 213–236. https://doi.org/10.2307/3626562

Beaver RA (1989) Insect-fungus relationships in the bark and ambrosia beetles. In: Wilding N, Collins NM, Hammond PM, Webber JF (Eds) Insect-fungus interactions. Academic Press, London: 121–143. https://doi.org/10.1016/b978-0-12-751800-8.50011-2

Beaver RA, Sittichaya W, Liu L-Y (2014) A synopsis of the scolytine ambrosia beetles of Thailand (Coleoptera: Curculionidae: Scolytinae). Zootaxa 3875: 1–82. https://doi.org/10.11646/zootaxa.3875.1.1

Beenken L, Brodtbeck T, De Marchi R (2020) First record of *Erysiphe corylacearum* on *Corylus avellana* in Switzerland and in central Europe. New Disease Reports 41: 11. https://doi.org/10.5197/j.2044-0588.2020.041.011

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26: 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Branco M, Nunes P, Roques A, Fernandes MR, Orazio C, Jactel H (2019) Urban trees facilitate the establishment of non-native forest insects. NeoBiota 52: 25–46. https://doi.org/10.3897/neobiota.52.36358

Breitenmoser S, Sanchez A, Chittaro Y (2022) Première mention de *Silvanus recticollis* Reitter, 1876 (Coleoptera: Silvanidae) en Suisse. Entomo Helvetica 15: 171–174.

Brockerhoff EG, Bain J, Kimberley M, Knížek M (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Canadian Journal of Forest Research 36(2): 289–298. https://doi.org/10.1139/X05-250

Brustel H (2012) Polytrap™ 2010: new "soft design" window flight trap for saproxylic beetles. In: Jurc M (Ed.) Saproxylic beetles in Europe: monitoring, biology and conservation. Ljubljana, Slovenian Forestry Institute, Silva Slovenica, 91–92.

Chittaro Y, Sanchez A, Szallies A, Gossner MM, Lachat T (2023) On the occurrence of relic populations of *Pytho abieticola* J. R. Sahlberg, 1875 in Switzerland (Coleoptera, Pythidae). Alpine Entomology 7: 1–11. https://doi.org/10.3897/alpento.7.98799

Derron J, Bertossa M, Brunetti R, Colombi L (2005) Phénologie du vol de la chrysomèle des racines du maïs (*Diabrotica virgifera virgifera*) dans le sud des Alpes suisses. Revue Suisse Agricole 37(2): 61–64.

Dodelin B (2018) *Cyclorhipidion fukiense* installé en Europe. EntomoData. https://entomodata.wordpress.com/2018/04/24/cyclorhipidion-fukiense-installe-en-europe/ [accessed on 1st December 2022]

Dodelin B, Saurat R (2017) *Xyloterinus politus* a traversé l'Atlantique. https://entomodata.wordpress.com/2017/07/08/xyloterinus-politus-a-traverse-latlantique/ [accessed on 1 December 2022]

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso AC, Eschen R, Gallardo B, Galil B, García-Berthou E, Genovesi P, Groom Q, Harrower C, Hulme PE, Katsanevakis S, Kenis M, Kühn I, Kumschick S, Martinou AF, Nentwig W, O'Flynn C, Pagad S, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roques A, Roy

HE, Scalera R, Schindler S, Seebens H, Vanderhoeven S, Vilà M, Wilson JRU, Zenetos A, Jeschke JM (2015) Crossing frontiers in tackling pathways of biological invasions. Bioscience 65: 769–782. https://doi.org/10.1093/biosci/biv082

EPPO (2017) First report of *Popillia japonica* in Switzerland. European and Mediterranean Plant Protection Organization (EPPO) Reporting Service No. 09-2017:2017/2160.

EPPO (2020) Pest information sheet on *Hypothenemus eruditus*. In: EPPO Study on the risk of bark and ambrosia beetles associated with imported non-coniferous wood. EPPO Technical Document no. 1081: 90–95. https://www.eppo.int/media/uploaded_images/RESOURCES/eppo_publications/TD-1081_EPPO_Study_bark_ambrosia.pdf

Fiala T, Knížek M, Holuša J (2021) Continued eastward spread of the invasive ambrosia beetle *Cyclorhipidion bodoanum* (Reitter, 1913) in Europe and its distribution in the world. BioInvasions Records 10(1): 65–73. https://doi.org/10.3391/bir.2021.10.1.08

Flacio E, Engeler L, Tonolla M, Müller P (2016) Spread and establishment of *Aedes albopictus* in southern Switzerland between 2003 and 2014: an analysis of ovideposition data and weather conditions. Parasites & Vectors 9: 304. https://doi.org/10.1186/s13071-016-1577-3

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoaninvertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.

Forster B, Castellazzi T, Colombi L, Fürst E, Marazzi C, Meier F, Tettamanti G, Moretto G (2009) Die Edelkastaniengallwespe *Dryocosmus kuriphilus* (Yasumatsu) (Hymenoptera, Cynipidae) tritt erstmals in der Südschweiz auf. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 82: 271–279. https://doi.org/10.5169/seals-402995

Fujii T, Toyoura K, Uda T, Kasamatsu S (2020) Theoretical Study on Proton Diffusivity in Y-Doped BaZrO3 with Realistic Dopant Configurations. ChemRxiv 23(10): 1–33. [Preprint., June 11, 2020] [accessed 2020 August 14] https://doi.org/10.26434/chemrxiv.13193858.v2

Galko J, Dzurenko M, Ranger C, Kulfan J, Kula E, Nikolov C, Zúbrik M, Zach P (2018) Distribution, habitat preference, and management of the invasive ambrosia beetle *Xylosandrus germanus* (Coleoptera: Curculionidae, Scolytinae) in European forests with an emphasis on the West Carpathians. Forests 10(1): 10. https://doi.org/10.3390/f10010010

Garonna AP, Dole SA, Saracino A, Mazzoleni S, Cristinzio G (2012) First record of the black twig borer *Xylosandrus compactus* (Eichhoff) (Coleoptera: Curculionidae, Scolytinae) from Europe. Zootaxa 3251(1): 64–68. https://doi.org/10.11646/zootaxa.3251.1.5

GBIF.org [23 February 2023] (2023) GBIF Occurrence Download. https://doi.org/10.15468/dl.27x8n4

Gebhardt H (2014) Erstfund des Ambrosiakäfers *Cyclorhipidion pelliculosum* (Eichhoff) in Deutschland (Coleoptera, Curculionidae, Scolytinae). Mitteilungen des Entomologischen Vereins Stuttgart 49: 67–69.

Gebhardt H, Doerfler I (2018) Erster Nachweis von *Xyloterinus politus* (Say, 1826) (Coleoptera, Curculionidae, Scolytinae) in Deutschland. Mitteilungen des Entomologischen Vereins Stuttgart 53: 61–63.

Hawkins CL, Bacher S, Essl F, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Vilà M, Wilson JRU, Genovesi P, Blackburn TM (2015) Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT). Diversity and Distributions 21: 1360–1363. https://doi.org/10.1111/ddi.12379

Hoebeke ER, Rabaglia RJ, Knížek M, Weaver JS (2018) First records of *Cyclorhipidion fukiense* (Eggers) (Coleoptera: Curculionidae: Scolytinae: Xyleborini), an ambrosia beetle native to Asia, in North America. Zootaxa 4394: 243–250. https://doi.org/10.11646/zootaxa.4394.2.7

Huang YT, Hulcr J, Johnson AJ, Lucky A (2016) A Bark Beetle *Hypothenemus eruditus* Westwood (1836) (Insecta: Coleoptera: Curculionidae: Scolytinae). EDIS 8: 1–5. https://doi.org/10.32473/edis-in1147-2016

Hulme PE, Roy DB, Cunha T, Larsson T-B (2009) A pan-European inventory of alien species: rationale, implementation and implications for managing biological invasions. In: Daisie (Ed.) The Handbook of European Alien Species. Invading Nature - Springer Series in Invasion Ecology 3: 1–14. https://doi.org/10.1007/978-1-4020-8280-1_1

Inward D (2020) Three new species of ambrosia beetles established in Great Britain illustrate unresolved risks from imported wood. Journal of Pest Science 93(1): 117–126. https://doi.org/10.1007/s10340-019-01137-1

Johnson AJ, Hulcr J, Knížek M, Atkinson TH, Mandelshtam MY, Smith SM, Cognato AI, Park S, Li Y, Jordal BH (2020) Revision of the bark beetle genera within the former Cryphalini (Curculionidae: Scolytinae). Insect Systematics and Diversity 4(3): 1–81. https://doi.org/10.1093/isd/ixaa002

Kambestad M, Kirkendall LR, Knutsen IL, Jordal BH (2017) Cryptic and pseudo-cryptic diversity in the world's most common bark beetle-*Hypothenemus eruditus*. Organisms Diversity & Evolution 17: 633–652. https://doi.org/10.1007/s13127-017-0334-6

Kirkendall L, Ødegaard F (2007) Ongoing invasions of old-growth tropical forests: establishment of three incestuous beetle species in Central America. Zootaxa 1588: 53–62. https://doi.org/10.11646/zootaxa.1588.1.3

Kirkendall L, Faccoli M (2010) Bark beetles and pinhole borers (Curculionidae, Scolytinae, Platypodinae) alien to Europe. ZooKeys 56: 227–251. https://doi.org/10.3897/zookeys.56.529

Lantschner MV, Corley J, Liebhold A (2020) Drivers of global Scolytinae invasion patterns. Ecological Applications 30(5): 1–12. https://doi.org/10.1002/eap.2103

López Romero S, Romón Ochoa P, Iturrondobeitia Bilbao JC, Goldaracena Lafuente A (2007) Los escolítidos de las coníferas del País Vasco: guía práctica para su identificación y control. Eusko Jaurlaritzaren Argitalpen Zerbitzu Nagusia, Servicio Central de Publicaciones del Gobierno Vasco. Donostia-San Sebastián, Vitoria-Gasteiz, 198 pp.

Mandelshtam MYu, Yakushkin EA, Petrov AV (2018) Oriental ambrosia beetles (Coleoptera: Curculionidae: Scolytinae): new inhabitants of Primorsky krai in Russia. Russian Journal of Biological Invasions 9(4): 355–365. https://doi.org/10.1134/S2075111718040082

Mandelshtam MYu, Yakushkin EA, Kovalenko YaN, Petrov AV (2022) New Invasive *Hypothenemus* Westwood, 1834 (Coleoptera, Curculionidae: Scolytinae) species in the Caucasus and in the Southern Primorskii Territory, Russia. Entomological Review 102: 485–491. https://doi.org/10.1134/s0013873822040078

Mangili S, Schönenberger N, Frey D (2016) Ritrovamento di tre specie vegetali nuove per la Svizzera e di un taxon raro considerato regionalmente scomparso. Bolletino della Società Ticinese di Scienze Naturali 104: 29–36.

Marchioro M, Faccoli M, Dal Cortivo M, Branco M, Roques A, Garcia A, Ruzzier E (2022) New species and new records of exotic Scolytinae (Coleoptera, Curculionidae) in Europe. Biodiversity Data Journal 10: e93995. https://doi.org/10.3897/BDJ.10.e93995

Masutti L (1968) Notizie sulla distribuzione in Italia dell'*Hypothenemus eruditus* Westwood (Coleoptera, Scolytidae). Annali Museo Civico Storia Naturale Genova 77: 360–370.

Mayers CG, Harrington TC, Biedermann PHW (2022) Mycangia define the diverse ambrosia beetle-fungus symbioses. In: Schultz TR, Gawne R, Peregrine PN (Eds) The Convergent Evolution of Agriculture in Humans and Insects, The MIT Press, Cambridge, MA, 105–142. https://doi.org/10.7551/mitpress/13600.003.0013

Mifsud D, Knížek M (2009) The Bark Beetles (Coleoptera: Scolytidae) of the Maltese Islands (Central Mediterranean). Bulletin of the Entomological Society of Malta 2: 25–52.

Noblecourt T (2004) Note sur les Coléoptères Scolytidae : espèces rare sou peu communes en France. Le Coléoptériste 7(1): 33–36.

OFEV [Éd.] (2022) Espèces exotiques en Suisse. Aperçu des espèces exotiques et de leurs conséquences. 1re édition actualisée 2022. 1re parution 2006. Office fédéral de l'environnement, Berne. Connaissance de l'environnement no 2220, 62 pp.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JP, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for global biodiversity in the 21st century. Science 330: 1496–1501. https://doi.org/10.1126/science.1196624

Prospero S, Rigling D (2012) Invasion genetics of the chestnut blight fungus *Cryphonectria parasitica* in Switzerland. Phytopathology 102(1): 73–82. https://doi.org/10.1094/PHYTO-02-11-0055

Pureswaran DS, Meurisse N, Rassati D, Liebhold AM, Faccoli M (2022) Climate change and invasions by nonnative bark and ambrosia beetles. In: Gandhi K, Hofstetter R (Eds) Bark beetle management, ecology, and climate change. Academic Press, Cambridge, 438 pp. https://doi.org/10.1016/b978-0-12-822145-7.00002-7

Ragusa E (1924) Gli Ipidae della Sicilia. Bollettino Società Entomologica Italiana 56: 114–118.

Ribeiro Correia JP, Prospero S, Beenken L, Biedermann PHW, Blaser S, Chittaro Y, Frey D, Hölling D, Kaya SO, Knížek M, Mittelstrass J, Branco M, Ruffner B, Sanchez A, Brockerhoff EG (2023[in prep.]) Detection of Anisandrus maiche (Coleoptera: Curculionidae, Scolytinae) and its associated ambrosia fungus in Switzerland. bioRxiv. [Preprint] April 3, 2023. https://doi.org/10.1101/2023.03.30.534995

Roques A, Shi J, Auger-Rozenberg M-A, Ren L, Augustin S, Luo Y-q (2020) Are invasive patterns of non-native insects related to woody plants differing between Europe and China? Frontiers in Forests and Global Change 2: 91. https://doi.org/10.3389/ffgc.2019.00091

Ruzzier E, Bani L, Cavaletto G, Faccoli M, Rassati D (2022) *Anisandrus maiche* Kurentzov (Curculionidae: Scolytinae), an Asian species recently introduced and now widely established in Northern Italy. BioInvasions Records 11(3): 652–658. https://doi.org/10.3391/bir.2022.11.3.07

Ruzzier E, Ortis G, Vallotto D, Faccoli M, Martinez-Sañudo I, Marchioro M (2023) The first full host plant dataset of Curculionidae Scolytinae of the world: tribe Xyleborini LeConte, 1876. Scientific Data 10: 166. https://doi.org/10.1038/s41597-023-02083-5

Sanchez A, Chittaro Y, Bense U (2021) Redécouverte d'*Eustrophus dermestoides* (Fabricius, 1792) en Suisse (Coleoptera, Tetratomidae). Entomo Helvetica 14: 131–134.

Sanchez A, Chittaro Y, Germann C, Knížek M (2020) Annotated checklist of Scolytinae and Platypodinae (Coleoptera, Curculionidae) of Switzerland. Alpine Entomology 4: 81–97. https://doi.org/10.3897/alpento.4.50440

Sauvard D, Branco M, Lakatos F, Faccoli M, Kirkendall L (2010) Weevils and Bark Beetles (Coleoptera, Curculionoidea). Chapter 8.2. In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. BioRisk 4(1): 219–266. https://doi.org/10.3897/biorisk.4.64

Schönenberger N, Röthlisberger J, Carraro G (2014) La flora esotica del Cantone Ticino (Svizzera). Bollettino della Società Ticinese di Scienze Naturali 102: 13–30.

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, vanKleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communication 8(1): 14435. https://doi.org/10.1038/ncomms14435

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: What's what and the way forward. Trends in Ecology and Evolution 28: 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Smith SM, Beaver RA, Cognato AI (2020) A monograph of the Xyleborini (Coleoptera, Curculionidae, Scolytinae) of the Indochinese Peninsula (except Malaysia) and China. ZooKeys 983: 1–442. https://doi.org/10.3897/zookeys.983.52630

Turner CR, Beaver RA (2015) *Hypothenemus eruditus* Westwood and *Hypothenemus seriatus* (Eichhoff) (Curculionidae: Scolytinae: Cryphalini) in Britain. The Coleopterist 24(1): 12–15.

Tuncer C, Knížek M, Hulcr J (2017) Scolytinae in hazelnut orchards of Turkey: clarification of species and identification key (Coleoptera, Curculionidae). ZooKeys 710: 65–76. https://doi.org/10.3897/zookeys.710.15047

Urvois T, Auger-Rozenberg MA, Roques A, Rossi JP, Kerdelhue C (2021) Climate change impact on the potential geographical distribution of two invading *Xylosandrus* ambrosia beetles. Scientific Reports 11: 1339. https://doi.org/10.1038/s41598-020-80157-9

Vega FE, Infante F, Johnson AJ (2015) The genus *Hypothenemus*, with emphasis on *H. hampei*, the coffee berry borer. In: Vega FE, Hofstetter RW (Eds) Bark Beetles, Biology and Ecology of Native and Invasive Species (1st edn.), Elsevier, London, 427–494. https://doi.org/10.1016/B978-0-12-417156-5.00011-3

Wood SL (1977) Introduced and exported American Scolytidae (Coleoptera). Great Basin Naturalist 37: 67–74.

Wood SL, Bright DE (1992) A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic index (Vol. A & Vol. B). Great Basin Naturalist Memoirs 13: 1–1553.

Wood SL (2007) Bark and ambrosia beetles of South America (Coleoptera: Scolytidae). Monte L. Bean Science Museum. Provo, Utah, 900 pp.

Alpine Entomology 7 2023, 57–62 | DOI 10.3897/alpento.7.102534

Alpine Entomology

Laufkäfer und ihre Habitatpräferenzen entlang eines Höhentransekts von 2100 bis 2500 m ü. M. oberhalb der Alp Flix in den Schweizer Alpen (Coleoptera, Carabidae)

Ground beetles and their habitat preferences along a high altitude transect from 2100 to 2500 m a.s.l. in the Swiss Alps (Coleoptera, Carabidae)

Marie Lüdeke[1,2], Christoph Germann[3], Matthias Jentzsch[2]

1 *Technische Universität Dresden, Institut für Hydrobiologie, D-01217, Dresden, Germany*
2 *Hochschule für Technik und Wirtschaft Dresden, Fakultät Landbau/Umwelt/Chemie, D-01326, Dresden, Germany*
3 *Abteilung Biowissenschaften, Naturhistorisches Museum Basel, Augustinergasse 2, CH-4051, Basel, Switzerland*

https://zoobank.org/411587A3-145E-41D3-A436-867475EAF0C9

Corresponding authors: Marie Lüdeke (anna_marie.luedeke@mailbox.tu-dresden.de); Christoph Germann (christoph.germann@bs.ch)

Academic editor: Charles Huber ♦ **Received** 22 February 2023 ♦ **Accepted** 31 May 2023 ♦ **Published** 16 June 2023

Zusammenfassung

Während einer Saison im Jahr 2020 wurden in den östlichen Zentralalpen der Schweiz im Gebiet Sur, Alp Flix, bodenlebende Makroarthropoden mittels Barberfallen erfasst. Hauptziel war es, entlang eines ausgewählten Höhentransekts von 2100 bis 2500 m ü. M. die vorhandene Biodiversität zu erfassen. Entlang des Bergbaches Ava dallas Tigias wurden von Juni – November 2020 an sieben Standorten je drei Barberfallen aufgestellt und durchgehend betrieben. Vorliegend werden die Carabidae vorgestellt. Durch Berechnungen von Ähnlichkeitindices wurden deren Habitate innerhalb des untersuchten Höhentransekts abgegrenzt. Es konnten 393 Laufkäferindividuen aus 21 Arten erfasst und bestimmt werden. Sieben Arten wurden erstmals für die Alp Flix nachgewiesen. Davon sind die seltene *Amara nigricornis* und *Leistus montanus rhaeticus* besonders hervorzuheben. Aus den Berechnungen konnten drei Habitate der Laufkäfer im Transekt unterschieden werden: subalpines Grünerlengebüsch mit halbschattiger und mäßig feucht-frischer Ausprägung; alpines Habitat mit starker Krautschicht und frischer bis trockener Ausprägung und ein kurzrasiger hochalpiner Lebensraum mit xerothermer Ausprägung.

Abstract

During one season in the year 2020 terrestrian Arthropods were collected using barber traps in the eastern Central Alps in Switzerland in the area Sur, Alp Flix. The main goal was the monitoring of the biodiversity along a vertical transect from 2100 to 2500 m a.s.l. Along the rivulet Ava dallas Tigias at seven localities each three barber traps were kept open from June 2020 till November 2020. Here the caught Carabidae are presented and using similarity- and dominance indices, the respective habitats are differentiated from each other along the vertical transect. 393 Carabid beetles out of 21 species were found and determined. Seven species are recorded for the first time from Alp Flix. Among them the rarely found *Amara nigricornis* and *Leistus montanus rhaeticus*. Based on the calculations, three habitats could be differentiated: subalpine green alder bush habitat with half shaded and moderately humid characteristics; alpine habitat with dense herb cover and more or less humid characteristics, and a short grassy high alpine habitat with a xero-thermophilous characteristics.

Key Words

Swiss Alps, ecology, alpine habitats, Carabidae, dominance indices, similarity indices

Einleitung

Eine der vielfältigsten und artenreichsten Ordnungen im Tierreich stellen die Coleoptera dar. Trotz des hohen Wissenstands zur Ökologie und Verbreitung vieler Arten in Mitteleuropa scheint die Erforschung der Käferfauna gerade in schwer zugänglichen Lebensräumen wie dem Hochgebirge noch unzureichend (Germann et al. 2014). Dieses Wissen um das Vorkommen von Zönosen in verschiedensten Hochgebirgen wie den Schweizer Alpen ist aber entscheidend, um dieses empfindliche Ökosystem zu verstehen und deren Entwicklung verfolgen zu können. Um eine Vergleichsgrundlage zu schaffen, wurde im Jahre 2020 anlässlich des 20-jährigen Jubiläums der Stiftung ‹‹Schatzinsel Alp Flix›› im Gebiet Oberhalbstein (Graubünden, Schweiz) ein Projekt zur Erforschung der Biodiversität initiiert und durch das Naturhistorische Museum Basel betreut. Ziel des Projektes war die Erfassung der bodenlebenden Makroarthropoden in den noch unerforschten subalpinen und alpinen Höhenlagen sowie die Untersuchung ökologischer Aspekte wie der Biozönose (vgl. Hänggi et al. 2022). Für den Vergleich der Faunenähnlichkeit zweier oder mehrerer Standorte bedarf es eines einheitlichen Masses, um Ähnlichkeiten der Zönosen anhand von Zahlenwerten zu beschreiben. Eine Möglichkeit, die Gemeinsamkeiten und Unterschiede von Tierbeständen festzustellen, bietet die Ermittlung der Art- und Dominanzidentitäten. Im Allgemeinen weisen hohe Ähnlichkeitsindices große Übereinstimmungen der verglichenen Käferfaunen auf. Daraus lassen sich ähnliche ökologische Standortbedingungen ableiten, die zu einem Habitat zusammengefasst werden können (Zandler 2012). Als Vergleichsgruppe wurden die Carabidae herangezogen. Zum einen sind die Laufkäfer als Bioindikatoren gut etabliert und vergleichsweise einfach mit Barberfallen zu fangen (Thiele and Weiss 1976; Spang 1999). Zum anderen gibt es bereits einen sehr guten taxonomischen und ökologischen Wissensstand betreffend den jeweiligen Artansprüchen (Marggi 1992; Luka et al. 2009; Trautner 2017). In der hier vorliegenden Arbeit soll, basierend auf einer vom Naturhistorischen Museum Basel initiierten und begleiteten Bachelorarbeit der Hochschule für Technik und Wirtschaft Dresden (Lüdeke 2022), die Carabidenfauna der Alp Flix ab 2100 m ü. M. inventarisiert und deren Habitate mit Hilfe von Ähnlichkeitsindices abgegrenzt werden.

Material und Methoden

Das Untersuchungsgebiet liegt in den östlichen Zentralalpen im Gebiet ‹‹Sur – Alp Flix›› (Oberhalbstein, Graubünden, Schweiz) am Julierpass. Die Alp Flix ist auf einem Hochplateau auf rund 1950 m ü. M. gelegen und befindet sich mitten im größten Naturpark der Schweiz, dem Parc Ela. Der in dieser Arbeit untersuchte Höhentransekt wurde so gewählt, dass er das Gebiet oberhalb der Alp abdeckte. Er schließt sich in östliche Richtung ab 2067 m ü. M. oberhalb an und führt entlang des Bergbaches Ava dallas Tigias. Er endet auf 2498 m ü. M. unterhalb der Gipfelkette zwischen Piz d´Err (3378 m ü. M.) und Piz d´Agnel (3205 m ü. M.). Unterhalb und auf Höhe der Alp Flix fanden bereits mehrfach Untersuchungen statt (Wildermuth and Knapp 1998; Hänggi and Müller 2001; Burckhardt et al. 2007; Müller and Briner 2007; De Rond 2007; Germann et al. 2022). Da die Erfassung der Biodiversität im Vordergrund stand, wurde versucht, möglichst alle Habitate im untersuchten Transekt zu erfassen. Die Abgrenzung der Habitate erfolgte durch Ermittlung der verschiedenen pflanzensoziologischen Lebensraumtypen nach Delarze et al. (2015). Eine eineindeutige Zuordnung der Lebensraumtypen war nicht möglich. Eine kurze Beschreibung der Standorte mit dem jeweiligen Lebensraumtyp ist Table 1 zu entnehmen. Die vollständige Liste aller Funde nach Fallen und Datum ist als Suppl. material 1 hinterlegt.

Im Zeitraum vom 20.06.2020 bis 11.11.2020 wurden mittels Barberfallen eine volle Vegetationsperiode lang gefangen. Die Leerungen erfolgten in zweiwöchigem Rhythmus. Im Oktober wurde wegen anhaltender Schneefälle keine Leerung vorgenommen. Pro Standort (Table 1) wurden drei Barberfallen gesetzt. Eine Falle bestand aus einem weißen Plastikbecher (7 cm Durchmesser und Höhe), welcher ebenerdig in den Boden eingelassen wurde, einem Drahtgeflecht und einem transparenten Plexiglasdach. Als Fanglösung kam eine vierprozentige Formalinlösung mit Detergenzien zum Einsatz. Der Fang wurde in 70%igem Ethanol konserviert. Anschließend wurden die Tiere präpariert. Dafür wurden die Tiere zunächst mit Kirschlorbeerblättern (*Prunus laurocerasus*), nach Wechsler et al. (2001), aufgeweicht. Genitalpräparate wurden von *Bembidion glaciale* (Heer, 1837), *Pterostichus unctulatus* (Duftschmid, 1812), *Trichotichnus laevicollis* (Duftschmid, 1812) sowie allen Arten der Gattung *Amara* angefertigt. Die Carabidae wurden mittels „Die

Table 1. Charakterisierung der Fangstandorte entlang des Höhentransekts oberhalb der Alp Flix.

Standort	Lebensraumtyp nach Delarze et al. (2016)	m ü. M.	Exp.	Neigung
STO 1	Grünerlengebüsch (Alnenion viridis)	2067	W/NW	mässig
STO 2	feuchter Krautsaum höherer Lagen (Petasition officinalis)	2146	W	mässig
STO 3	mesophile subalpine Zwergstrauchheide (Rhododendro-Vaccinion)	2241	WSW	mässig
STO 4	mesophile subalpine Zwergstrauchheide (Rhododendro-Vaccinion)	2310	WSW	steil
STO 5	Krummseggenrasen (Caricion curvulae)/ Windheide (Loiseleurio-Vaccinion)	2375	WSW	flach/stufig
STO 6	Krummseggenrasen (Caricion curvulae) mit Nacktriedrasen (Elynion)	2432	–	flach
STO 7	trockenwarme Silikatschuttflur (Galeopsion segetum)	2498	WNW	steil

Käfer Mitteleuropas“ von Freude et al. (2004) bestimmt und die Belegtiere sind am Naturhistorischen Museum Basel hinterlegt. Die Verbreitung der Laufkäferarten der Schweiz wurden mittels des Kartenservers des Info Fauna – Schweizerisches Zentrum für die Kartographie der Fauna (Info Fauna 2021) überprüft. Die Nomenklatur richtet sich nach Freude et al. (2004). Als Referenz der bereits im Gebiet der Alp Flix angetroffenen Arten diente eine Artenliste, die im Rahmen des „GEO-Tages 2000“ zur Erfassung der Biodiversität auf der Alp Flix in der Zeitschrift GEO (2000) erschien und den Beiträgen von Hänggi and Müller (2001).

Ähnlichkeitsindices

Als Grundannahme wird jeder Standort (Table 1) als Habitat mit eigenem Artinventar betrachtet und mit allen anderen Standorten im Höhentransekt verglichen. Für den Vergleich von Faunenähnlichkeiten wurde die Artidentität nach Sørensen (1948) und Jaccard (1901, 1902) sowie die Dominanzidentität nach Renkonen (1938) berechnet. Ebenfalls wurde der Wainstein-Index (Mühlenberg 1993) ermittelt. Die Einordnung der Werte in niedrige oder hohe Übereinstimmungen der Käferfaunen richtet sich nach Schuster (2003). Durch die Multiplikation zweier Prozentwerte ist der Wainstein-Index deutlich niedriger als der Dominanzidentitätswert oder des Gemeinschaftskoeffizienten und muss separat betrachtet werden.

Resultate

Während der Fangsaison 2020 wurden oberhalb der Alp Flix insgesamt 393 Carabidae (Table 2) gefangen. Diese können 21 Arten aus 9 Gattungen zugeordnet werden. Die Art *Pterostichus multipunctatus* war mit insgesamt 108 Individuen am häufigsten in den Fallen gefangen. Am seltensten vertreten waren die Arten *Amara equestris*, *Amara lunicollis*, *Amara nigricornis* (Fig. 1), *Harpalus solitaris* und *Leistus montanus rhaeticus* (Fig. 2). Im Fangzeitraum 2020 oberhalb der Alp Flix wurden sie jeweils in nur einem Individuum nachgewiesen. Von den insgesamt 21 Arten konnten 7 Arten (Table 2) neu für die Alp Flix nachgewiesen werden. Es handelt sich um die Arten *Amara lunicollis*, *Amara nigricornis*, *Calathus micropterus*, *Cymindis vaporariorum*, *Leistus nitidus*, *Leistus montanus rhaeticus* und *Trichotichnus laevicollis*. Zwei der neu gefundenen Arten, *Amara nigricornis* (Fig. 1) und *Leistus montanus rhaeticus* (Fig. 2) werden in der Schweiz als sehr selten eingestuft.

Der Vergleich der Laufkäferfaunen aller Standorte ergibt, dass manche Habitate (Tables 1, 3) eine hohe Übereinstimmung zeigen, wie die Standorte 2 und 4, die Standort 2 und 5, die Standort 3 und 4 oder die Standorte 6 und 7. Andere Standorte zeigen hingegeben kaum oder überhaupt keine Übereinstimmung der Laufkäferfaunen, beispielsweise die Standorte 1 und 7, die Standorte 3 und 7 oder die Standorte 4 und 6 und die Standorte 4 und 7.

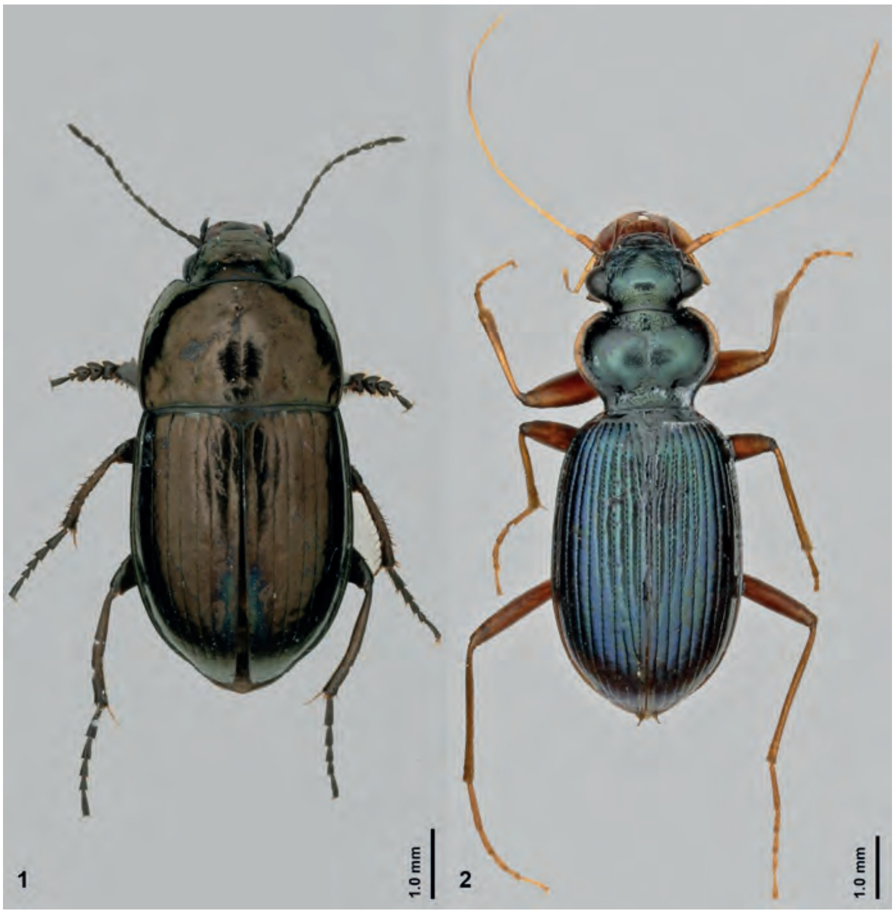
Diskussion

Aus der Berechnung der Ähnlichkeitsindices der Laufkäferfaunen können 3 Gruppen von Habitaten im untersuchten Höhentransekt unterschieden werden:

1. **Subalpines Habitat** des Standortes 1: halbschattiges Grünerlengebüsch mit mäßig feucht-frischer Ausprägung und hoher Deckung der Strauchschicht und Krautschicht auf 2067 m ü. M.
2. **Alpines Habitat** der Standorte 2, 3 und 4: ohne Strauchschicht aber stark ausgeprägter Krautschicht, mäßig feucht-frische bis trockene Standorte, die sonnenexponiert sind, dabei aber halbschattige Plätze aufweisen, zwischen 2146 m ü. M. bis 2375 m ü. M.
3. **Hochalpines Habitat** der Standorte 5, 6 und 7: ohne Strauchschicht und kurzrasiger oder schwacher Krautschicht xerothermer Standorte durch volle Sonnenexposition über 2432 m ü. M.

Diese Einteilung lässt sich weitestgehend anhand der Ökologie der einzelnen Laufkäferarten (Marggi 1992; Freude et al. 2004; Trautner 2017) erklären: *Leistus nitidus* kommt im subalpinen Habitat 1 (Table 2) vor. Diese Art ist montan bis alpin in den Alpen verbreitet, zeigt allerdings eine Präferenz für die subalpine Stufe zwischen 1000–2500 m a.s.l. (Marggi 1992). Die Arten *Notiophilus aquaticus* und *Calathus micropterus* (Table 2) fanden sich schwerpunktmäßig im alpinen Habitat 2. Beide Arten sind ausschließlich montan bis alpin verbreitet (Marggi 1992). Allerdings kann *Notiophilus aquaticus* vereinzelt bis 3000 m ü. M. aufsteigen. *N. aquaticus* und *C. micropterus* finden im alpinen Habitat 2 ideale Lebensbedingungen (Freude et al. 2004; Marggi 1992), könnten aber bis in das hochalpine Habitat 3 aufsteigen, was sie hier nicht taten. Daher wird die Vermutung von Hänggi et al. (2022), dass der Einfluss der Höhenlage durch die Ökologie der einzelnen Lebensraumtypen in Untersuchungstransekt oberhalb der Alp Flix überprägt sein könnte, geteilt. Dahingegen kommt *Amara erratica* vorrangig im hochalpinen Habitat 3 der Standorte 6 und 7 vor. *A. erratica* steigt subalpin bis alpin in den Alpen auf, kann aber bis 3000 m ü. M. vorkommen (Marggi 1992) und wird daher als Vertreter des hochalpinen Habitats betrachtet.

Von den insgesamt 21 festgestellten Laufkäferarten im Untersuchungszeitraum konnten sieben Arten (33,33%) neu für die Alp Flix nachgewiesen werden. Dieser hohe Anteil zeigt auf, dass die Kenntnisse über die Carabidaenfauna in den Alpen und besonders der Alp Flix noch bei Weitem nicht vollständig sind. Zum Vergleich konnten in der Untersuchung 2000 zum „GEO-Tag der Artenvielfalt“ (Hänggi and Müller 2001) insgesamt 33 Laufkäferarten



Figures 1, 2. 1. *Amara nigricornis* Alp Flix, 2241 m ü. M. **2.** *Leistus montanus rhaeticus* Alp Flix, 2498 m ü. M. Beide Arten werden in der Schweiz nur sehr selten gefunden (Fotos: C. Germann).

bestimmt werden. Dass oberhalb der Alp Flix 2020 12 Arten weniger als 2000 gefunden wurden, scheint eher an der Methodik zu liegen. Im Jahr 2000 wurden auf der Alp Flix gezielte Handfänge von mehreren Experten vorgenommen. In weiteren Arbeiten am Albulapass aus dem Jahr 2008 (Schmid and Müller 2010) und auf dem Furkapass aus dem Jahr 2012 (Germann et al. 2014) wurden in der subalpinen bis alpinen Stufe ebenfalls Artaufnahmen vorgenommen. Abweichend zur hier durchgeführten Arbeit wurde methodisch mittels Handfang, Kescherfang, Klopfschirm, Nachtfang oder Käfersieb gefangen und andere Untersuchungszeiträume gewählt. Die nachgewiesene Artenanzahl am Furkapass ist mit der Zahl der Alp Flix 2020 erfassten Arten vergleichbar. Auf der Alp Flix 2020 wurde nur eine Art mehr nachgewiesen. Ebenfalls vergleichbar ist die Artenanzahl, welche in der Untersuchung 2008 vom Albulapass stammt. Hier wurden drei Arten weniger als auf der Alp Flix 2020 determiniert. Die gefangene Artenanzahl im untersuchten Transekt 2020 scheint für diese Höhenlagen somit durchaus repräsentativ zu sein.

Die im untersuchten Höhentransekt festgestellten sechs pflanzensoziologischen Lebensraumtypen (Table 1) konnten durch die berechneten Ähnlichkeitsindices der Carabidae nicht abgegrenzt werden. Es scheint Unterschiede in der Abgrenzung von Habitaten zwischen der Flora und der Laufkäferfauna zu geben. Die Mehrzahl an pflanzensoziologischen Lebensraumtypen könnte durch das Mosaik unterschiedlicher Böden rund um die Alp Flix (Wildermuth and Knapp 1998) erklärt werden. Interessant wäre eine weiterführende Arbeit im Gebiet, in der geklärt werden könnte, inwieweit Lebensraumtypen mittels Ähnlichkeitsindices der vorhandenen Pflanzenarten abzugrenzen sind.

Das auf der Alp Flix begonnene Monitoring der Biodiversität sollte weiter vorangetrieben werden. Hier wurde eine gute Ausgangslage geschaffen, um die zukünftige Entwicklung der Biodiversität in den Schweizer Alpen zu verfolgen. Die Wissenslücken zur Artenvielfalt müssen aber kontinuierlich weiter geschlossen werden, um den empfindlichen Lebensraum „Hochgebirge“ besser zu verstehen. Nur so lässt sich dieses vielschichtige Ökosystem schützen und auch für zukünftige Generationen bewahren.

Danksagung

Die vorliegende Arbeit wurde an der Fakultät Landbau/ Umwelt/ Chemie der Hochschule für Technik und Wirtschaft Dresden unter Betreuung von Prof. Dr. Matthias Jentzsch geschrieben.

Table 2. In der Fangsaison 2020 nachgewiesene Laufkäferarten der Alp Flix mit Angabe der pro Standort gefangenen Individuen- und Artenzahl. Die Anordnung entspricht ihrer Verteilung über die Höhenstufen im Transekt. Die Gefährdung richtet sich nach Luka et al. (2009); n = nicht gefährdet; R = sehr seltene Art.

Standort		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**Total pro Art**	**Gefährdung**
Art	**neu für Alp Flix**									
***Leistus nitidus* (Duftschmid, 1812)**	**x**	7						1	**8**	**n**
***Trichotichnus laevicollis* (Duftschmid, 1812)**	**x**	27	1						**28**	**n**
***Pterostichus unctulatus* (Duftschmid, 1812)**		3		13					**16**	**n**
***Amara nigricornis* (Thomson, 1857)**	**x**			1					**1**	**R**
***Amara equestris* (Duftschmid, 1812)**				1					**1**	**n**
***Harpalus solitaris* (Dejean, 1829)**				1					**1**	**n**
***Carabus violaceus neesi* (Linnaeus, 1758)**			1	2				1	**4**	**n**
***Carabus sylvestris* (Panzer, 1793)**				2				2	**4**	**n**
***Notiophilus aquaticus* (Linnaeus, 1758)**			1	4	3				**8**	**n**
***Calathus micropterus* (Duftschmid, 1812)**	**x**	5	1	9	6	2			**23**	**n**
***Calathus melanocephalus* (Linnaeus, 1758)**			7		6	1	4		**18**	**n**
***Amara lunicollis* (Schiødte, 1837)**	**x**				1				**1**	**n**
***Pterostichus multipunctatus* (Dejean, 1828)**			1	44	45	10	6	2	**108**	**n**
***Amara praetermissa* (C. R. Sahlberg, 1827)**				1			5		**6**	**n**
***Oreonebria castanea* (Bonelli, 1810)**				1		1	9	6	**17**	**n**
***Pterostichus jurinei* (Panzer, 1803)**		6	1	19	5	18	31	1	**81**	**n**
***Amara erratica* (Duftschmid, 1812)**			1			8	48	3	**60**	**n**
***Cymindis vaporariorum* (Linnaeus, 1758)**	**x**						1	1	**2**	**n**
***Bembidion glaciale* (Heer, 1837)**							1	1	**2**	**n**
***Amara quenseli* (Schönherr, 1806)**							2	1	**3**	**n**
***Leistus montanus rhaeticus* (Herr, 1837)**	**x**							1	**1**	**R**
Individuenanzahl pro Standort		**48**	**14**	**98**	**66**	**40**	**107**	**20**		
Artenanzahl pro Standort		**5**	**8**	**12**	**6**	**6**	**9**	**11**		

Table 3. Zusammenfassung der Ergebnisse der Artidentität nach Sørensen (1948) und Jaccard (1901, 1902) der Dominanzidentität nach Renkonen (1938) sowie des Wainstein-Index (Mühlenberg 1993); die Interpretationen der Übereinstimmungen der Faunenähnlichkeit/ -unähnlichkeit zwischen den Standorten folgen Schuster (2003).

Überein-stimmung	**Standorte der Faunenähnlichkeiten/ -unähnlichkeiten nach**			
	Sørensen´s “quotient of similarity” I_A	**Jaccard´s Gemeinschaftskoeffizient I_A**	**Renkonen´s Dominanzidentitätswert I_D**	**Wainstein-Index KW**
hoch (≥ 60%) **(Wainstien-Index [≥ 15%])**	2 und 4 2 und 5 4 und 5 5 und 6 6 und 7	–	3 und 4	2 und 4 2 und 5 3 und 4 4 und 5 5 und 6 6 und 7
gering (≤ 20%) **Wainstein-Index (≤ 10%)**	1 und 6	1 und 6 1 und 7 4 und 7	1 und 4 1 und 5 1 und 6 1 und 7 4 und 7 4 und 6	1 und 2 1 und 3 2 und 3 2 und 6 2 und 7 3 und 6 3 und 7 5 und 7
sehr gering (<5%)	–	–	–	1 und 4 1 und 5 1 und 6 1 und 7 4 und 6 4 und 7

Unser Dank gilt der Abteilung Biowissenschaften des Naturhistorischen Museums Basel für die Unterstützung und Ermöglichung des Projektes. Besonderer Dank geht an Herrn Dr. Ambros Hänggi für die Unterstützung und Betreuung und an Herrn Dr. h.c. Werner Marggi für seine Überprüfung der Artbestimmungen. Ebenso gilt unser Dank der Stiftung Schatzinsel Alp Flix. Den Reviewern danken wir herzlich für Ihre hilfreichen Anmerkungen und Korrekturen.

Referenzen

Burckhardt D, Mühlethaler R, Lauterer P, Malenovsky I, Kunz G (2007) Die Blattflöhe und Zikaden der Alp Flix (Insecta, Hemiptera: Psylloidea und Auchenorrhyncha). Jahresbericht der Naturforschenden Gesellschaft Graubünden 114: 191–197.

Delarze R, Gonseth Y, Eggenberg S, Vust M (2015) Lebensräume der Schweiz, 3. Auflage. Bern, Ott-Verlag, 456 pp.

De Rond J (2007) Wasp and bee expedition on the Alp Flix. Jahresbericht der Naturforschenden Gesellschaft Graubünden 114: 107–112.

Freude H, Harde KW, Lohse GA, Klausnitzer B (2004) Adephaga: Carabidae (Laufkäfer). 2. Auflage. In: Müller-Motzfeld G (Hrsg.) Die Käfer Mitteleuropas. Band 2 Heidelberg: Spektrum Akademischer Verlag, 521 pp.

Germann C, Geiser M, Luka H, Sprecher E, Schatz I (2014) Käfer (Coleoptera) im Gebiet des Furkapasses, Kantone Uri und Wallis. Entomo Helvetica 8: 29–37.

Germann C, Borer M, Burckhardt D, Charran M, Coray A, Frick H, Klopfstein S, Marques DA, Rendón-Mera D, Spasojevic T, Urfer K, Viertler A, Zürcher I, Hänggi A (2022) Sammel-Exkursion auf die Alp Flix – ein Teambildungsprozess mit Folgen. Jahresberichte Naturforschende Gesellschaft Graubünden 122: 123–134.

GEO (2000) GEO-Tag der Artenvielfalt 2000. Alp Flix – das Ergebnis. Artenliste als Sonderheft zur Auflage in der Schweiz. GEO 9.

Hänggi A, Müller JP (2001) Eine 24-Stunden Aktion zur Erfassung der Biodiversität aus der Alp Flix (Graubünden): Methoden und Resultate. Jahresbericht der Naturforschenden Gesellschaft Graubünden 110: 5–36.

Hänggi A, Germann C, Lüdeke M, Borer M (2022) Bodenlebende Makroarthropoden oberhalb der Alp Flix – Unterschiede zu den Beständen der Alp Flix. Jahresbericht der Naturforschenden Gesellschaft Graubünden 122: 75–85.

Info Fauna (2021) Verbreitungskarten. Schweizerisches Zentrum für Kartographie der Fauna. CSCF/ SZKF. [online] https://lepus.unine.ch/carto/ [Stand: 04.08.2021]

Jaccard P (1901) Étude comparative de la distribution florale dans une portion des Alpes et du Jura. Bulletin de la Société Vaudoise des Sciences Naturelles 37: 547–579.

Jaccard P (1902) Lois de distribution florale dans la zone alpine. Bulletin de la Société Vaudoise des Sciences Naturelles 38: 69–130.

Luka H, Marggi W, Huber C, Nagel P (2009) Coleoptera, Carabidae Ecology-Atlas. In: Centre suisse de cartographie de la faune (CSCF/SZKF) und Schweizerische Entomologische Gesellschaft (SEG/SES) (Hrsg.) Fauna Helvetica 24, CSCF & SEG Neuchâtel, 677 pp.

Lüdeke M (1922) Art- und Dominanzidentitäten von Laufkäfervorkommen eintlang eines ausgewählten Höhentransektes in den Schweizer Hochalpen. Hochschule für Technik und Wirtschaft Dresden. Fakultät Landbau/Umwelt/Chemie. Dresden: Bachelorarbeit zur Erlangung des akademischen Grades Bachelor of Science.

Marggi W (1992) Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz (Cicindelidae & Carabidae) Coleoptera unter besondere Berücksichtigung der „Roten Liste“. Documentae Faunistica Helvetiae 12/13, Teil 1 /2. – Neuchâtel. 477 pp. [und 243 S.]

Mühlenberg M (1993) Freilandökologie – UTB für Wissenschaft. Uni-Taschenbücher.

Müller J-P, Briner T (2007) Schatzinsel Alp Flix – Übersicht über die Forschung in den Jahren 2000 bis 2007. Jahresbericht der Naturforschenden Gesellschaft Graubünden 114: 59–63.

Renkonen O (1938) Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. Societas zoologica-botanica Fennica Vanamo 6(1): 1–231.

Schmid M, Müller JP (2010) Der GEO-Tag der Artenvielfalt 2008 am Albulapass Eine 24-Stunden-Aktion zur Erfassung der Biodiversität: Methoden und Resultate. Jahresbericht der Naturforschenden Gesellschaft Graubünden 116: 5–58.

Schuster R (2003) Faunistische und ökologische Untersuchungen an moosbewohnenden Tardigraden. Mathematisch- Naturwissenschaftliche Fakultät der Heinrich-Heine-Universität Düsseldorf. Düsseldorf: Inaugural-Dissertation zur Erlangung des Doktorgrades.

Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. Kongelige Danske videnskabernes selskab 5(4): 1–34.

Spang WD (1999) Laufkäfer als Indikatoren hydrologischer Rahmenbedingungen in der Oberrheinaue. Angewandte Carabidologie Supplementum 1: 103–114.

Thiele HU, Weiss HE (1976) Die Carabiden eines Auwaldgebietes als Bioindikatoren für anthropogen bedingte Änderungen des Mikroklimas. Schriftenreihe Vegetationskunde 10: 359–374.

Trautner J (2017) Die Laufkäfer Baden-Württembergs. 2 Bände. Stuttgart, Verlag Eugen Ulmer, 848 pp.

Wechsler K, Fiebig J, Henche A, Plackinger U, Rauer-Gömann M, Scheidt H (2001) Über das Weichen trockengefallener Alkohol- und Formalinpräparate, Herbarblätter und Tapagewebe. Der Präparator 47(1): 15–31.

Wildermuth H, Knapp E (1998) Die Libellen der Alp Flix (GR); ein Beitrag zur Odonatenfauna an der Waldgrenze. Mitteilung der entomologischen Gesellschaft Basel 48(1): 2–24.

Zandler K (2012) Der Einfluss von Restwasser auf das Makrozoobenthos des Gampadelsbaches. Universität für Bodenkultur Wien. Department für Wasser-Atmosphäre-Umwelt. Institut für Hydrobiologie und Gewässermanagement. Wien: Diplomarbeit zur Erlangung des akademischen Grades Diplomingenieur.

Supplementary material 1

Urtabelle Feldaufnahmen

Authors: Marie Lüdeke
Data type: full samples list (excel document)
Explanation note: Data of all Carabidae species and specimens from all localities is included.

Link: https://doi.org/10.3897/alpento.7.102534.suppl1

Alpine Entomology 7 2023, 63–68 | DOI 10.3897/alpento.7.103164

Prey handling and feeding habits of the snail predator *Licinus depressus* (Coleoptera, Carabidae)

Bruno Baur[1], José D. Gilgado[2], Armin Coray[3]

1 *Department of Environmental Sciences, University of Basel, CH-4056 Basel, Switzerland*
2 *Grupo de Investigación de Biología del Suelo y de los Ecosistemas Subterráneos, Departamento de Ciencias de la Vida, Facultad de Ciencias, Universidad de Alcalá, Alcalá de Henares, E-28805 Madrid, Spain*
3 *Natural History Museum, Augustinergasse 2, CH-4051 Basel, Switzerland*

https://zoobank.org/DB686EFF-7D14-4077-92DF-0F62C0C5675E

Corresponding author: Bruno Baur (bruno.baur@unibas.ch)

Academic editor: Thibault Lachat ♦ **Received** 7 March 2023 ♦ **Accepted** 23 June 2023 ♦ **Published** 4 July 2023

Abstract

Carabid beetles of the tribe Licinini use their asymmetric mandibles to open the shells of land snails. Prey handling of large snails has been described in a few Licinini species. We observed for the first time how a male of *Licinus depressus* (Paykull, 1790) opens the shells of small prey snails (*Chondrina arcadica* (Reinhardt, 1881)) and eats their soft bodies. The beetle holds the conical snail shell with its forelegs and breaks the wall of the right-hand coiled shell. In doing so, the beetle rotates the shell counter-clockwise opening it stepwise along the dorsal part of the whorls towards the apex. After some bites, the beetle interrupts the opening process and begins to feed on the snail's soft tissue. Then the beetle continues to break up the shell, shortly after which there is another feeding phase. The alternating sequence of shell breaking and feeding ends after 2 to 2.5 whorls when the beetle can no longer hold the prey's remaining intact shell. We compare this previously unknown way of prey handling with the reported predatory behaviour in large snails by other Licinini species. Our observations confirm the high plasticity of predatory behaviour in Licinini beetles.

Key Words

Insect, feeding behaviour, asymmetrical mandibles, shell coiling, gastropod, predator-prey interaction

Introduction

Asymmetric morphology and function have been described in several groups of insects (Palmer 1996). Carabid beetles of the tribe Licinini have asymmetric mandibles (Forsythe 1983; Ball 1992). Their mouthparts are adapted to a specialized diet, mainly land snails. The mandibles crush the prey's shell to reach the soft tissues inside (Erwin et al. 2015; Hayashi and Sugiura 2021). However, the Licinini beetles' feeding behaviour has only been studied in a few species. Adult individuals of *Badister pictus* Bates, 1873 begin their attacks by breaking the outer lip of the prey snail's dextral (right-handed coiled) shell, which lies on the ground (Hayashi and Sugiura 2021). The left and the right mandible are always placed against the external and internal shell wall, respectively. When the outer lip of a shell is broken by biting, the beetle breaks open the shell further along the dorsal part of the whorls towards the apex (Hayashi and Sugiura 2021). During the whole process the beetle fixes the shell with its forelegs and moves around the prey snail. A very similar cracking of snail shells has been described in three *Licinus* species (*L. cassideus* (Fabricius, 1792), *L. hoffmannseggi* (Panzer, 1797), *L. italicus* Puel, 1925; Brandmayr and Zetto Brandmayr (1986)). Through repeated bites, the beetles open the first whorl of the shell and – in most cases – a part of the second whorl (420° and more; figs 2, 3 in Brandmayr and Zetto Brandmayr (1986)). Breaking the shell wall takes four or more hours. The actual feeding begins after the shell wall has broken through at least a whole whorl. Depending on the size of the snail, it takes 12 hours or more to consume the prey's soft tissue (Brandmayr and Zetto Brandmayr 1986). However, the soft tissue of the inner whorls is never consumed. In the cases described, the prey snail was at least half the size, and often significantly larger, than the predatory beetle (Brandmayr and Zetto Brandmayr 1986; Hayashi and Sugiura 2021).

During field work on the population dynamics of land snails in the grassland Great Alvar on the Baltic island of Öland, Sweden, we found a male of *Licinus depressus* (Paykull, 1790) feeding on a small snail under a flat piece of limestone. The prey was a *Chondrina arcadica* (Reinhardt, 1881) (formerly *Chondrina clienta*), a snail with a cylindro-conical shell that has about seven moderately convex whorls and is 5–6 mm high in fully-grown individuals (Fig. 1). Under the same piece of stone we found several shells of *C. arcadica* showing typical traces of beetle predation. We captured the beetle in order to investigate its shell-breaking and feeding behaviour in the laboratory under near-natural conditions.

Licinus depressus is considered an obligate snail predator, at least as a larva (Lindroth 1949; Kinnunen 1996). However, its predatory behaviour has never been documented. Here we show how *L. depressus* opens the shells of small prey snails and eats their soft bodies. We compare this previously unknown way of prey handling with the reported predatory behaviour in large snails by other species of the tribe Licinini.

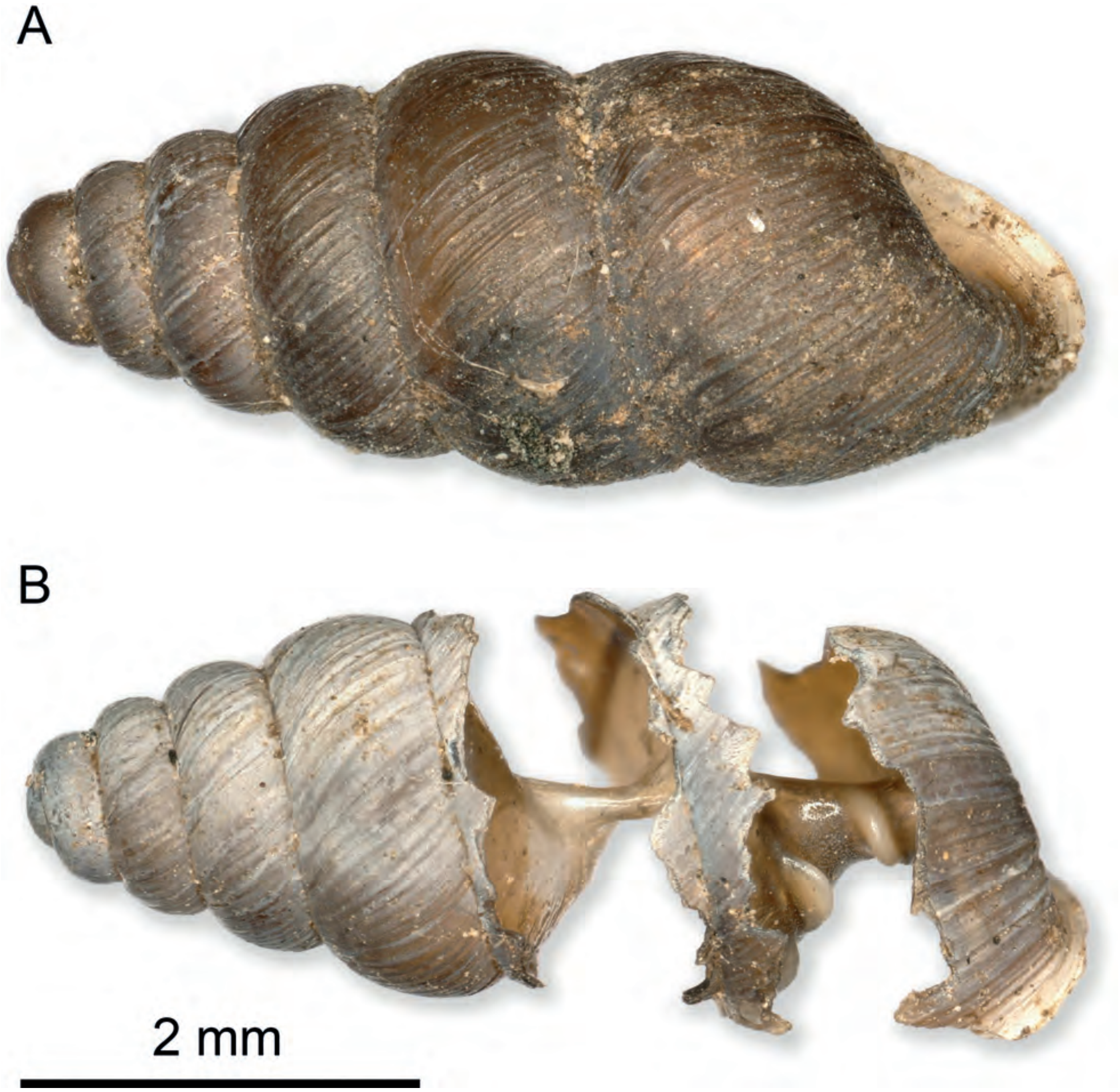


Figure 1. Intact shell of *Chondrina arcadica* (**A**), and shell opened by *Licinus depressus* (**B**). The bite marks of the mandibles are clearly visible. Photo: José D. Gilgado.

Material and method

The xerophilous *Licinus depressus* (body length 9.5–11.8 mm) occurs in Central and Eastern Europe, in Southern Scandinavia, on the British Islands, and in Russia (GBIF 2023). In Switzerland, the xerophilous species has been reported mainly in the Jura mountains and in valleys of the Alps (cantons of Valais and Grison; Info fauna 2023). Individuals of *L. depressus* are found scattered in calcareous areas with dry, sandy or gravelly soils at somewhat shaded sites in grasslands, on overgrown dunes, and in dry forests (Lindroth 1986).

We captured a male of *L. depressus* feeding on a snail under a piece of limestone at the foot of a stone pile in the grassland Great Alvar (56.61565°N, 16.49963°E) on the Baltic island of Öland, Sweden, on 8 October 1995. *Licinus depressus* has been found previously in the Great Alvar on Öland (Lundberg 1983). The beetle was kept in a transparent plastic box (14 × 10 × 7 cm in size) containing a flat piece of limestone. The bottom of the container was covered with moistened paper towel. We collected adult *C. arcadica* as prey from the beetle's place of origin. *Chondrina arcadica* is abundant on rock habitats (limestone pavements, stone walls, piles of stones) in the Great Alvar (Baur 1988; Baur and Baur 1995). We offered the beetle a prey snail on each of four consecutive days. In each case, the active snail was placed on the moistened stone. We observed the beetle's prey handling and feeding under dimmed light conditions.

We photographed the shell of both an intact and a cracked shell of *C. arcadica* using a digital microscope Keyence VHX-6000 (Keyence Corporation, Osaka, Japan). Based on photographs, A. Coray made a drawing of the typical prey handling of *L. depressus*. The specimen of *L. depressus* examined has been deposited in the Natural History Museum of Basel, Switzerland.

Results

Within a few minutes, the *L. depressus* male found the prey snail. The beetle grabbed the snail with its forelegs while maintaining a stable position with its middle and hind legs (Fig. 2). The snail is held at the first and second whorl, with the apex of the shell pointing towards the back of the beetle. After breaking the outer lip of the dextral (right-hand coiled) shell, the beetle rotated the conical shell 20–30 degrees counter-clockwise and bit again, opening the shell stepwise along the dorsal part of the whorls towards the apex. The cracking of the shell was clearly audible. After six to eight bites (approximately 120 degrees of a whorl), the beetle interrupted the opening process and began to pull the snail's soft tissue out of the opened shell (Fig. 3). While feeding, the beetle continued to hold the shell with its forelegs and did not change its position. Then the beetle continued to break up the shell, shortly after which there was another feeding phase. The alternating sequence of shell breaking and feeding ended after 2 to 2.5 whorls (out of a total of 6–7 whorls) when the beetle could no longer hold the remaining unbroken shell of the prey (Fig. 1). In this way the beetle was able to consume about two thirds of the snail's soft body. In the four observed cases, prey handling and feeding was rather rapid with a total duration of 2.5 to 4 minutes.

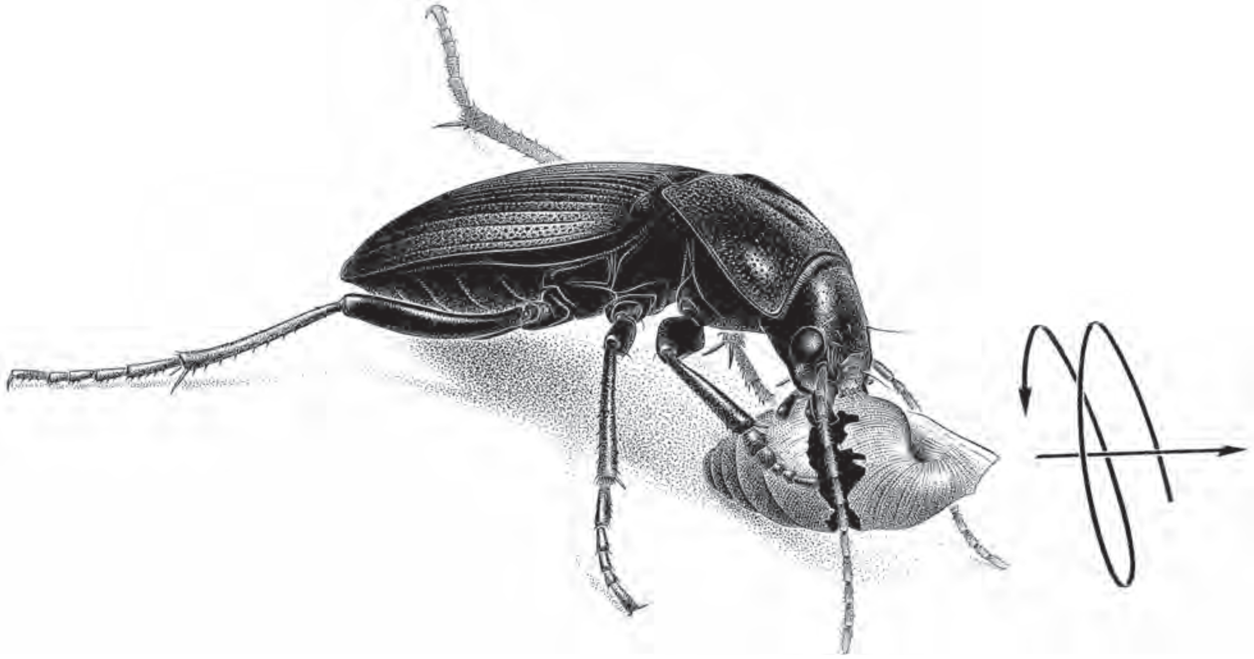


Figure 2. The predatory beetle *Licinus depressus* holds onto a prey snail (*Chondrina arcadica*) with its forelegs and breaks through the shell wall with its asymmetrical mandibles. Drawing: Armin Coray.

Figure 3. The predatory beetle *Licinus depressus* interrupts the opening process of the shell and begins to feed on the soft tissue of the prey snail. Photo: Bruno Baur.

Discussion

The handling and feeding behaviour described here differs significantly from previous descriptions of this behaviour in other Licinini species. In the reported cases, the prey snail was, in relation to the size of the predatory beetle, significantly larger, often exceeding the predator size (Brandmayr and Zetto Brandmayr 1986; Hayashi and Sugiura 2021). Any holding of the prey with the forelegs was therefore not possible. Large prey snails are held on the ground while the predatory beetle moves around the shell, gradually opening it. In all detailed descriptions of shell crushing, the beetle only began to feed after finishing the opening process, which itself lasted 12 and more hours (Brandmayr and Zetto Brandmayr 1986; Hayashi and Sugiura 2021). In contrast, *L. depressus* held the prey snail with its forelegs during both shell breaking and feeding, alternated between shell breaking and feeding several times, and prey handling and feeding lasted only a few minutes. On the other hand, what is common to both forms of prey handling is that a considerable part of the snail's soft tissue (approximately one third) is not eaten. Possible explanations for this are that the inner whorls of the shell are too narrow to open them with the mandibles, or that the further energy intake from the additional food is low in relation to the handling time. In addition, in the case of *L. depressus*, the beetle is no longer able to hold the partially opened shell with its forelegs.

It is interesting to compare the food intake of the two forms of prey handling. Shell length-biomass relationships are a reliable method to estimate the dry weight of gastropod soft bodies (Calow 1975; Hawkins et al. 1997). According to Brandmayr and Zetto Brandmayr (1986), a *Licinus italicus* female devoured one snail (shell diameter 13 to 20 mm) every five days. Snails of this size range have a soft body dry weight of 13 to 27 mg compared to 3 mg of a 5.5 mm long *Chondrina arcadica*. This indicates that a beetle would need to eat one to two *C. arcadica* per day to have the similar food intake as a beetle that chooses large snails as prey. In the Great Alvar, *C. arcadica* occurs in high densities, mainly on stone walls, in stone piles and on limestone pavements (Baur and Baur 1990). Large snails are rare in this grassland, an exception being *Helicigona lapicida* (Linneus, 1758) in abandoned limestone quarries (Baur and Baur 2006). It is therefore not surprising that *L. depressus* frequently eats small prey snails, such as *C. arcadica* and *Cochlicopa lubrica* (O. F. Müller, 1774), which can be found in the grassland with little search effort (B. Baur, unpubl. data).

Specific external or internal traces on shells left by the predators indicate who killed the snail (birds, rodents, beetles, or parasitoid flies; Němec and Horsák 2019). In limestone steppes in Slovakia and the Czech Republic, beetles have been found to be the most common predators of snails (Němec and Horsák 2019). Similarly, among numerous empty shells collected from dry grasslands in the Swiss Jura mountains, shells of similar size and shape such as *C. arcadica* (*C. lubrica*, *C. lubricella* (Rossmässler, 1834), *Abida secale* (Draparnaud, 1801)) with traces of Licinini predation have been regularly found (Boschi and Baur 2008). In addition, empty shells of *Chondrina avenacea* (Bruguière, 1792) and *A. secale* with the same feeding marks were regularly found in the Alps (B. Baur, unpubl. data). However, it is not possible to assign shells to a specific beetle species using traces from predation.

Our observations are based on one individual and five predation events (one field observation, four laboratory observations). However, the numerous empty snail shells found in the field with these specific feeding marks (Fig. 1) indicate that this form of prey handling occurs regularly in *L. depressus* and possibly other Licinini beetles. However, their prey handling and feeding behavior under stones and in the dense ground vegetation are hardly observed.

Land snails exhibit a great diversity of shell forms (Kerney and Cameron 1979). Many of the shell traits (e.g., whorl number and size, aperture shape and size, shell shape, shell thickness and size) are adaptive responses to abiotic ecological factors, while some shell traits (e.g., aperture shape and size, shell size, shell wall thickness, and shell coiling direction) are known to provide a selective advantage when faced with predation (Goodfriend 1986; Liew and Schilthuizen 2014). Land snails are prey for different predators and are accordingly exposed to different selection pressures (Schilthuizen et al. 2006; Němec and Horsák 2019).

With its asymmetrical mandibles and particular behaviour of holding the small conical shell with its forelegs, *L. depressus* can only open right-handed coiled shells, but not left-handed coiled shells (Fig. 2). *Balea perversa* (Linnaeus, 1758) is a snail of similar size to *C. arcadica* and both species coexist in stony habitats of the Great Alvar (Baur and Baur 1990). However, we have never found a shell of *B. perversa* with traces of beetle predation in the Great Alvar. In contrast to *C. arcadica*, shell coiling in *B. perversa* is left-handed (sinistral). The unusual (rare) shell coiling may give this species an advantage against *L. depressus* attacks. This argument is supported by other studies showing that predatory insects with asymmetrical mandibles specialize in snails with a specific shell coiling direction (Hoso and Hori 2008).

Brandmayr and Zetto Brandmayr (1986) proposed high plasticity of predatory behaviour in Licinini. For example, *Licinus cassideus latus* opened shells of juveniles *Helix aspersa* (= *Cornu aspersum* (O. F. Müller, 1774)) with a shell diameter of 7–12 mm by breaking the whorls as described above. In individuals with a shell diameter larger than 20 mm, however, the beetle simply entered through the shell aperture and began feeding (Brandmayr and Zetto Brandmayr 1986). Our observations on how to deal with small prey snails expand the repertoire of known predatory behaviour. At the same time, our observations confirm the high plasticity of predatory behaviour in Licinini beetles.

Acknowlegements

We thank J. Niemelä for confirmation of the species determination, and B. Braschler, J. Litman and an anonymous reviewer for valuable comments on the manuscript.

References

Ball GE (1992) The tribe Licinini (Coleoptera: Carabidae): A review of the genus-groups and of the species of selected genera. Journal of the New York Entomological Society 100: 325–380.

Baur B (1988) Microgeographical variation in shell size of the land snail *Chondrina clienta*. Biological Journal of the Linnean Society 35: 247–259. https://doi.org/10.1111/j.1095-8312.1988.tb00469.x

Baur B, Baur A (1990) Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. Journal of Animal Ecology 59: 301–315. https://doi.org/10.2307/5174

Baur B, Baur A (1995) Habitat-related dispersal in the land snail *Chondrina clienta*. Ecography 18: 123–130. https://doi.org/10.1111/j.1600-0587.1995.tb00332.x

Baur B, Baur A (2006) Dispersal of the land snail *Helicigona lapicida* in an abandoned limestone quarry. Malakologische Abhandlungen 24: 135–139.

Boschi C, Baur B (2008) Past pasture management affects the land snail diversity in nutrient-poor calcareous grasslands. Basic and Applied Ecology 9: 752–761. https://doi.org/10.1016/j.baae.2007.09.006

Brandmayr P, Zetto Brandmayr T (1986) Food and feeding behaviour of some *Licinus* species (Coleoptera, Carabidae, Licinini). Monitore Zoologico Italiano New Series 20: 171–181.

Calow P (1975) Length-dry weight relationships in snails: some explanatory models. Proceedings of the malacological Society London 41: 357–375. https://doi.org/10.1093/oxfordjournals.mollus.a065283

Erwin TL, Micheli C, Chaboo CS (2015) Beetles (Coleoptera) of Peru: a survey of the families. Carabidae. Journal of the Kansas Entomological Society 88: 151–162. https://doi.org/10.2317/kent-88-02-151-162.1

Forsythe TG (1983) Mouthparts and feeding of certain ground beetles (Coleoptera: Carabidae). Zoological Journal of the Linnean Society 79: 319–376. https://doi.org/10.1111/j.1096-3642.1983.tb01170.x

GBIF (2023) Global Biodiversity Information Facility. Distribution of *Licinus depressus*. https://www.gbif.org/en/species/9414758 [accessed on 8 February 2023]

Goodfriend GA (1986) Variation in land-snail shell form and size and its causes: a review. Systematic Biology 35: 204–223. https://doi.org/10.1093/sysbio/35.2.204

Hawkins JW, Lankester MW, Lautenschlager RA, Bell FW (1997) Length-biomass and energy relationships of terrestrial gastropods in northern forest ecosystems. Canadian Journal of Zoology 75: 501–505. https://doi.org/10.1139/z97-061

Hayashi M, Sugiura S (2021) Shell-breaking predation on gastropods by *Badister pictus* (Coleoptera, Carabidae) with strikingly asymmetric mandibles. ZooKeys 1044: 815–830. https://doi.org/10.3897/zookeys.1044.62293

Hosi M, Hori M (2008) Divergent shell shape as an antipredator adaptation in tropical land snails. American Naturalist 172: 726–732. https://doi.org/10.1086/591681

Info fauna (2023) Schweizerisches Zentrum für die Kartografie der Fauna. Distribution of *Licinus depressus* in Switzerland. https://lepus.unine.ch/carto/18526 [accessed on 8 February 2023]

Kerney MP, Cameron RAD (1979) A Field Guide to the Land Snails of Britain and North-west Europe. Collins, London, 288 pp.

Kinnunen H (1996) *Licinus depressus* (Coleoptera, Carabidae) – a new species for Tavastia – Finland. Entomologica Fennica 7: 5–6. https://doi.org/10.33338/ef.83880

Liew T-S, Schilthuizen M (2014) Association between shell morphology of micro-land snails (genus *Plectostoma*) and their predator's predatory behaviour. PeerJ 2: e329. https://doi.org/10.7717/peerj.329

Lindroth CH (1949) Die Fennoskandischen Carabidae. Eine tiergeographische Studie. III. Allgemeiner Teil. Meddelanden från Göteborgs Musei Zoologiska Avdelning 122: 1–911.

Lindroth CH (1986) The Carabidae (Coleoptera) of Fennoscandia and Danmark. Fauna Entomologica Scandinavia 15: 233–497. https://doi.org/10.1163/9789004267503

Lundberg S (1983) Skalbaggar på Ölands Stora alvar. Entomologisk Tidskrift 104: 121–126.

Němec T, Horsák M (2019) Specific damage recognised on land snails as a tool for studying predation intensity: differences related to habitat and predator types. Contributions to Zoology 88: 277–296. https://doi.org/10.1163/18759866-20191402

Palmer AR (1996) From symmetry to asymmetry: phylogenetic patterns of asymmetric variation in animals and their evolutionary significance. Proceedings of the National Academy of Sciences of the USA 93: 14279–14286. https://doi.org/10.1073/pnas.93.25.142

Schilthuizen M, van Til A, Salverda M, Liew T-S, James SS, Elahan BB, Vermeulen JJ (2006) Microgeographic evolution of snail shell shape and predator behavior. Evolution 60: 1851–1858. https://doi.org/10.1111/j.0014-3820.2006.tb00528.x

Alpine Entomology 7 2023, 69–82 | DOI 10.3897/alpento.7.105937

Alpine Entomology

A review of the *Chrysolina* species – subgenus *Stichoptera* Motschulsky, 1860 – in Switzerland, with notes on distribution, conservation and preimaginal stages (Coleoptera, Chrysomelidae)

Christoph Germann[1], Michael Geiser[2], Matthias Borer[1]

1 *Naturhistorisches Museum, Augustinergasse 2, CH-4051, Basel, Switzerland*
2 *Department of Life Sciences, Natural History Museum, London SW7 5BD, UK*

https://zoobank.org/C0FEB30F-8600-4783-8C42-2AC07B4F8323

Corresponding author: Christoph Germann (germann.christoph@gmail.com)

Academic editor: Yannick Chittaro ♦ **Received** 4 May 2023 ♦ **Accepted** 26 June 2023 ♦ **Published** 7 July 2023

Abstract

The species of the subgenus *Stichoptera* occurring in Switzerland are revised, based on a combination of literature data, old museum specimens and recent material. Four species, one with two subspecies, *Chrysolina kuesteri* (Helliesen, 1912), *Ch. latecincta latecincta* (Demaison, 1896), *Ch. latecincta norica* (Holdhaus, 1914), *Ch. rossia* (Illiger, 1802) and *Ch. sanguinolenta* (Linnaeus, 1758) are confirmed to occur in Switzerland, while *Ch. gypsophilae* (Küster, 1845) has to be excluded from the Swiss fauna due to insufficient evidence. Errors and unclarities in the older literature are discussed. *Ch. kuesteri* was found abundantly in central Valais, allowing some notes on its larval biology. Larvae of the alpine *Ch. latecincta* are also illustrated, along with notes on its habitat and some past and present distribution records. Illustrations for all Swiss members of the subgenus, as well as distribution maps with all confirmed records, are provided.

Zusammenfassung

Die Arten der Untergattung *Stichoptera*, welche in der Schweiz vorkommen, wurden auf der Grundlage einer Kombination von Literaturdaten, alten Museumsbelegen und aktuellen Funden revidiert. Vier Arten, dabei eine mit zwei Unterarten, *Chrysolina kuesteri* (Helliesen, 1912), *Ch. latecincta latecincta* (Demaison, 1896), *Ch. latecincta norica* (Holdhaus, 1914), *Ch. rossia* (Illiger, 1802) und *Ch. sanguinolenta* (Linnaeus, 1758) werden als in der Schweiz vorkommend bestätigt, während *Ch. gypsophilae* (Küster, 1845) ohne bestätigende Belege ausgeschlossen werden muss. Fehler und Unklarheiten in historischer Literatur werden diskutiert. *Ch. kuesteri* wurde häufig im Zentralwallis gefunden, was zu Beobachtungen über die Larvalbiologie führte. Larven der alpin verbreiteten *Ch. latecincta* werden auch abgebildet, zusammen mit Bemerkungen über das Habitat und historischen sowie rezenten Verbreitungsdaten. Abbildungen für alle schweizerischen Arten des Subgenus, sowie Fundortkarten aller überprüften Funde werden gegeben.

Key Words

Chrysomelinae, biology, larvae, faunistics, Switzerland

Introduction

Leaf beetles (Chrysomelidae) are the third most diverse beetle family in Switzerland and worldwide (Leschen and Beutel 2014), after the Staphylinidae and Curculionidae. Unfortunately, it is also the largest family, which at present still lacks an updated checklist for the Swiss fauna, although both of the larger families have been reviewed in recent times (Luka et al. 2009; Germann 2010). The total number of the Swiss Chrysomelidae species can therefore only be estimated, but may be hovering around 580 according to Löbl and Smetana (2010), and own investigations. Within the Swiss Chrysomelidae, it is not only the smaller and less apparent species like those of the Alticinae that have not yet been thoroughly studied (Döberl 1995; Germann 2011), but also the larger-sized species still show considerable gaps regarding their occurrences and distribution data. Recently, Borer and Chittaro (2016) published the first records of *Lilioceris schneideri* (Weise, 1900), and Germann et al. (2020) discussed some of the rarely recorded *Cryptocephalus* species. Also the large-bodied and therefore easily spotted *Chrysolina* species are in lack of specialist attention. As entomologists in neighbouring countries have found alarming population declines in multiple *Chrysolina* species (e.g. Rheinheimer and Hassler 2018), a critical assessment of the situation in Switzerland has become more urgent. In order to inform future conservation measures, a critical re-assessment of the past and present situation has become crucial.

At present, 38 species and subspecies of the genus *Chrysolina* are recorded from Switzerland (unpublished data), five of which in the subgenus *Stichoptera* Motschulsky, 1860: *Ch. gypsophilae* (Küster, 1845), *Ch. kuesteri* (Helliesen, 1912), *Ch. latecincta* (Demaison, 1896), *Ch. rossia* (Illiger, 1802) and *Ch. sanguinolenta* (Linnaeus, 1758). In total, this subgenus contains fifteen valid species and numerous subspecies (Bieńkowski 2001; Kippenberg 2010; Bourdonné et al. 2013; Bienkowski 2019; Kippenberg 2020).

The central European members of *Stichoptera* form a rather difficult species complex, hence *Chrysolina* species with a red coloured margin of the elytra were often confused or misinterpreted in the literature. The 19th century literature cites the species names *Ch. marginalis* Duftschmid, 1825 and *Ch. sanguinolenta* (Linnaeus, 1758) as separate species, even though they are now considered synonyms (Kippenberg 2010), and it seems likely that both names refer to a mixture of species!

Helliesen (1912) was the first to provide a thorough revision of these morphologically similar species within Europe based on a study of the type material, including that of *Ch. sanguinolenta* at the Linnaean Society in London. His excellent identification key is still usable today, in conjunction with illustrations of the genitalia. A more up-to-date key was provided by Winkelman and Debreuil (2008), which also proved useful for the present study.

Kippenberg (2020) recently revised the predominantly alpine *Ch. latecincta* and its subspecies, including specimens from Switzerland. The subspecies *Ch. latecincta vallesiaca* (Franz, 1949), until recently considered endemic to Switzerland (Germann et al. 2013), was synonymised with the nominotypical subspecies. The subspecies *Ch. latecincta norica* (Holdhaus, 1914) was recorded for the first time from Switzerland by Kippenberg (2020).

The present study aims at summarising the current state of knowledge on all members of the subgenus *Stichoptera* in Switzerland, as far as reliable specimens were available, in order to paint a clearer picture of their distribution within the country. We also provide additional data on newly discovered populations of *Ch. kuesteri* in central Valais and details on the larval biology of this species, alongside some notes on the larvae of the alpine *Ch. latecincta latecincta*.

Material and method

The initial idea for this study came after *Chrysolina kuesteri*, a species only recently published as new to the Swiss fauna (Blanc et al. 2012), was observed in surprisingly high abundance in Valais, near Sion, by Annette Geiser-Barkhausen and Urs Lemmenmeier in October 2020. One of us (CG) re-visited the locality later in 2020 and collected adults and larvae. Furthermore, we analysed pitfall trap samples from vineyards around Salgesch and Varen (Valais) made available to us by Lukas Lischer.

We then revised all specimens of *Stichoptera* from Switzerland and immediately adjacent areas contained within the following collections: **AGRO** – Agroscope-Changins, Nyon. **BMNH** – Natural History Museum, London. **MHNG** – Muséum d'Histoire Naturelle, Genève. **NMB** – Naturhistorisches Museum Basel. **NMBE** – Naturhistorisches Museum Bern. **NMSG** – Naturmuseum St. Gallen. **NMCH** – Naturmuseum Chur. **MCSN** – Museo Cantonale di Storia Naturale, Lugano. Collections: **cAS** – Alexander Szallies, Reutlingen. **cCG** – Christoph Germann, Rubigen. **cCM** – Christian Monnerat, Neuchâtel. **cHB** – Hermann Blöchlinger, Erschmatt. **cMB** – Matthias Borer, Liestal. **cRG** – Roman Graf, Kriens. **cSB** – Stève Breitenmoser, Prangins. **cYC** – Yannick Chittaro, Conthey. Data is given verbatim, additions are set in square brackets ([]). The Swiss coordinates are given verbatim.

Pairs of live *Ch. kuesteri* from Mont d'Orge (Sion, Valais) and *Ch. latecincta* from Griespass (Ulrichen, Valais) were kept in multiuse plastic boxes (see Germann 2021) with a diameter of 45 mm and 28 mm hight from autumn until the next summer, and they were generally fed with *Linaria purpurea* (L.) Mill., in order to observe and document their larval development.

Results

Literature review

Stierlin and Gautard (1867) mention *Ch. sanguinolenta* («Ziemlich häufig überall auf Wegen, in Gras.»), *Ch. marginalis* («Selten, wie der vorige [= *sanguinolenta*]. Schaffhausen (St.), Genf (Tourn.)») and *Ch. rossia* [spelt as «*rossii*»] («Selten. Lugano (Meyer)»). Favre (1890) cites only *Ch. sanguinolenta* (« Par places très-commune. Isérables, Fully, Sierre, Niouc (Fav.); Sion (Buy.); aussi à Lully (Jac.) [Kanton VD].») and *Ch. marginalis* («Rare. Val d'Entremont (Rätz.).»). Stierlin (1898) repeated the record of *Ch. rossia* with the general indication «Selten. Im Tessin.», and also listed *Ch. sanguinolenta* «Ziemlich häufig überall auf Wegen und im Gras», but additionally also *Ch. marginalis*: «Seltener als der vorige, Genf, Tessin, Puschlav, Schaffhausen».

Based on the above treatments, we are not able to determine which species these early authors had at hand, considering that *Ch. marginalis* is treated as synonymous with *Ch. sanguinolenta* in the current literature (Kippenberg 2010). Only the information given for *Ch. rossia* matches with our own observations based on voucher specimens in various collections (see below).

Hugentobler (1966) mentions *Ch. sanguinolenta* in his treatment of the beetles of northeast Switzerland and gave the locality «Churfirsten leg. Rietmann». However, no voucher specimen was found in the collection of the Naturmuseum St. Gallen.

Blanc et al. (2012) recorded *Ch. gypsophilae* and *Ch. kuesteri* from Geneva, the latter as a new record for Switzerland. We were able to examine the specimens that formed the base for these records at MHNG.

Records given by Kippenberg (2020) for *Ch. latecincta latecincta* and *Ch. latecincta norica* are based on a thorough morphological revision of these taxa, so we can accept them without hesitation. However, he also points out certain unresolved taxonomic issues with this species complex. *Ch. latecincta* shows considerable morphological variability across its many geographically isolated populations. First results using the barcode sequence (COI) seem promising and may help to shed further light into those populations and/or potential subspecies. For this purpose, we also collected and will continue to collect specimens in alcohol.

General results

Four species and one additional subspecies of *Stichoptera* are here confirmed to occur in Switzerland. All registered specimens and records (Suppl. material 1), and a summary map of both recent and historical records (Fig. 3) shows that three of them were recorded North of the main watershed of the Alps, while all of them except *Ch. latecincta norica* occur in the southern parts of the country (Valais and/or Ticino). The northernmost records from «Basel», «Liestal» and «Schaffhausen» should however be taken with caution, as there might have been a confusion between the collector's home and the actual collecting locality in some of the older specimens (see also Monnerat et al. 2015).

In the following we provide data for all species, including habitus photos (Fig. 1a–g) and those of their male genitalia (Fig. 2a–e). Faunistic records are shown in chronological order.

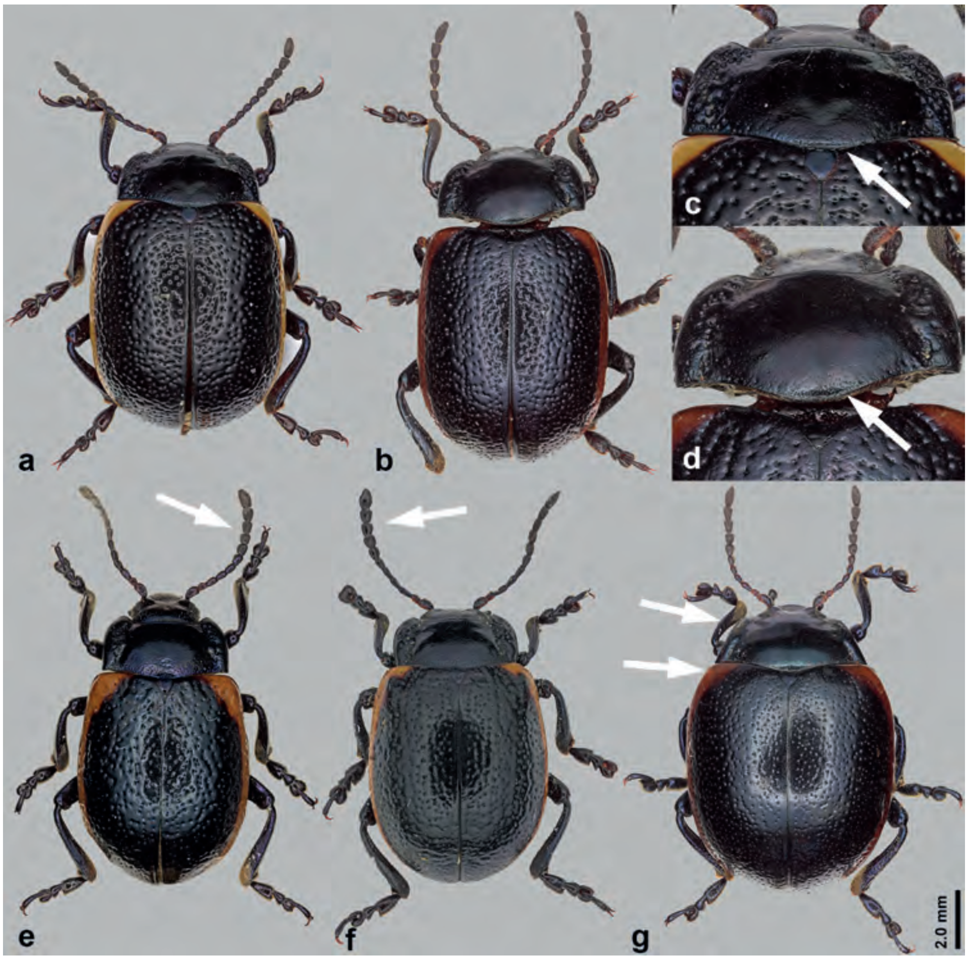


Figure 1. a–g. Dorsal habitus of males of *Chrysolina* (*Stichoptera*) from Switzerland. **a, c.** *Ch. kuesteri*, Raron VS; **b, d.** *Ch. sanguinolenta*, Scuol GR; **e.** *Ch. latecincta latecincta* Griespass VS; **f.** *Ch. latecincta norica* Fusio TI. Arrows indicate relevant differences; pronotum more shiny and glabrous in *Ch. sanguinolenta* (**d**), antennal segments shorter and thicker in *Ch. latecincta* (**e, f**), shape of pronotum trapezoid and circular elytra in *Ch. rossia* (**g**) (Photos: M. Borer, C. Germann).

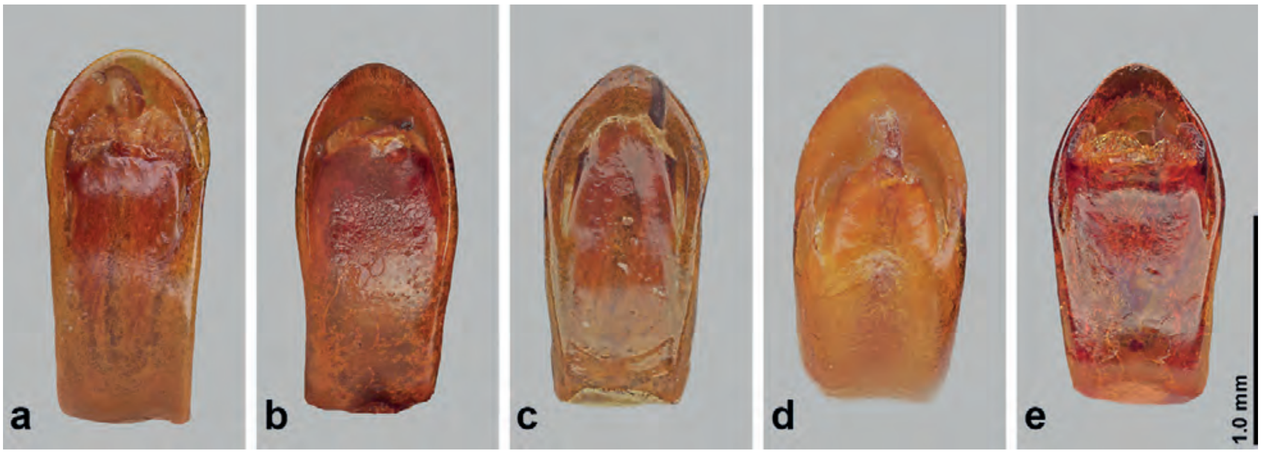


Figure 2. a–e. Apex of the penis (median lobe) of *Chrysolina* (*Stichoptera*) occurring in Switzerland in dorsal view. **a.** *Ch. kuesteri*; **b.** *Ch. sanguinolenta*; **c.** *Ch. latecincta latecincta*; **d.** *Ch. latecincta norica*; **e.** *Ch. rossia* (Photos: M. Borer).

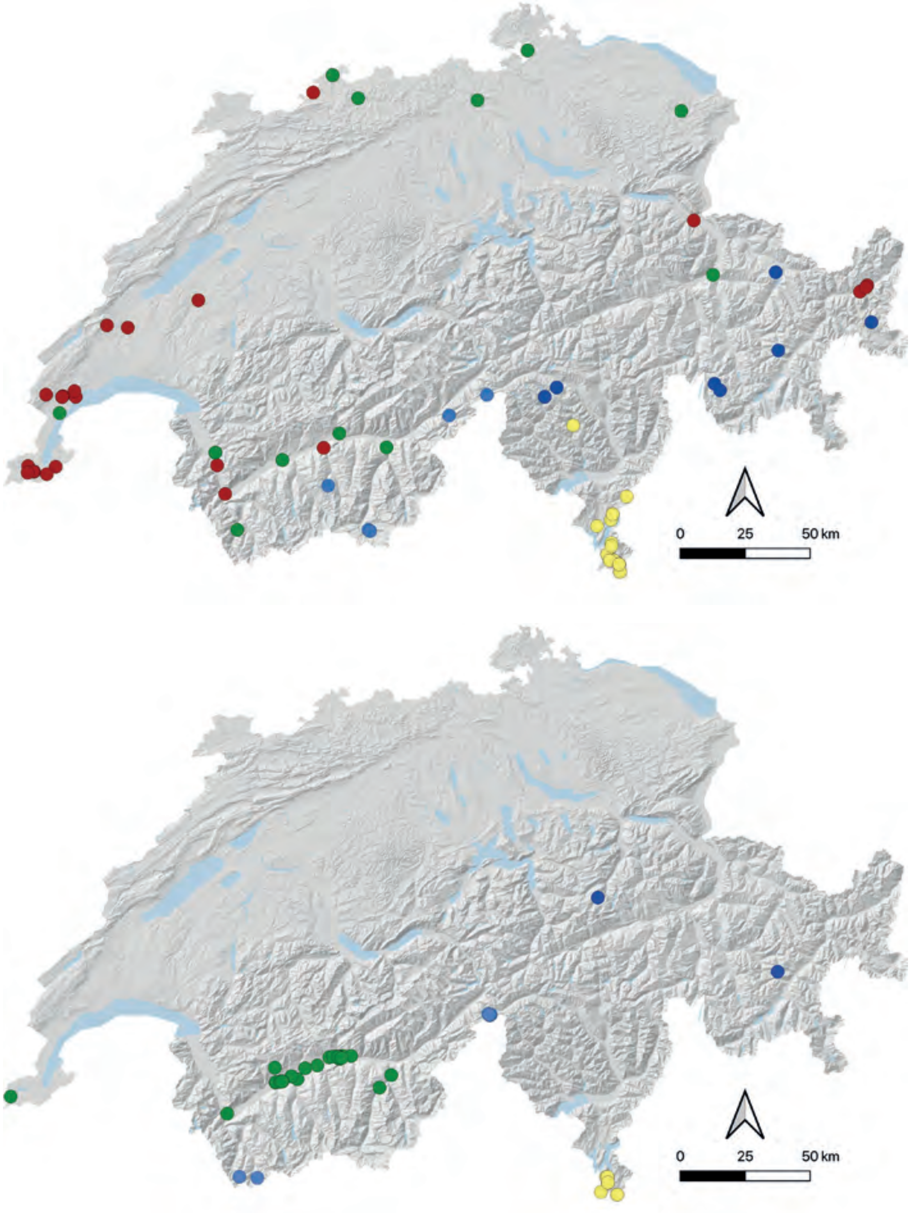


Figure 3. Localities of all revised specimens of the subgenus *Stichoptera* from Switzerland, before the year 2000 (above), and after (below). Colour code: green *Ch. kuesteri*, red *Ch. sanguinolenta*, dark blue *Ch. latecincta norica*, light blue *Ch. latecincta latecincta*, yellow *Ch. rossia* (Background map: swisstopo.ch).

Chrysolina (*Stichoptera*) *gypsophilae* (Küster, 1845)

Note. This species occurs in large parts of Europe, particularly in the South, as well as in the Near East, Caucasus and Central Asia (Kippenberg 2010). There are published records from all countries surrounding Switzerland. In adjacent Baden-Württemberg (Germany), *Ch. gypsophilae* has recently been listed as extinct (Rheinheimer and Hassler 2018), for Germany it is listed as "vulnerable" (Fritzlar et al. 2021).

Material. 1 ♀: «Coll. Ch. Maerky Grammont» [Le Grammont, VS?] (MHNG). 1 ♀: Chandolin [VS], 21.6. [before 1929], coll. Maerky (MHNG). 1 ♀: Kippel [VS, almost illegible, handwritten], 21.6. [before 1929], coll. Maerky (MHNG).

Remarks. Blanc et al. (2012) reported this species from «Genève», based on likely misinterpreted historical specimens at the MHNG (the handwritten labels are difficult to interprete). These are likely the same specimens cited above, all from the collection of Charles Maerky. This collection has a reputation for containing frequent labelling errors, making the data altogether unreliable (see Monnerat et al. 2015). The three specimens are all females, and all are supposedly from localities at montane altitudes, which seems odd for this species, otherwise known from lowlands areas (Rheinheimer and Hassler 2018). Because of this unreliability and the lack of other material in collections, we consider the occurrence of this species in Switzerland dubious and advise not to add it onto faunistic lists unless new data become available.

Chrysolina (*Stichoptera*) *kuesteri* (Helliesen, 1912)

Note. This species is widespread in Europe. Kippenberg (2010) cites the nominotypical subspecies from Belarus, Bosnia-Herzegovina, Bulgaria, Germany, France, Latvia, Netherlands, Austria, Poland, Romania, Switzerland, Serbia, Montenegro, Slovakia, Slovenia, Czech Republic, Ukraine and Hungary, while the subspecies *Ch. kuesteri friderici* (Wagner, 1927) occurs in Portugal and Spain. Rheinheimer and Hassler (2018) listed it as thermophilous, localised and rare in SW Germany. Blanc et al. (2012) only recently confirmed the occurrence in Switzerland, but likely based on the specimen in the coll. Charles Maerky at MHNG (see comments under *Ch. gypsophilae* above).

Historical data. 1 ♂, 2 ♀: St. Gallen, ex coll. Täschler [without date] (NMSG). 1 ♂, 1 ♀: Basel coll. Burghold [without date] (NMBE). 1 ♀: Wallis, coll. Burghold [without date] (NMBE). 1 ex.: Genève, La Praille, 7-V. coll. Maerky (MHNG). 1 ♀: «Schweiz» coll. Stähelin-Bischoff [without date], det. J.C. Bourdonné 2005 (NMB). 3 ex. «Basel» (NMB). 3 ex. E. Handschin «Liestal» [without date], coll. E. Handschin (NMB). 1 ♀: Chur [yellow label, without date] coll. Killias, coll. J. B. Jörger (NMB). 4 ex. Basel, coll. [E.] Liniger [1880ies] (NMB). 1 ♂: coll. Chevrier, Nyon, Oct. [18]80 (MHNG). 1 ex. Sion [VS] 22.VI.[18]92 (MHNG). 1 ♀: Rheinau, 6.99 [1899], coll. J.B. Jörger (NMB). 1 ♂: Praz de F [Praz-de-Fort, Orsières, VS] 5.VI.1911 (MHNG). 1 ♀: Rheinau 19.11.[19]12, coll. J. B. Jörger (NMB). 1 ♀ Bex [VD] 14.X.[19]22 (MHNG). 1 ♀: Lägern, Kt. Aarg., Helv. 5.6.1933, coll. V. Allenspach (NMB). 1 ex. VS, Leuk, oberhalb, 30.5.1966, leg. P. Scherler (NMBE). 1 ex. Zeneggen [VS] 4.8.[19]72 (MHNG).

Recent data (2000 onwards). 1 ♀: VS, Kalpetran, 3.6.2000, ex. coll. G. Carron (cYC). 1♀: Helv, VS, Leuk, 615/129, PR2, 26.V.2001, leg. C. Monnerat, det. M. Borer, 2017 (cCM). 1 ex. VS, Sierre, Route Sion 46, 606.247, 126.219, 23.10.2012 (cYC), 1 ♀: VS, St. Léonard, 599, 122, 13.5.2013, leg. R. Graf (cRG). 2 ex.: Hell 662 m, CH-VS-Salgesch, 610787, 129327, 9.xi.[20]14, leg. and det. L. Lischer (cCG). 1 ex.: Marjunne, 709 m, CH, VS, Varen, 613582, 129671, 9.vi. [20]14, leg. and det. L. Lischer (cCG). 1 ♂: Helv, VS, Visperterminen, 634730/122500, 1098 m, 11.V.2017, leg. Y. Chittaro, det. M. Borer 2019 (cYC). 1 ♀: Helv, VS, Varen, 612270-129590, 791 m, 28.V.2017, leg. C. Monnerat, det. M. Borer, 2019 (cCM). 1 ♀: Helv, GE, La Touvière, 488042/114263, 348 m, 24.V.2018, leg. Y. Chittaro, det. M. Borer 2019 (cYC). 1 ♀: Helv, VS, Flanthey, 601540/125155, 952 m, 14.V.2019, leg. Y. Chittaro det. M. Borer 2020 (cYC). 1 ♀: Helv, VS, Brentjong, 616030/129985, 962 m, 31.V.2019, leg. Y. Chittaro, det. M. Borer 2020 (cYC). 1 ♀: Sion, Bisse de Clavau, cours d'eau, vigne [46.25000 / 7.39000], 30.05.2019, leg. S. Breitenmoser (cSB). 1 ♀: Sion, Bisse de Clavau, vigne bosquet [46.25000 / 7.39000], 30.05.2019, leg. S. Breitenmoser (cSB). 1 ex. VS, Conthey, près du Torrent 47, 510 m, 2.II.2020, leg. M. C. Chittaro (cYC). 1 ex. VS, Conthey, près du Torrent 47, 510 m, 27.10.2020, leg. M. C. Chittaro (cYC). 13 ex. VS, Pt. de la Morge, Route de Vuisse, 523 m, 22.4.2020, coll. A. Schmidt (cYC). 1 ♀: Helv, VS, Mayentset, 589812/125364, 1510 m, 22.V.2020, leg. Y. Chittaro, det. M. Borer 2021 (cYC). 1 ♂: CH, VS, Leuk, Erschmatt (Bl), 619.250, 129.925, 1210 m, 13.10.2020, leg. H. Blöchlinger (cHB). 1 ♂: CH, VS, Fully, Les Follatères, 30.9.2020, leg. C. Germann. 1 ♂, 1♀: Sion, Mont d'Orge, 660 m, 592380, 120130 (46°13'58"N, 7°20'24"E), 9.x.2020, leg. A. Geiser-Barkhausen and U. Lemmenmeier (BMNH). 4 ex. 359_20.2 CH, VS, Sion, Montorge, Umgb., 592'590, 120'067, 589 m, 17.10.2020, leg. C. Germann (NMB). 3 ex. 359_20.3. CH, VS, Sion, Montorge, Umgb., 592'490, 120'047, 611 m, 17.10.2020, leg. C. Germann (NMB). 2 ex.: 359_20.4. CH, VS, Sion, Montorge, Umgb., 592'394, 120'144, 660 m, 17.10.2020, leg. C. Germann (NMB). 2 ex.: 359_20.5. CH, VS, Sion, Montorge, Umgb., 591'900, 119'866, 785 m, 17.10.2020, leg. C. Germann (NMB). 1 ex.: 360_20.1 CH, VS, Leuk, Ringacker, 615'119, 129'245, 678 m, 22.10.2020, leg. C. Germann (NMB). 1 ex.: 360_20.2 CH, VS, Leuk, Ringacker, 615'079, 129'260, 675 m, 22.10.2020, leg. C. Germann (NMB). 1 ♂, 1 ex.: 360_20.3 CH, VS, Leuk, ob Ringacker, 615'100, 129'352, 696 m, 22.10.2020, leg. C. Germann (NMB). 3 ex.: 360_20.4 CH, VS, Leuk, Dorf, altes Bahntrassee, 614'965, 129'462, 713 m, 22.10.2020, leg. C. Germann (NMB). 1 ♂: 360_20.5 CH, VS, Leuk, Dorf, 614'840, 129'595, 704 m, 22.10.2020, leg. C. Germann (NMB). 3 ex.: 360_20.6 CH, VS, Leuk, 614'558, 129'576, 672 m, 22.10.2020, leg. C. Germann (NMB). 1♂, 1 ex.: 360_20.7 CH, VS, Leuk, 614'487, 129'538, 22.10.2020, 657 m, leg. C. Germann (cCG, NMB). 1 ♀: 360_20.8 CH, VS, Leuk, 614'274, 129'486, 636 m, 22.10.2020, leg. C. Germann (NMB). 1 ♀: 360_20.9 CH, VS, Leuk, 615'571, 129'138, 632 m, 22.10.2020, leg. C. Germann (cCG). 2 ex. (Larve und Ei) CH, VS, Sion, Montorge, Umgb., 592'748, 120'105, 560 m, 22.3.2021, vid. C. Germann. 1 ex. CH, VS, Sion, Montorge, 592'600, 120'065, 580 m, 3.6.2021, leg. C. Germann (NMB).

Remarks. Based on our own investigations in Valais, plus the data provided to us by colleagues, *Ch. kuesteri* is locally common around Sion and Leuk. Several previously unknown localised populations were found between in late 2020 and 2021. For a precise map see Fig. 4. All of the older Swiss records we found in museum collections were previously misidentified, mostly standing under *Ch. sanguinolenta*, obscuring the real distribution of this species. Recently « citizen science » observations have become available thanks to iNaturalist (https://www.inaturalist.org/, accessed 1th February 2023), but unfortunately, they leave no possibility of examining characters such as the genitalia more close up. Observations from Sion (8th October 2020), Zeneggen (17th October 2021) and Varen (17th February 2022), all Valais, can be tentatively assigned to *Ch. kuesteri*, but users of this website often seem to confuse this species with *Ch. sanguinolenta* or *Ch. rossia*.

Ch. kuesteri rearing experiments

Note. Six couples of *Ch. kuesteri* from Mont d`Orge (=Montorge Sion, Valais) collected in October 2020 were kept in plastic boxes. As its local host plant in Valais was not exactly determined (but presumed to be *Linaria* sp.), both adults and larvae were fed on *Linaria purpurea*, a readily available garden plant. Oviposition was observed on *L. purpurea* from November until January. In early February 2021 the first larvae were noticed (Fig. 5b), which accepted *L. purpurea* without problems. The first moult took place in mid-February (Fig. 5c), the second towards the end of the same month. In early March,

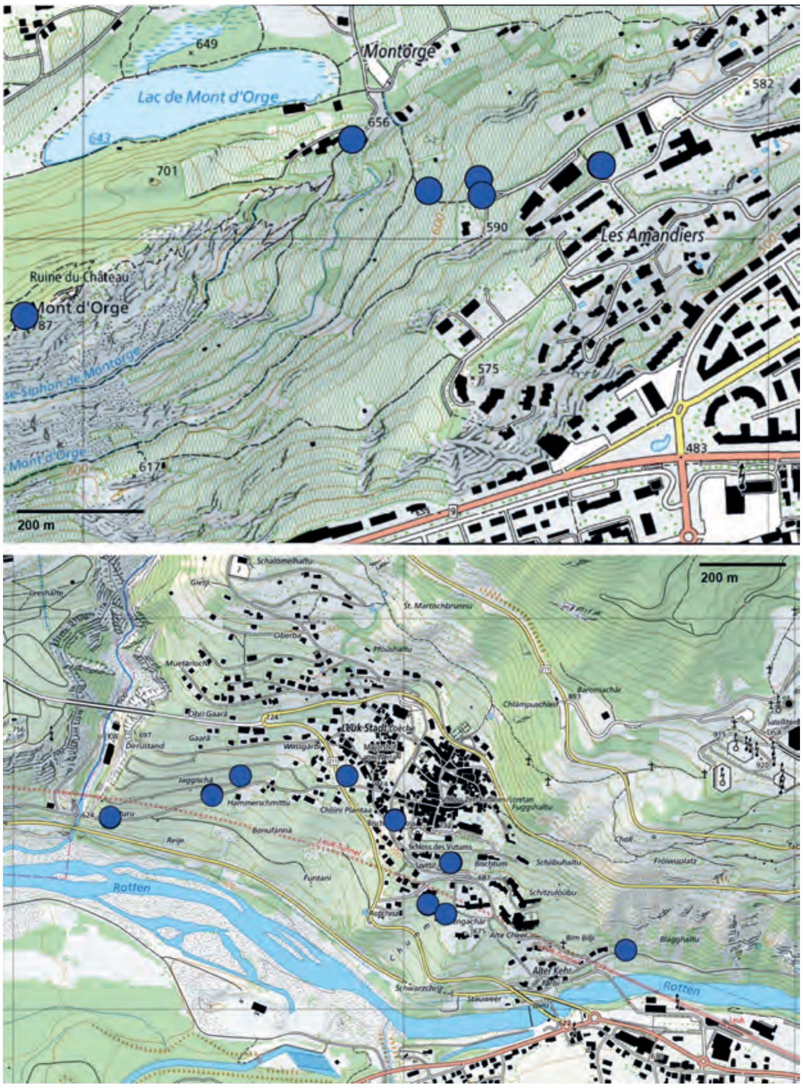


Figure 4. Detailed maps of local *Ch. kuesteri* populations around Mont d`Orge (Sion, Valais) and Leuk (Valais) showing records made in 2020 and 2021 (Background map: map.geo.admin.ch).

Figure 5. a–g. Preimaginal stages of *Chrysolina kuesteri*. **a.** Eggs shortly before hatching, late January; **b.** First larval instar; **c.** Larva after first moult in middle of February; **d.** Larva after fourth moult mid-March; **e.** Fifth (and last) larval instar, April; **f, g.** Pupa, lateral and ventral view; **h.** Freshly hatched adult, end of May (Photos: C. Germann).

more larval skins were found, suggesting a third moult. A fourth moult was observed in mid-March (Fig. 5d), a fifth and final one in mid-April (Fig. 5e). The first pale yellowish pupa (Fig. 5f, g) was found on 30rd April. The larvae pupated at the bottom of the boxes, where some quartz sand had been added earlier. Further pupae followed in May. The first adult hatched on May 29th (Fig. 5h). Part of the adults from autumn 2020 were still alive at that time (Fig. 6a). In addition to those results in captivity (under environmental conditions in Rubigen, outside in

Figure 6. a. Adult of *Chrysolina kuesteri* from Mont d`Orge in October; **b.** Habitat in the vineyards at Mont d'Orge; **c.** Fifth larval instar at the same locality in March 2021 feeding on *Veronica hederifolia* (Photos: C. Germann).

the garden), 5th instar larvae were found in the field near Sion on March 22nd 2021 (Fig. 6c), which shows a somewhat faster development at Mont d`Orge, a locality with exceptionally mild climatic conditions. Only later on, on 22nd March 2021, we found evidence of *Veronica hederifolia* L. acting as the host plant at Mont d d`Orge (Fig. 6b, c).

Some insights into the development of *Ch. kuesteri* were already provided by Bourdonné et al. (2013), who also noted a larval development from October to May, in agreement with our observations and experiments. However, they noted a «quiescence» during the coldest season, which we did not observe. The same authors mentioned *Linaria supina* (L.) Chaz. and *Antirrhinum majus* L. as additional host plants. Rheinheimer and Hassler (2018) reported *Linaria vulgaris* P. Mill. and *L. nivea* Boiss. and Reut. and also quote an observation by Peter Sprick in Lower Saxony (Germany), confirming *Veronica hederifolia* as host plant, matching our field observations.

Chrysolina (*Stichoptera*) *latecincta latecincta* (Demaison 1896)

Note. Based on the recent revision by Kippenberg (2020), this subspecies occurs in the French Alps, NW Italy and southern Switzerland, generally at altitudes above 2000 m. The former subspecies *Ch. latecincta vallesiaca* (Franz, 1949), based on material from Switzerland (Valais), is now included in *Ch. latecincta latecincta*.

Material. 1 ex. [VS] Binn, Eggerhorn, 2400 m, 6.8.[19]46, leg. and coll. E. Handschin (NMB). 4 ex. Rothenboden s. Gornergrat, sous une pierre, alt. 2950, 26.VI.1961 (MHNG). 1 ♂: VS, V. Moiry, 2500 m, 29.7.[19]66, leg. J. Steffen (MHNG). 1 ex.: Valais, Gornergrat, 13.IX.[19]69, s. Pierre 3000–3100 m, Cl. Besuchet (MHNG). 1 ex.: Valais, Gornergrat, 7.VIII.[19]76, 3000–3100 m, Cl. Besuchet (MHNG). 1 ♂: Valais, Gornergrat, 12.VIII.[19]82, s. pierres 3050 m, Cl. Besuchet (MHNG). 10 ex. VS, Ulrichen, Griessee, 16.8.1993, unter Steinplatte im Bereich von kriechender

Salix-Art, leg. E. Kobel (NMBE). 5 ♂, 1 ♀: CH, TI, Cornosee, Geröllhalde, unter Steinen mit *Saxifraga* cf. *oppositifolia*, 2486 m, 46.45805 / 8.38344, 04.VIII.2011, leg. M. Borer, (cMB). 4 ♂, 4 ♀: CH, TI, Cornosee, Geröllhalde, unter Steinen mit *Saxifraga* cf. *oppositifolia,* 2502 m, 46.46004 / 8.38977, 04.VIII.2011, leg. M. Borer, (cMB). 2 ♂, 2 ♀: CH, TI, Cornosee, Geröllhalde, unter Steinen mit *Saxifraga* cf. *oppositifolia,* 2495 m, 672705 / 145639, 11.VIII.2015, leg. M. Borer, (NMB).1 ex. 153_11.2 SCHWEIZ, VS, Orsières, Val Ferret, Ferret, 576.206 / 083.399, 2420 m, 8.9.2011, GS Moos Blocksteinhalde, leg. C. Germann (cCG). 4 ex.: VS, Zwischbergen, Zwischbergengletscher, Moräne, 2700 m, 27.7.2012 (cAS). 5 ex.: 203_13.3 SCHWEIZ, VS, Ulrichen, Nufenenpass, ob. Griessee, Mändeli, 672.090 / 146.080, 2500 m, 29.8.2013, leg. C. Germann (cCG). 11 ex. Ticino, Bedretto, Passo del Corno, hand collecting, 672 550 / 145 700, 2490 m (46°27'32"N, 8°22'59"E), 5. VIII.2019, leg. M. Geiser (BMNH). 15 ex. 386_21.4 CH, TI, Nufenenpass, Val Corno, Cornopass Umgb., 672'589, 145'729, 2400 m, 2.9.2021, leg. C. Germann and M. Borer (NMB). 1 ♂: Helv. VS, Bg-St-Bernard, Troistorr, 583123 / 82917, 2543 m, 20.06.2022 (cYC).

Ch. latecincta latecincta rearing experiments

Note. 15 adults from Griespass (Ulrichen, Valais) were kept alive in couples in the same multiuse boxes (Germann 2021) and kept on *Linaria purpurea* (after the 2nd instar *Linaria vulgaris* was used temporarily), as with *Ch. kuesteri*, which was well accepted. In the middle of September 2021 already three eggs were laid, one of the larvae survived and moulted a fist time till 23rd September, and a second time on 3rd October. From middle of December to February 2022 the larva did not feed anymore and hardly moved. Beginning of March the larva died of unknown reason and despite (or because?) of the mild winter. Three females laid more than 20 eggs (Fig. 7a) from middle to end of March 2022. The larvae hatched in the beginning of April (Fig. 7b, c) and moulted a first time till middle of April, a second (Fig. 7d), third (Fig. 7e, f) and fourth time in May and likely a fifth time till beginning of June (Fig. 7g), when a first pupa was found (Fig. 7h).

Bourdonné et al. (2013) reported, that *Ch. latecincta latecincta* develops on an *Linaria alpina* and *L. supina*, as well as *Antirrhinum latifolium* Mill. in the French Alps (800–1500 m) and they develop from September to April, with a quiescence inbetween. The same authors reported a larval development from May to June for *Ch. latecincta decipiens* (Franz, 1938) from the Pyrenees.

C*hrysolina* (*Stichoptera*) *latecincta norica* (Holdhaus, 1914)

Note. Kippenberg (2020) lists this subspecies from the Alps of Austria and Switzerland.

Material. 1 ♀: Fusio // Campolungo Fusio 21.7.[19]10 // COF06499 coll. Fontana (MCSN). 2 ♂: Fusio // Campolungo Fusio II.7.[19]12 // *Chrysomela sanguinolenta* // COF06497 coll. Fontana (MCSN). 3 ♂, 4 ♀: Fusio, Ticino, G. C. C. // G. C. Champion Coll. M.B. 1927-409 (BMNH). 1 ♂: Fusio // VII.7.[19]36 // COF06498 coll. Fontana (MCSN). 1 ♂: Parsenn, 11.9.[19]38, leg. Dr. J. P. Wolf (MHNG). 2 ♂: Avers-Cresta, VII-VIII. [19]39, coll. V. Allenspach (NMBA). 1 ♀: Valetta [Piz Vallatscha?], 13.7.(19)45, 2900 m, Schuel [or Schuls, hardly legible], E. Handschin (NMCH). 2 ♂: Albula[pass], 24.VII. [19]49, Dr. J.P. Wolf (MHNG). 2 ex. GR, Avers, Juppa, Bergalga, 25.7.1989, 2007 m, leg. E. Kobel (NMBE). 9 ex.: GL, Claridenfirn, oberhalb Claridenhütte, 2400–2500 m, 22.8.2012 (cAS). 5 ex.: dito 15.8.2013, leg. Schnetzler and Tanaka (cAS). 7 ex. GR, Albula[pass], 783624/ 162365, 2532 m, 15.VIII. 2014, leg. Y. Chittaro (cYC).

Remarks. One of us (MG) revisited the area around Bergalga (Avers) on two occasions, in September 2012 and August 2017. Despite two days of intensive searching, no *Ch. latecincta* were found. Further literature records are adopted from Kippenberg (2020), and Szallies and Brenneisen (2015): Pizol, Albulapass.

A remarkable locality of *Ch. latecincta norica* is Passo Campolungo near Fusio (Ticino), separated from the nearest known populations by some 70 km and several mountain ranges. A single female specimen from this locality was discussed in Franz (1949) and Kippenberg (2020). Seven specimens, including males, collected before 1927 and labelled simply « Fusio, Ticino » were collected by G.C. Champion (BMNH). The Fontana collection (MCSN) contains four specimens from Passo Campolungo dating from 1912 to 1936. These specimens do not show any relevant differences to the other Swiss specimens of ssp. *norica* examined here. A targeted field trip undertaken 1st and 2nd September 2021 by MB and CG did not yield any specimens. The occurrence of the host plants *Linaria alpina* in the area was confirmed (Fig. 8), however, the small, scattered plants might not have provided enough food to sustain a population of the *Chrysolina*. Further exploration of the area, particularly on the Fusio side of the pass, is planned. Unfortunately, it is possible that this interesting, isolated population has already gone extinct in the 87 years since its last sighting.

Chrysolina (*Stichoptera*) *rossia* (Illiger, 1802)

Note. A species primarily distributed in the Balkan Peninsula and Italy but reaching also France and Central Europe. Kippenberg (2010) lists it for Austria, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Greece, Hungary, Italy, Romania, Slovakia, Slovenia, Switzerland and Serbia. In Switzerland, it is restricted to Ticino.

Material. 1 ex. TI, Lugano [without date nor collector] (MHNG). 1 ex. Lugano [without date], leg. and coll. Andrewes (BMNH). 1 ex.: Castello [Castel San Pietro], [without date], COFO6475, GBIFCH00227782, coll. Fontana (MCSN). 4 ex.: Castello [Castel San Pietro], [without date], COFO6478, GBIFCH00227788, coll. Fontana (MCSN). 2 ex.: Castello [Castel San Pietro],

Figure 7. a-f. Preimaginal stages of *Chrysolina latecincta latecincta* from Griespass. **a.** Egg; **b.** Freshly hatched larva; **c.** First instar larval; **d.** Third instar Larva; **e.** Freshly moulted larva after 3rd moult; **f.** Fourth instar larva in February; **g.** Fifth (Last) larval instar; **h.** Pupa (Photos: C. Germann).

[without date], COFO6479, GBIFCH00227789, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], [without date], COFO6479, GBIFCH00227790, coll. Fontana (MCSN). 1 ex. Lugano, Windrath (MHNG). 1 ex. VS, Martigny [without date nor collector, misplaced or mislabelled specimen] (MHNG). 1 ex. Capolago-Meride, 7.IX.[19]19, Fruhstorfer (MHNG). 2 ex. [TI] Monte Bré, 30.9.[19]22, coll. E. Handschin (NMB). 1 ex. [TI] Rancate, 3.10.[19]22, coll. E. Handschin (NMB). 1 ex.: Castello [Castel San Pietro], 10.1923, COFO6479, GBIFCH00227791, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], 6.2 [5?].1926, COFO6475, GBIFCH00227783, coll. Fontana (MCSN).1 ex.: Chiasso, 3.6.1928, COFO6473, GBIFCH00227775, coll. Fontana (MCSN). 1 ex.: Chiasso, 10.10.1931, COFO6473, GBIFCH00227776, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], 3.7.1932, COFO6475, GBIFCH00227784, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], 11.5.1932, COFO6475, GBIFCH00227785, coll. Fontana (MCSN). 2 ex.: Frasco,

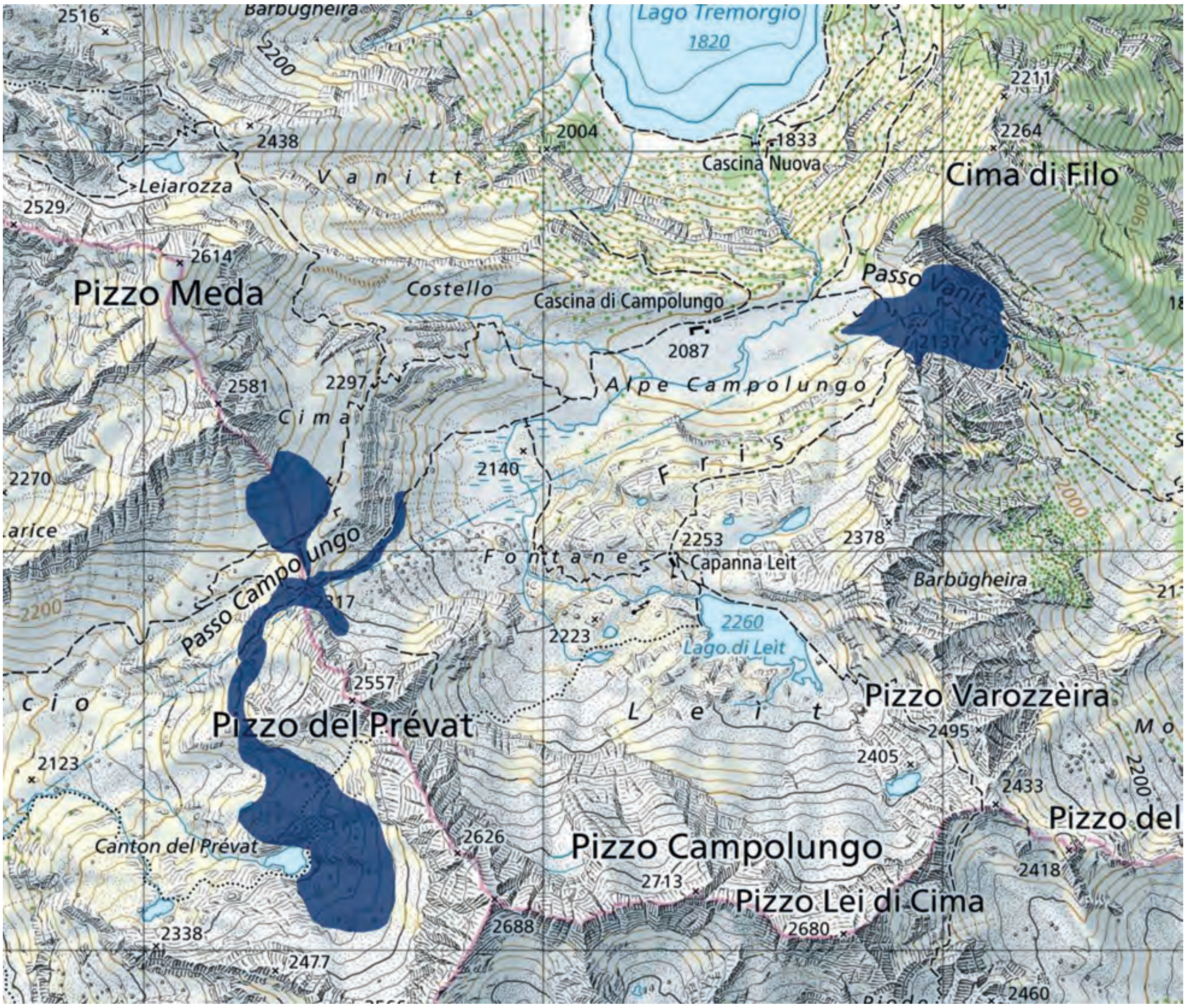


Figure 8. Investigated area around the Passo Campolungo with confirmed occurrences of the host plant (*Linaria alpina*), but without any recent records of *Chrysolina latecincta* (Background map: map.geo.admin.ch).

6.10.1932, COFO6477, GBIFCH00227787, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], 20.6.1937, COFO6474, GBIFCH00227781, coll. Fontana (MCSN). 1 ex.: Chiasso, 21.6.1939, COFO6473, GBIFCH00227777, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], 4.3.1939, COFO6474, GBIFCH00227778, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], 9.6.1939, COFO6474, GBIFCH00227779, coll. Fontana (MCSN). 1 ex.: Castello [Castel San Pietro], 16.6.1939, COFO6474, GBIFCH00227780, coll. Fontana (MCSN).1 ex. Kt. Tess. Salorino 4.[19]40, leg. and coll. J. Lautner (NMB). 6 ex. Kt. Tess. Salorino 8.[19]40, leg. and coll. J. Lautner (NMB). 3 ex.: Chiasso, 29.5.1944, COFO6476, GBIFCH00227786, coll. Fontana (MCSN). 1 ex. [TI] Muzano [Muzzano] 8.10.[19]50, leg. and coll. E. Handschin (NMBA). 2 ex. 1 ex. Comer See [Lago di Como, TI?] coll. Killias, in coll. J.B. Jörger (NMB). 1 ex. TI, Bogno, 5.8.1963, leg. and coll. P. Scherler (NMBE). 1 ex. TI, Rovio, 26.8.1971, leg. and coll. P. Scherler (NMBE). 1 ex. TI, Rancate, 30.7.1975, leg. and coll. P. Scherler (NMBE). 2 ex. TI, Melano, 29.8.1989, leg. and coll. P. Scherler (NMBE). 1 ex.: Helv, TI, Mendrisio, Besazio, Vigna, 718130/80940, 392 m, 07.X.2002, leg. C. Monnerat, det. M. Borer (cCM). 1 ex.: Helv, TI, Chiasso, Pedrinate, 721750/76500, 07.VIII.2003, leg. C. Monnerat, det. M. Borer (cCM). 1 ex.: Helv, TI, Mendrisio, Meride, village, 717625/83270, 05.V.2005, leg. C. Monnerat, det. M. Borer (cCM). 1 ex.: Helv, TI, Stabio, Gerette, 715500/77500, 13.X.2007, leg. C. Monnerat, det. M. Borer (cCM). 1 ex. TI, Meride, 550 m, 718030/ 083360, 4.6.2013, leg. Y. Chittaro, det. M. Borer (cYC). 1 ex.: Helv, TI, Chiasso, Pedrinate, San Stefano, 721818/76517, 450 m, 05.V.2014, leg. C. Monnerat, det. M. Borer (cCM). 2 ex.: Helv., TI, Rancate, 718274/81169, 396 m, 31.V.2016, leg. Y. Chittaro, det. M. Borer 2019 (cYC).

As this species is recognisable even on photographs, recent « citizen science » data are usually trustworthy. iNaturalist (https://www.inaturalist.org/, accessed 1th February 2023) provide supplementary observations (without voucher specimen) from Chiasso (30th April 2015, 27th April 2020), Brissago (19th October 2016), Giumaglio (24th December 2020) and Aquila (30th May 2022).

***Chrysolina* (*Stichoptera*) *sanguinolenta* (Linné, 1758)**

Note. Arguably the most widespread species of the subgenus, found across the Palaearctic Region from Great Britain to eastern Siberia and Mongolia, but absent from the Iberian Peninsula (Kippenberg 2010). Rheinheimer and Hassler (2018) noted that this species has recently seen a sharp population decline in Germany but were not able to name any causes for this.

Material. 1 ex. Genève, Veyrier, 7.VI. [without year] coll. Maerky (MHNG). 2 ♂, 2 ♀: «Basel» [without date, historical collection] (NMBA). 1 ex.: VD, Bavois, 5 [without date], coll. G. Toumayeff (MHNG). 2 ex.: GE, Genève, Bernex, dans rails du Tram, 452 m, coll. Ruchat [without date] (MHNG). 1 ♀: Sargans, leg. Meli 1878, ex coll. Tr [Täschler? Record mentioned in Hugentobler 1966] (NMSG). 1 ex. Niouc [Anniviers] e.V.[18]90 (MHNG). 1 ♂: VS, Sion, 8.V.[18]97 (MHNG). 1 ex.: GE, Chèvres [Bernex] 5.7.[19]03, coll. J. Simonet (MHNG). 1 ♂ : Bex, 9. V. [19]04, leg. and coll. G.E. Bryant (BMNH). 1 ex. Genève, Bel-Air, Rte. d'Ambi[lly], 22.4.[19]17 (MHNG). 1 ♂: VD, St Cergues V. [St-Cergue] 7.VII.[19]21 (MHNG). 1 ♀: Schuls, 28.7.[19]21, leg. E. Handschin (NMCH). 1 ex.: GR, Tarasp, 8.1938, coll. G. Toumayeff (MHNG). 1 ex.: GR, Schuls, 6.1939, coll. G. Toumayeff (MHNG). 1 ex.: Boulex [VD], 7.8.1941 (AGRO). 1 ex. VD, Bursinel, 26.IV.1943, coll. Audéoud (MHNG). 1 ex. [VS] La Bâtiaz, 5.6.[19]49, leg. and coll. E. Handschin (NMBA). 1 ♂: Scuol GR 24.VIII.-10.9.[19]53, coll. V. Allenspach (NMBA). 1 ex. VD, Vincy, 6.6.[19]54 (MHNG). 1 ex. GE, Genève, Onex, 24.4.[19]59, coll. J. Rappo (MHNG). 1 ♂ GE, Genève, Onex, 25.4.[19]59, coll. J. Rappo (MHNG). 1 ex. GE, Genève, Onex, 10.5.[19]59, coll. J. Rappo (MHNG). 1 ♂, 2 ex.: GE, Genève, Onex, 15.3.[19]60, coll. J. Rappo (MHNG). 1 ex. GE, Genève, Onex, 31.3.[19]60, coll. J. Rappo (MHNG). 3 ex. GE, Genève, Onex, 15.3.[19]61, coll. J. Rappo (MHNG). 1 ex.: VD, Lavey-Morcles, Savatan, 28.5.1964, leg. and coll. P. Scherler (NMBE). 1 ex. Genf, 9. [19]66 (MHNG). 1 ex.: VD, Romainmôtier, 5.[19]70, coll. G. Toumayeff (MHNG). 3 ex.: Begnins [VD] c/nous, 9.5.1970, C. Poluzzi (MHNG). 1 ex.: Begnins [VD] 5.10.[19]71, Poluzzi (MHNG). 1 ex.: Begnins [VD] 17.10.[19]71, Poluzzi (MHNG). 1 ex.: Begnins [VD] 18.10.[19]71, Poluzzi (MHNG). 2 ex.: Begnins [VD] 21.10.[19]71, Poluzzi (MHNG). 1 ex.: Begnins [VD] en Moinsel, 27.10.[19]71, Poluzzi (MHNG). 1 ex.: Begnins [VD] 28.10.[19]71, Poluzzi (MHNG). 1 ♂, 1 ♀ VD, Begnins, Villa Caendet 1971, leg. C. Poluzzi (MHNG). 165 ex. same locality, breeding experiments 1971–1973 (MHNG). 3 ex. Suisse-Vaud, Begnins-élevage, VII-VIII. 1972, [C.] Poluzzi (MHNG). 23 ex. Vaud, Begnins, 25.IX.[19]72, C. Poluzzi (MHNG).

Remarks. Even though this species seems to have been once common and widely distributed in Switzerland, our survey of the available data paints a rather alarming picture. The most recent records of this species in Switzerland date back to the early 1970ies! Given the amount of collecting activity in many of its former localities in recent decades, its sudden decline cannot be entirely attributed to a lack of sampling.

The larvae of this species are notable for being pale brownish in colour (Fig. 9), in contrast to the dark brown or black larvae we observed for *Ch. kuesteri* and *Ch. latecincta*. This is based upon observations by Carlo Poluzzi in the canton Vaud in the early 1970ies, when he was still able to find this species in abundance at Begnins. At the time, he also reared this species on *Linaria vulgaris* and carefully documented his results in a drawing, which is kept at MHNG alongside his collection (Fig. 9). Bourdonné et al. (2013) provided a photograph of the pale reddish brown larva of this species.

In September 2022, an attempt was made to find specimens of *Ch. sanguinolenta* in vineyards around Begnins (Vaud), where it was last observed, but unfortunately without success.

Discussion

Our revision of specimens in various museums and private collections often revealed a colourful mixture of species standing under the same name in the collection. We found specimens of *Ch. kuesteri*, *Ch. rossia*, as well as occasionally *Ch. latecincta*, and even *Ch. limbata* (Fabricius, 1775), a member of the subgenus *Zeugotaenia* Motschulsky, 1860, all standing as *Ch. sanguinolenta* or *Ch. marginalis*! A thorough revision of the determinations often including extraction of the male genitalia proved to be paramount for gathering faunistic data. We therefore

Figure 9. Preimaginal stages of *Chrysolina sanguinolenta* on *Linaria vulgaris*. Drawing by Carlo Poluzzi, original in the MHNG.

advise biological recorders and conservationists working on similarly complicated taxa to refrain from uncritically downloading data from online databases, even if those originate from a museum collection, unless these data are clearly shown to be recently verified by a specialist.

A browse through the «citizen science» data of *Stichoptera* currently available on iNaturalist (https://www.inaturalist.org/, accessed 4th January 2023) also revealed numerous misidentifications, including some labelled as «research grade».

Due to the historical confusion of *Ch. sanguinolenta* with its relatives, we were not able to use a large part of the data in the published literature, unless backed up by voucher specimens. The only literature records we were able to accept directly are those contained within Kippenberg (2020) and Szallies and Brenneisen (2015).

From a conservation point of view, our current state of knowledge is too poor to evaluate the Swiss *Stichoptera* taxa using IUCN criteria. However, we can make some tentative statements about the conservation status of the taxa in Switzerland: *Ch. kuesteri* is much more abundant than previously known, particularly in Valais, with many recent records. It appears to be the least threatened of all the Swiss taxa. Our recent field observations of *Ch. kuesteri* in Valais (Mont d'Orge), may help to shed some light on the ecology of this species. Most of the beetles were observed within the vineyards, smaller numbers at southern exposed sites in the rocky step towards the peak of Mont d'Orge. Around Leuk, our targeted search also revealed a large abundance in a similar habitat. It is notable that Valais is a particularly well sampled area for Coleoptera, and yet most collections made during the past decades did not contain any *Ch. kuesteri*. Of the 86 voucher specimens we examined, only 21 were collected before 2000, over a range of 120 years, but 65 were collected since 2000. We therefore assume that this species has markedly increased in abundance during the last 20 or so years. Rheinheimer and Hassler (2018) made some similar observations in SW Germany (Kaiserstuhl area), where they found a sharp increase in sightings in recent years, also in vineyards. The reasons for this apparent population increase remain unknown. We can only speculate that the warming climate might have had an influence, or a change in the use of insecticides in vineyards.

Ch. latecincta latecincta is a high-altitude species potentially threatened by anthropogenic climate change in the long term. However, no drastic population decline was apparent based on our data. *Ch. latecincta norica* seems to have habits similar to the nominotypical subspecies, but with more widely scattered populations. Our failure to find recent specimens of this species in two well-known localities so far may point to a population decline. A potential threat is climate change and associated greening (Choler et al. 2021) of alpine habitats.

Ch. rossia is restricted to Ticino, but its populations appear to be stable and not in decline, with a fair number of recent observations.

Ch. sanguinolenta, despite being locally common at least in some regions until the 1970ies, has not been recorded from Switzerland for 50 years and must be feared extinct! It turned out to be a particular problem that many records of *Ch. kuesteri* and occasionally other species were misidentified as this species, obscuring its recent decline. Targeted surveys are now urgently needed, to find surviving populations. Furthermore, the causes of this species' decline need to be better understood.

Our rearing experiments for *Ch. kuesteri* and *Ch. latecincta* confirm a remarkable plasticity in the developmental time for both species. We also confirm a certain oligophagy, already postulated in the relevant literature, for *Ch. kuesteri*, which readily accepts two different species of *Linaria*, even though the host plant of this particular population in the field seems to be *Veronica*. For *Ch. latecincta* we confirm that other species than *Linaria alpina* are accepted (both genera are part of the Plantaginaceae, but in different tribes). Hence, we assume that both species may handle uncomfortable environmental conditions and/or loss of host plants to a certain degree. A regular development in winter can be confirmed for *Ch. kuesteri*. *Ch. latecincta latecincta* may also develop in winter, depending on the altitude and population. A larval development from spring to summer is likely to be the rule for the population on Griespass (2400 m), where a thick snow cover remains until early summer, greatly slowing down plant growth.

Acknowledgements

We cordially acknowledge our colleagues Hannes Baur (NMBE), Hermann Blöchlinger (Erschmatt), Stève Breitenmoser (AGRO), Yannick Chittaro (Conthey), Roman Graf (Kriens), Michael Greff (ETHZ), Stefan Liersch (NMCH), Lukas Lischer (Zug), Christian Monnerat (Neuchâtel), Alexander Szallies (Reutlingen), Karin Urfer (Naturmuseum St. Gallen) and Lucia Pollini (MCSN) for access to their collections and valuable information, Vivien Cosandey (MHNG) kindly helped with specimens (and labels) from the MHNG, Andreas Sanchez (info fauna) kindly helped us with the maps, and Horst Kippenberg (Herzogenaurach) kindly provided expert's knowledge. We cordially acknowledge Annette Geiser-Barkhausen and Urs Lemmenmeier for providing specimens of *Ch. kuesteri* from Mont d'Orge, which initiated the present co-authored paper, and Maxwell Barclay (BMNH) for his general support to one of us (MG) during difficult months during pandemic times while the BMNH was closed. We cordially acknowledge the referees for their helpful comments on the manuscript.

References

Bieńkowski AO (2001) A study on the genus *Chrysolina* Motschulsky, 1860, with a checklist of all the described subgenera, species, subspecies, and synonyms (Coleoptera: Chrysomelidae: Chrysomelinae). Genus 12(2): 105–235.

Bieńkowski AO (2019) *Chrysolina* of the world (Coleoptera: Chrysomelidae). Taxonomic review. Mukhametov G. V., Livny, 920 pp.

Blanc M, Besuchet C, Reuteler C, Merz B (2012) Superfamille Chrysomeloidea. In: Merz B (Ed.) Liste Annotée des Insectes (Insecta) du Canton de Genève. Genève, Instrumenta Biodiversitatis VIII, Gilbert-E. Huguet, 166–176. [532 pp.]

Borer M, Chittaro Y (2016) Erstmeldung von *Lilioceris schneideri* (Weise, 1900) für die Schweiz (Coleoptera, Chrysomelidae, Criocerinae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 89: 69–72. https://doi:10.5281/zenodo.51889

Bourdonné J-C, Doguet S and Petitpierre E (2013) *Chrysolina* (*Stichoptera*) *oceanoripensis* nova species, endémique des dunes françaises des Landes de Gascogne et considérations sur le sous-genre *Stichoptera* Motschulsky, 1860 (Coleoptera, Chrysomelidae). Nouvelle Revue d'Entomologie (N.S.) 29: 33–52.

Choler P, Bayle A, Carlson BZ, Randin C, Filippa G, Cremonese E (2021) The tempo of greening in the European Alps: Spatial variations on a common theme. Global Change Biology 27(21): 1–15. https://doi.org/10.1111/gcb.15820

Döberl M (1995) Der heutige Alticinen-Artenbestand der Schweiz (Coleoptera, Chrysomelidae, Alticinae). Mitteilungen der entomologischen Gesellschaft Basel 45(2): 42–96.

Favre E (1890) Faune des Coléoptères du Valais et des régions limitrophes. Nouvelles Mémoires de la Société Helvétique des Sciences Naturelles 31: e448.

Franz H (1938) Revision der Verwandtschaftsgruppe der *Chrysomela gypsophilae* Küst. Entomologische Blätter 34(4): 190–210. [und 34(5): 249–273.]

Franz H (1949) Zur Kenntnis der Rassenbildung bei Käfern der ostalpinen Fauna. Zentralblatt für das Gesamtgebiet der Entomologie 3: 5–23.

Fritzlar F, Schöller M, Sprick P (2021) Rote Liste und Gesamtartenliste der Blatt-, Samen – und Resedakäfer (Coleoptera: Chrysomelidae, Bruchidae; Urodontinae) Deutschlands. Naturschutz und Biologische Vielfalt 70(5): 293–331.

Germann C (2010) Die Rüsselkäfer der Schweiz – Checkliste (Coleoptera, Curculionoidea) mit Verbreitungsangaben nach biogeografischen Regionen. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 83: 41–118.

Germann C (2011) *Aphthona nigriceps* (Redtenbacher, 1842) – neu für die Schweiz (Coleoptera, Chrysomelidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 84: 103–107.

Germann C (2021) Beitrag zur Praxis in der Entomologie: Zucht von phytophagen Käferlarven in Mehrzweckdosen (Coleoptera). Entomo Helvetica: 14: 105–108.

Germann C, Bernasconi M, Cordillot F (2013) Projektvorstellung «Aktualisierung Endemitenliste der Schweiz». Entomo Helvetica 6: 220–222.

Germann C, Borer M, Herger P (2020) Zum Vorkommen zweier heimlicher Blattkäfer in der Schweiz: *Cryptocephalus imperialis* (Laicharting, 1781) und *C. octomaculatus* Rossi, 1790 (Coleoptera, Chrysomelidae). Entomo Helvetica 13: 73–79.

Helliesen T (1912) La grupo *Chrysomela sanguinolenta*. Stavanger Museums Aarshefte 22 [1911]: 1–15.

Hugentobler H (1966) Beitrag zur Kenntnis der Käfer der Nordostschweiz. Naturwissenschaftliche Gesellschaft St. Gallen, 248 pp.

Kippenberg H (2010) Subfamily Chrysomelinae Latreille, 1802. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera (Vol. 6). Chrysomeloidea. Stenstrup, Apollo Books, 390–443. [924 pp.]

Kippenberg H (2020) *Chrysolina* (*Stichoptera*) *latecincta* (Demaison, 1896) und ihre Subspezies in den Alpen (Coleoptera, Chrysomelidae). Mitteilungen der Münchner Entomologischen Gesellschaft 110: 53–64.

Leschen R, Beutel R (2014) Coleoptera, Beetles (Vol. 3): Morphology and Systematics (Phytophaga). Walter de Gruyter GmbH, Berlin/Boston, 675 pp.

Löbl I, Smetana A [Eds] (2010) Catalogue of Palaearctic Coleoptera (Vol. 6), Chrysomeloidea. Apollo Books, Stenstrup, 924 pp. https://doi.org/10.1163/9789004260917

Luka H, Nagel P, Feldmann B, Luka A, Gonseth Y (2009) Checkliste der Kurzflügelkäfer der Schweiz (Coleoptera: Staphylinidae ohne Pselaphinae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 82: 61–100.

Monnerat C, Chittaro Y, Sanchez A, Gonseth Y (2015) Critères et procédure d'élaboration de listes taxonomiques nationales: le cas des Buprestidae, Cerambycidae, Lucanidae et Cetoniidae (Coleoptera) de Suisse. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 88: 155–172.

Rheinheimer J, Hassler M (2018) Die Blattkäfer Baden-Württembergs. Karlsruhe, Kleinsteuber Books, 928 pp.

Stierlin G (1898) Fauna Coleopterorum Helvetica. Teil II. Schaffhausen, Bolli und Boecherer, 662 pp.

Stierlin G, Gautard VV (1867) Fauna coleopterorum helvetica, die Käfer-Fauna der Schweiz. Schaffhausen und Vevey, 354 pp.

Szallies A, Brenneisen S (2015) Reliktpopulationen von endemischen Prioritätsarten aus den Schweizer Nordalpen. Schlussbericht. Zürich, Institut für Umwelt und Natürliche Ressourcen, 39 pp.

Winkelman J, Debreuil M (2008) Les Chrysomelinae de France (Coleoptera, Chrysomelidae). Supplément Rutilans, 188 pp.

Supplementary material 1

Label data, interpreted coordinates and collection references

Authors: Christoph Germann, Michael Geiser, Matthias Borer

Data type: collection data of all Chrysolina (Stichoptera) species investigated.

Explanation note: Label data, interpreted coordinates and collection references of all investigated specimens of the following species are given: *Chrysolina kuesteri* (Helliesen, 1912), *Ch. latecincta latecincta* (Demaison, 1896), *Ch. latecincta norica* (Holdhaus, 1914), *Ch. rossia* (Illiger, 1802) und *Ch. sanguinolenta*. These data are the basis for the maps provided (Fig 3).

Link: https://doi.org/10.3897/alpento.7.105937.suppl1

Alpine Entomology 7 2023, 83–134 | DOI 10.3897/alpento.7.106089

New species of *Labiobaetis* Novikova & Kluge from New Guinea (Ephemeroptera, Baetidae): a never-ending story of diversity

Thomas Kaltenbach[1,2], Laurent Vuataz[1,2], Jean-Luc Gattolliat[1,2]

1 *Muséum cantonal des Sciences Naturelles, Département de zoologie, Palais de Rumine, Place Riponne 6, CH-1005 Lausanne, Switzerland*
2 *University of Lausanne (UNIL), Department of Ecology and Evolution, CH-1015 Lausanne, Switzerland*

https://zoobank.org/EC4C4A0E-A1F0-4555-B5D4-A4F18AFED1AD

Corresponding author: Thomas Kaltenbach (thomas.kaltenbach@bluewin.ch)

Academic editor: Dávid Murányi ♦ **Received** 8 May 2023 ♦ **Accepted** 18 June 2023 ♦ **Published** 7 July 2023

Abstract

Investigations of material collected partly in 1999 and mainly between 2006 and 2016 in New Guinea, mostly along the high, central mountain chain of the island, further increased our knowledge of the diversity of the genus *Labiobaetis* Novikova & Kluge on this island. Previously, 37 species were reported from New Guinea. We have identified six new species using a combination of morphology and genetic analysis (COI). They are described and illustrated based on their larvae. Five of the six new species belong to the group *petersorum*, which is endemic to the island. Additionally, *Labiobaetis xeniolus* Lugo-Ortiz & McCafferty is also assigned to this group. The morphological characterisation of the group *petersorum* is enhanced, and a key to all species of this group is provided. Complementary descriptions and remarks to the morphology of known species of the group *petersorum* are provided. Additionally, a genetic analysis (COI) including most species and several additional Molecular Operational Taxonomic Units (MOTUs) of the group *petersorum* is discussed. One of the new species belongs to the group *vitilis*. The morphological characterization of this group is slightly enhanced, and the obtained COI sequence was added to the genetic analysis of the group *petersorum*. The total number of *Labiobaetis* species worldwide is augmented to 162.

Key Words

COI, integrative taxonomy, mayflies, morphology, MOTU

Introduction

The genus *Labiobaetis* Novikova & Kluge, 1987 is part of the Baetidae, which is the most divers family of Ephemeroptera, including approximately one third of all mayfly species worldwide (> 1160 species) in ca. 118 genera (Sartori and Brittain 2015; Jacobus et al. 2019; updated by the authors). *Labiobaetis* is the most divers genus of Baetidae and one of the most divers amongst mayflies in general, with 156 previously described species (Barber-James et al. 2013; Kaltenbach and Gattolliat 2018, 2019, 2020, 2021 and citations therein; Kaltenbach et al. 2020, 2022a and citations therein). The distribution of *Labiobaetis* is nearly worldwide, except for the Neotropical realm, New Zealand, New Caledonia and some remote islands. The history and concept of *Labiobaetis* were summarized in detail by Shi and Tong (2014) and Kaltenbach and Gattolliat (2018).

This contribution will focus on further new species of *Labiobaetis* from New Guinea. The first six species of *Labiobaetis* from New Guinea were reported by Lugo-Ortiz et al. (1999). Subsequently, a large study was carried out by Kaltenbach and Gattolliat (2018) with the description of 26 new species, followed by two smaller studies with additional new species (Kaltenbach et al. 2021a; Kaltenbach and Gattolliat 2021). Presently, a total of 37 species of *Labiobaetis* are reported from New Guinea. Six additional species are described in this study, augmenting the total number for New Guinea to 43 species, which is the highest density of different species worldwide for this genus. Five of the new species belong to the group *petersorum*, erected in Kaltenbach and Gattolliat (2018), which is the focus in this study. The morphological definition of the group is enhanced, another already known species was added (*L. xeniolus* Lugo-Ortiz & McCafferty, 1999), and COI sequences of the group are analysed. One of the new species belongs to the group *vitilis*, erected in Kaltenbach and Gattolliat (2018). The morphological characterization of the group is slightly enhanced, and the obtained COI sequence was added to the genetic analysis of the group *petersorum*.

New Guinea, the second largest island after Greenland, is known for its exceptional diversity. It is a geological composite consisting of many separate terranes; the evolutionary history of the biota involves connections to the Australian landmass, uplift, volcanism, and rifting that accompanied the tectonic events (Allison 2010). There is strong evidence that recent environmental change in the extremely structured central highlands of New Guinea with its ongoing formation of rich aquatic resources, remote valleys and mountain blocks has been the primary driver of diversification of aquatic insects in that area (Toussaint et al. 2013, 2014).

Given the extraordinary diversity of New Guinea, the limited collection efforts in the past, the presence of many unexplored areas, and the exceptional richness of *Labiobaetis* on the island, it is reasonable to anticipate the discovery of numerous additional species through future collection efforts.

Materials and methods

All specimens were preserved in 70%–96% ethanol. The dissection of larvae was done in Cellosolve (2-Ethoxyethanol) with subsequent mounting on slides with Euparal liquid, using an Olympus SZX7 stereomicroscope.

Photographs of larvae were taken using a Canon EOS 6D camera and processed with the programs Adobe Photoshop Lightroom (http://www.adobe.com) and Helicon Focus version 5.3 (http://www.heliconsoft.com). Photographs of larval parts on slides were taken with an Olympus BX43 microscope equipped with an Olympus SC 50 camera and the program Olympus CellSense v. 4.1. The SEM picture was taken using a FEI Quanta FEC 250 electron microscope (Thermo Fisher). All photographs were subsequently enhanced with Adobe Photoshop Elements 13.

The DNA of part of the specimens was extracted using non-destructive methods allowing subsequent morphological analysis (see Vuataz et al. 2011 for details). We amplified a 658 bp fragment of the mitochondrial gene cytochrome oxidase subunit 1 (COI) using the primers LCO 1490 and HCO 2198 (Folmer et al. 1994, see Kaltenbach and Gattolliat 2020 for details). Sequencing was done with Sanger's method (Sanger et al. 1977). Forward and reverse sequencing reads were assembled and edited in CodonCode Aligner 10.0.2 (Codon-Code Corporation, Dedham, MA), and aligned using MAFFT (Katoh et al. 2019) with default settings as implemented in Jalview 2.11.2.6 (Waterhouse et al. 2009). The number of parsimony-informative sites of the alignment was calculated in MegaX (Kumar et al. 2018; Stecher et al. 2020). Pairwise COI distances were calculated using the dist.dna function of the ape 5.7-1 package (Paradis and Schliep 2019) for R 4.2.3 (R Core Team 2023), under the raw model and the pairwise.deletion option, corresponding to uncorrected p-distances (see Srivathsan and Meier 2012) with missing data removed in a pairwise way. Mean, minimum and maximum distances within and between COI putative species, referred to as Molecular Operational Taxonomic Units hereafter (MOTUs), were calculated using the ddply function of the plyr 1.8.8 package (Wickham 2011). The COI sequences were attributed to species based on morphological evidence, with seven additional MOTUs within *L.* cf. *xeniolus* (*L.* cf. *xeniolus* A–G) defined according to the most conservative species delimitation method (i.e., GMYC; see below).

Before reconstructing the COI gene tree, the best evolutionary model (GTR+ Γ +I) was estimated following the second-order Akaike information criterion (AICc; Hurvich and Tsai 1989) implemented in JModelTest 2.1.10 (Darriba et al 2012) with five substitution schemes and six Γ categories and all other parameters set to default. To accommodate different substitution rates among COI codon positions, we analysed our data set in two partitions, one with first and second codon positions and one with third positions (1 + 2, 3). Bayesian inference (BI) gene tree reconstruction was conducted in MrBayes 3.2.7a (Ronquist et al. 2012). Two independent analyses of four MCMC chains run for three million generations with trees sampled every 1'000 generations were implemented, and the first 10% of generations were discarded as burn-in after visually verifying run stationarity and convergence in Tracer 1.7.2 (Rambaut et al. 2018). The sequence GBIFCH00975629, corresponding to *L. kokoda* sp. nov. (Table 1), was used as outgroup as it is the only non-member of the group *petersorum* (see Results). The consensus tree was visualized and edited in iTOL 6.7.4 (Letunic and Bork 2021).

To explore COI evolutionary divergence and compare it to our morphological identifications, we applied three single-locus species delimitation methods to our COI data set: the distance-based ASAP (Assemble Species by Automatic Partitioning; Puillandre et al. 2020), the tree-based PTP (Poisson Tree Processes; Zhang et al 2013) and GMYC (General Mixed Yule-Coalescent; Pons et al. 2006; Fujisawa and Barraclough 2013) approaches. The ASAP method, which is an improvement of the widely used ABGD (Automatic Barcode Gap Discovery; Puillandre et al. 2012) approach, has the advantage of providing a score (i.e., asap-score) that designates the most likely number of hypothetical species. The PTP approach exploits the differences between the relationships among and within species, using the number of substitutions from a phylogenetic tree. The GMYC model, which also exploits intra and interspecies phylogenetic differences, uses time rather than direct number of substitutions, and thus requires a time-calibrated ultrametric tree as input. ASAP was applied to our COI alignment using the ASAP webserver available at https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html, computing the genetic distances under simple p-distances with all other settings set to default. Input maximum likelihood tree for PTP was generated in RAxML-NG 1.1.0 (Kozlov et al. 2019) from our COI alignment, selecting the all-in-one (ML search + bootstrapping) option and MRE-based bootstrap convergence criterion. The best model of evolution and the partition scheme specified above, as well as 50 random and 50 parsimony starting trees were implemented. PTP was conducted on the web service available at https://mptp.h-its.org, selecting the partition with the lowest asap-score. Input BI ultra-metric tree for GMYC was generated in BEAST 1.10.4. (Suchard et al. 2018). To avoid potential biases in threshold estimation, the identical COI haplotypes were pruned (see Talavera et al. 2013) using Collapsetypes 4.6 (Chesters 2013). Input BEAST file was created in BEAUTi 1.10.4 (Suchard et al. 2018), implementing the best model of evolution and the partition scheme specified above, and selecting a relaxed molecular clock (uncorrelated lognormal) model, a coalescent (constant size) prior (see Monaghan et al. 2009) and a UPGMA starting tree. Two independent MCMC chains were run for 30 million generations, sampling trees every 1000 generations. Run stationarity and convergence was visually verified in Tracer and the independent log and tree files were combined using LogCombiner 1.10.4 (Suchard et al. 2018) after discarding the first 10% of the trees as burn-in. The maximum clade credibility tree, generated in TreeAnnotator 1.10.4 (Suchard et al. 2018) with all options set to default, was used as input for GMYC, which was run in R using the SPLITS package 1.0-20 (Ezard et al. 2021). We favoured the single-threshold version of the GMYC model because it was shown to outperform the multiple-threshold version (Fujisawa and Barraclough 2013).

Table 1. Sequenced specimens.

Species	Specimen voucher	GenBank #	GenSeq
	catalogue #	(COI)	Nomenclature
L. gladius	GBIFCH00465179	MH619486	genseq-4 COI
L. janae	GBIFCH00465181	MH619483	genseq-1 COI
	GBIFCH00465182	MH619489	genseq-2 COI
L. amber sp. nov.	GBIFCH00763716	OQ947296	genseq-2 COI
L. bilibil sp. nov.	GBIFCH00763602	OQ947297	genseq-2 COI
L. kinibeli sp. nov.	GBIFCH00829887	OQ947310	genseq-2 COI
	GBIFCH00975628	OQ947311	genseq-1 COI
	GBIFCH00975632	OQ947312	genseq-2 COI
	GBIFCH00763775	OQ947309	genseq-2 COI
L. nabire sp. nov.	GBIFCH00980888	OQ947313	genseq-1 COI
	GBIFCH00980889	OQ947314	genseq-2 COI
L. cf. *petersorum*	GBIFCH00763702	OQ955856	genseq-4 COI
L. cf. *xeniolus* A	GBIFCH00829891	OQ947299	genseq-4 COI
	GBIFCH00829892	OQ947300	genseq-4 COI
	GBIFCH00829890	OQ947298	genseq-4 COI
L. cf. *xeniolus* B	GBIFCH00829889	OQ947302	genseq-4 COI
	GBIFCH00829888	OQ947301	genseq-4 COI
L. cf. *xeniolus* C	GBIFCH00763703	OQ947303	genseq-4 COI
L. cf. *xeniolus* D	GBIFCH00975631	OQ947304	genseq-4 COI
L. cf. *xeniolus* E	GBIFCH00975627	OQ947305	genseq-4 COI
L. cf. *xeniolus* F	GBIFCH00763704	OQ947306	genseq-4 COI
	GBIFCH00975630	OQ947307	genseq-4 COI
L. cf. *xeniolus* G	GBIFCH00829894	OQ947308	genseq-4 COI
L. sp. 1	GBIFCH00763711	OQ947315	genseq-4 COI
L. kokoda sp. nov.	GBIFCH00975629	OQ947316	genseq-1 COI

The GenBank accession numbers are given in Table 1, nomenclature of gene sequences follows Chakrabarty et al. (2013).

The distribution maps were generated with the program SimpleMappr (https://simplemappr.net, Shorthouse 2010).

The dichotomous keys were elaborated with the support of the program DKey v. 1.3.0 (http://drawwing.org/dkey, Tofilski 2018).

The terminology follows Hubbard (1995), Kluge (2004) and Kluge 2005 (term “protopteron”). The term “blank” is used to describe an unpigmented area of cuticle (Kluge et al. 2023).

Results

New species descriptions

Abbreviations:

MZB	Museum Zoologicum Bogoriense (Indonesia);
MZL	Muséum cantonal des Sciences Naturelles, Lausanne (Switzerland);
ZSM	Zoologische Staatssammlung München (Germany).

List of *Labiobaetis* species treated in this paper

petersorum group

1. *L. petersorum* (Lugo-Ortiz & McCafferty, 1999)
2. *L. xeniolus* (Lugo-Ortiz & McCafferty, 1999)
3. *L. gladius* Kaltenbach & Gattolliat, 2018
4. *L. janae* Kaltenbach & Gattolliat, 2018
5. *L. amber* sp. nov.
6. *L. bilibil* sp. nov.
7. *L. kinibeli* sp. nov.
8. *L. nabire* sp. nov.
9. *L. simbuensis* sp. nov.

vitilis group

10. *L. kokoda* sp. nov.

Labiobaetis petersorum group of species

(diagnosis enhanced from Kaltenbach and Gattolliat 2018)

Following combination of characters: A) antennal scape without distolateral process; antennal pedicel distally with triangular scales; flagellum usually with dots in middle part (Fig. 6a, b); B) labrum sub-rectangular, wide; dorsal, submarginal arc of setae well developed, composed of long, simple setae (Fig. 2a, b); C) both mandibles with outermost denticle blade-like enlarged (Fig. 9c, d, f, g); D) hypopharynx apically with well-developed tuft of stout setae, distolaterally with two additional tufts of setae; superlinguae distolaterally protruding (Fig. 3a); E) maxillary palp segment II distally pointed, constricted (Fig. 3c); F) labial palp segment II with thumb-like distomedial protuberance, apically rounded (Fig. 4d); G) hind protoptera absent; H) femur wide; dorsal margin with numerous short to medium, spine-like setae (usually > 40); apex on posterior side with stout setae on fore and middle leg, not on hind leg (Fig. 5a, e); I) claw with convex ventral margin; with long, fine, subapical seta in anterior position (between apex and first denticle. Subapical setae fine and transparent, sometimes difficult to see; seems to break easily and may also stick to the claw) (Fig. 12j, k); J) tergalii present on segments II–VII; usually large, tracheae strongly pigmented; anal margin with both long and short setae (Fig. 13d, e).

The *L. petersorum* group is known from New Guinea only, including the following species:

Labiobaetis petersorum
Labiobaetis xeniolus (new assignment to the group)
Labiobaetis gladius
Labiobaetis janae
Labiobaetis amber sp. nov.
Labiobaetis bilibil sp. nov.
Labiobaetis kinibeli sp. nov.
Labiobaetis nabire sp. nov.
Labiobaetis simbuensis sp. nov.

1. *Labiobaetis petersorum* (Lugo-Ortiz & McCafferty, 1999)

Pseudocloeon petersorum: Lugo-Ortiz et al. 1999.
Labiobaetis petersorum: Kaltenbach and Gattolliat 2018: fig. 16a–d.

Remarks to morphology. Larva. Based on the original description and the figures in Lugo-Ortiz et al. 1999, most of the diagnostic characters of group *petersorum* are present. Exceptions are: the presence of dots on the flagellum; two additional distolateral tufts of setae on hypopharynx; stout setae on posterior apex of fore and middle legs; anal margin of the tergalii with both short and long setae. These characters remain unknown until reexamination of type material. Subapical setae are also not described for this species.

Labiobaetis cf. *petersorum*: we studied specimens morphologically very similar to *L. petersorum,* but collected in a location far away from the type locality of *L. petersorum* (Fig. 38a, b). Unfortunately, we cannot compare COI sequences, because of the lack of a sequence from the type locality or nearby. Because of the geographical distance, we prefer to remain prudent and denominate these specimens as “cf. *petersorum*”. Interestingly, they have all characters of the group *petersorum,* except subapical setae.

Material examined (*L.* cf. *petersorum*). INDONESIA • 7 larvae; Papua Barat, Tamrau, Mts N of Kebar, sandy sunny riverbank; 00°47'02"S, 133°04'20"E; 758 m; 07.xi.2013; leg. M. Balke; (BH032); 1 on slide; GBIFCH00763702; 6 in alcohol; GBIFCH00975710; MZL.

2. *Labiobaetis xeniolus* (Lugo-Ortiz & McCafferty, 1999)

Pseudocloeon xeniolum: Lugo-Ortiz et al. 1999.

Remarks to morphology. Larva. Based on the original description and the figures in Lugo-Ortiz et al. 1999, most of the diagnostic characters of group *petersorum* are present. Exceptions are: the presence of dots on the flagellum; two additional distolateral tufts of setae on hypopharynx; stout setae on posterior apex of fore and middle legs; anal margin of the tergalii with both short and long setae. These characters remain unknown until complete re-examination of type material. Additionally, subapical setae are also not mentioned in the original description, but may have been overlooked. However, based on stacking videos, the fore legs of two paratypes have no subapical setae, other legs are not embedded in the slides (Lugo-Ortiz et al. 1999: 20).

MOTUs (see discussion in Kaltenbach et al. 2020). We studied specimens with the same morphology as *L. xeniolus*, collected in different locations far away from the type locality of *L. xeniolus* (Fig. 38a, b). The most important characters for the species assignment are: short, conical labial palp segment III; tergalii with remarkably strong development and pigmentation of tracheae; paraproct with poorly developed marginal spines. Based on COI sequences, we can distinguish seven different MOTUs (*L.* cf. *xeniolus* A–G; Table 1; Fig. 39). Unfortunately, a sequence from the type locality of *L. xeniolus* or nearby is lacking. We remain prudent and denominate these specimens as “cf. *xeniolus*”. Interestingly, these specimens have all characters of the group *petersorum*, including subapical setae. This is pointing into the direction that *L. xeniolus* from the type locality equally might have all characters of the group *petersorum*, incl. subapical setae.

Material examined. *Labiobaetis xeniolus*. ***Paratypes***. PAPUA NEW GUINEA • 2 larvae; Morobe Prov., Poverty Cr., Mt. Missim; 1600 m; 18.ix.1983; J.T. and D.A. Polhemus; on slides; PERC0012578, PERC0012579; Purdue University.

Labiobaetis cf. *xeniolus* A. PAPUA NEW GUINEA • larva; Western Highlands Prov., Simbai, Kairong River; 05°14'50"S, 144°28'27"E; 1850 m; 02.iii.2007; leg. Kinibel; (PNG 139); on slide; GBIFCH00829891; MZL • larva; Enga Prov., Wapanamanda; 05°38'06"S, 143°55'20"E; 1500 m; 06.xii.2006; leg. M. Balke and Kinibel; (PNG 128); on slide; GBIFCH00829892; MZL • larva; Madang Prov., Simbai area; 05°12'42"S, 144°35'31"E; 1800–2400 m; 08.iii.2007; leg. Kinibel; (PNG 151); on slide; GBIFCH00975618; MZL.

Labiobaetis cf. *xeniolus* B. PAPUA NEW GUINEA • 2 larvae; Central Prov., Tapini; 08°20'31"S, 146°59'49"E;

870 m; 29.x.2007; leg. Kinibel; (PNG 161); in alcohol; GBIFCH00515640, GBIFCH00829889; MZL • 1 larva; Central Prov., Kokoda Trek; 09°14'20"S, 147°40'32"E; 1400 m; i.2008; leg. Posman; (PNG 171); on slide; GBIFCH00829888; MZL.

Labiobaetis cf. *xeniolus* C. PAPUA NEW GUINEA • 16 larvae; Morobe Prov., Menyamya, Mt. Inji; nr 07°14'49"S, 146°01'20"E; 1700 m; 14.xi.2006; leg. M. Balke and Kinibel; (PNG 96); 1 on slide; GBIFCH00763703; 15 in alcohol; GBIFCH00829886; MZL.

Labiobaetis cf. *xeniolus* D. PAPUA NEW GUINEA • 2 larvae; Western Highlands Prov., Kundum; 05°16'06"S, 144°27'52"E; 1400 m; 03.iii.2007; leg. Kinibel; (PNG 142); 1 on slide; GBIFCH00975631; 1 in alcohol; GBIFCH00515635; MZL.

Labiobaetis cf. *xeniolus* E. PAPUA NEW GUINEA • 2 larvae; Central Prov., Kokoda Trek; 09°01'57"S, 147°44'27"E; 1400 m; i.2008; leg. Posman; (PNG 172); 1 on slide; GBIFCH00975627; 1 in alcohol; GBIFCH00515638; MZL.

Labiobaetis cf. *xeniolus* F. PAPUA NEW GUINEA • 6 larvae; Madang Prov., Simbai area; 05°13'23"S, 144°37'17"E; 1200 m; 10.iii.2007; leg. Kinibel; (PNG 152); 2 on slides; GBIFCH00515634, GBIFCH00763704; 4 in alcohol; GBIFCH00975619, GBIFCH00975668, GBIFCH00829896; MZL • 2 larvae; Madang Prov., Simbai area; 05°13'20"S, 144°37'37"E; 1200 m; 11.iii.2007; leg. Kinibel; (PNG 153); on slides; GBIFCH00515637, GBIFCH00975630; MZL.

Labiobaetis cf. *xeniolus* G. PAPUA NEW GUINEA • 4 larvae; Central Prov., Woitape; 08°31'35"S, 147°14'06"E; 1600 m; i.2008; leg. Posman; (PNG 165); 3 on slides; GBIFCH00592681, GBIFCH00975666, GBIFCH00829894; 1 in alcohol; GBIFCH00515627; MZL.

3. *Labiobaetis gladius* Kaltenbach & Gattolliat, 2018

Labiobaetis gladius: Kaltenbach and Gattolliat 2018.

Additional description. Larva. Re-examination of type material confirmed that the species has all of the diagnostic characters of the group *petersorum* as listed above. This includes characters not or not correctly described or illustrated in the original description (Kaltenbach and Gattolliat 2018: figs 17–18): flagellum with brown dots in middle part (as Fig. 6b); hypopharynx distolaterally with two additional tufts of setae (as Fig. 3a); anal margin of tergalii with both short and long, fine setae (as Fig. 6e); claw with convex ventral margin and with subapical seta (as Fig. 5k, l); femur posterior apex with stout setae on fore and middle legs, not on hind leg (as Fig. 5e).

Material examined. ***Paratypes.*** PAPUA NEW GUINEA • 3 larvae; Simbu Prov., Mt. Wilhelm, Pindaunde Creek, S5 (oria 6); 05°49'58"S, 145°06'08"E; 2350 m; 18.viii.1999; leg. L. Čížek; on slides; GBIFCH00456173, GBIFCH00465177, GBIFCH00456178; MZL.

4. *Labiobaetis janae* Kaltenbach & Gattolliat, 2018

Labiobaetis janae: Kaltenbach and Gattolliat 2018.

Additional description. Larva. Re-examination of type material confirmed that the species has most of the diagnostic characters of the group *petersorum* as listed above. This includes characters not or not correctly described or illustrated in the original description (Kaltenbach and Gattolliat 2018: figs 19–20): hypopharynx distolaterally with two additional tufts of setae (as Fig. 3a); anal margin of tergalii with both short and long, fine setae (as Fig. 6e); claw with very slightly convex ventral margin; claw with subapical seta (as Fig. 5l); femur posterior apex with stout setae on fore and middle legs, not on hind leg (as Fig. 5e). The flagellum has no brown dots, as it is usually the case in the group *petersorum*.

Material examined. ***Paratypes.*** INDONESIA • Papua Prov., Lake Habemma, stream; 04°07'46"S, 138°40'46"E; 3200 m; 19.x.2011; leg. M. Balke; (PAP07); on slide; GBIFCH00465182; MZL.

5. *Labiobaetis amber* sp. nov.

https://zoobank.org/289249EE-9562-44D6-A5F5-A602900CB96A

Figs 1–7, 38

Diagnosis. Larva. Following combination of characters differentiates *L. amber* sp. nov. from other species of the group *petersorum*: A) labrum length 0.6× maximal width (Fig. 2a); B) both mandibles without denticles between prostheca and mola (Fig. 2d, f); C) labial palp segment II with broadly rounded, thumb-like, distomedial protuberance; segment III nearly oblong (Fig. 4d); D) paraglossa dorsally with row of four long, spine-like setae near inner, distal margin (Fig. 4c); E) tibia with row of medium, stout, apically rounded setae on dorsal margin (Fig. 5f); posterior surface scattered with short, lanceolate setae (Fig. 5h); F) claw with ca. ten denticles (Fig. 5k); G) posterior margin of abdominal tergum IV with triangular, pointed spines, mostly slightly wider than long (Fig. 6c).

Description. Larva (Figs 1–7). Body length 6.2–8.2 mm. Cerci: ca. 3/4 of body length. Paracercus: ca. 1/2 of cerci length. Antenna: approx. twice as long as head length.

Cuticular colouration (Fig. 1a, b). Head, thorax and abdomen dorsally mainly brown, with pattern as in Fig. 1a. Forewing pads light brown with dark brown and grey stripes; abdominal tergum I grey with brown streak along distal margin; terga II–IV grey-brown, laterally brighter, with distolateral brown spots; terga V–VI off-white, laterally with darker areas; terga VII–VIII dark brown, laterally with whitish streak, medially with light brown line; tergum IX grey-brown with bright area medially; tergum X off-white. Thorax and abdomen ventrally grey-white, sterna VII–VIII darker. Legs off-white, femur medially with large grey area, with large blanks in distal and proximal area; tarsus distally grey-brown. Caudalii grey.

Figure 1. *Labiobaetis amber* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars: 1 mm.

Hypodermal colouration (Fig. 6b). Antenna with dark brown dots in middle part of flagellum.

Antenna (Fig. 6a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 2a, b). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. ten long, simple setae. Ventrally with marginal row of setae composed of lateral and anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 2c, d). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with four denticles, inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, smooth. Tuft of setae at apex of mola present.

Left mandible (Fig. 2e, f). Incisor and kinetodontium fused. Incisor with four denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, smooth. Subtriangular process rather short, basally broad, above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 3a). Lingua approx. as long as superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally protruding; lateral margins angulate; fine, long, simple setae along distal margin.

Maxilla (Fig. 3b, d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered, spine-like seta and ca. six long, simple setae. Maxillary palp slightly longer than length of galea-lacinia; 2-segmented; palp segment II slightly longer and narrower than segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 4a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. nine spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. five spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area and ca. two short, simple setae in anteromedial area; dorsally with four long, spine-

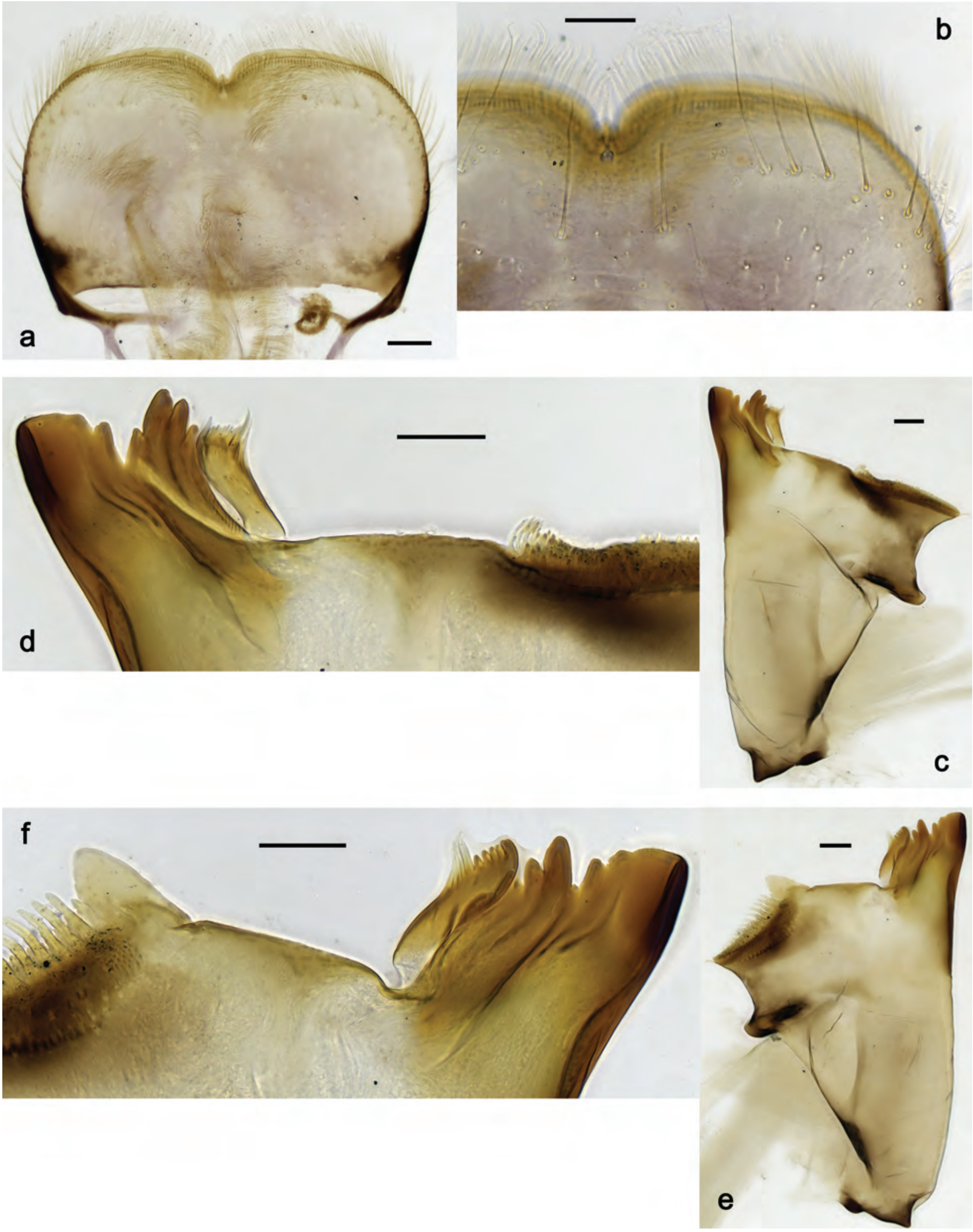


Figure 2. *Labiobaetis amber* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e, f.** Left mandible. Scale bars: 50 µm.

like setae near inner margin. Labial palp with segment I slightly shorter than length of segments II and III combined. Segment II with broadly rounded, thumb-like, distomedial protuberance; distomedial protuberance 0.5× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. six spine-like setae near outer margin. Segment III nearly oblong; length 1.1× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

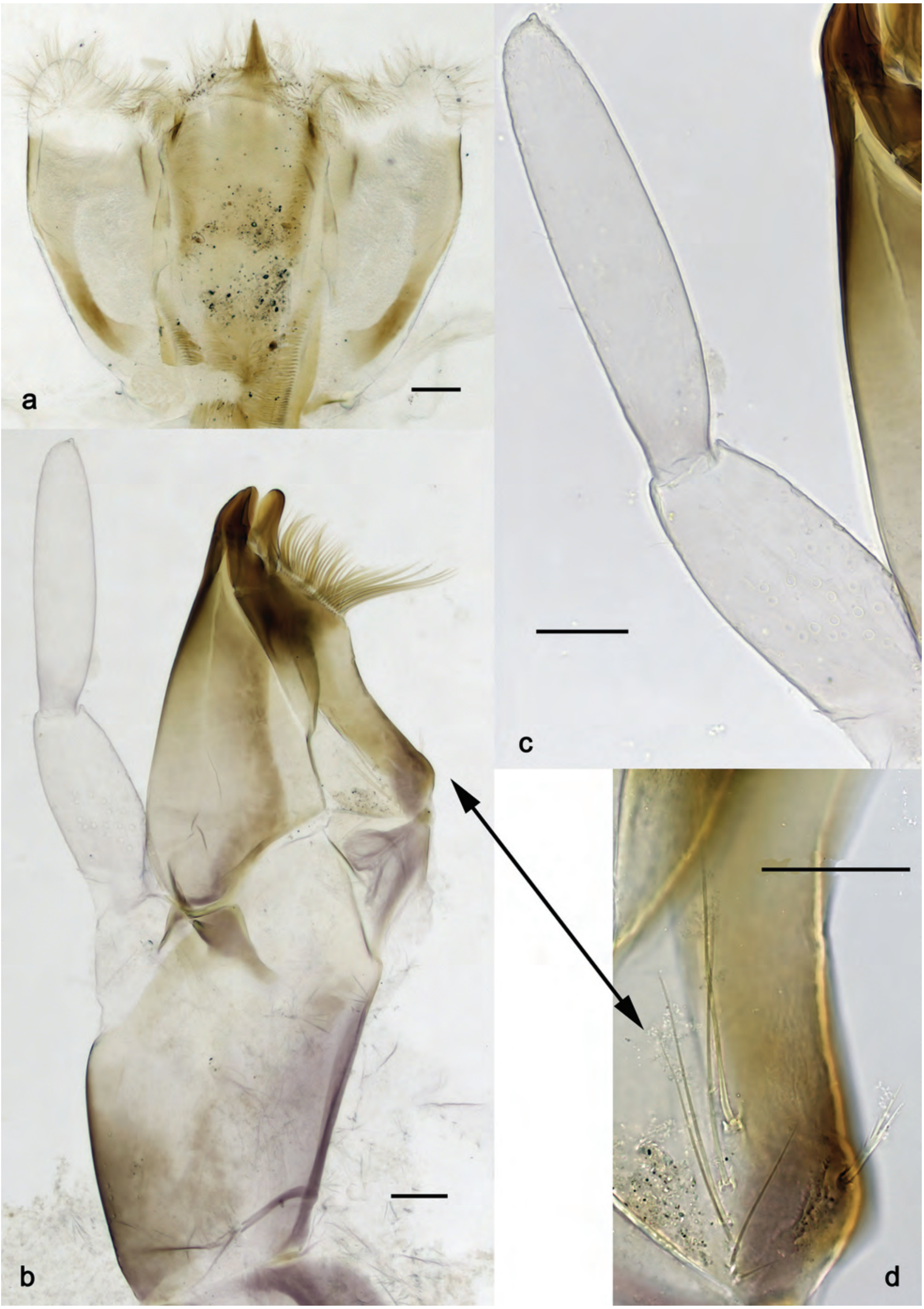


Figure 3. *Labiobaetis amber* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

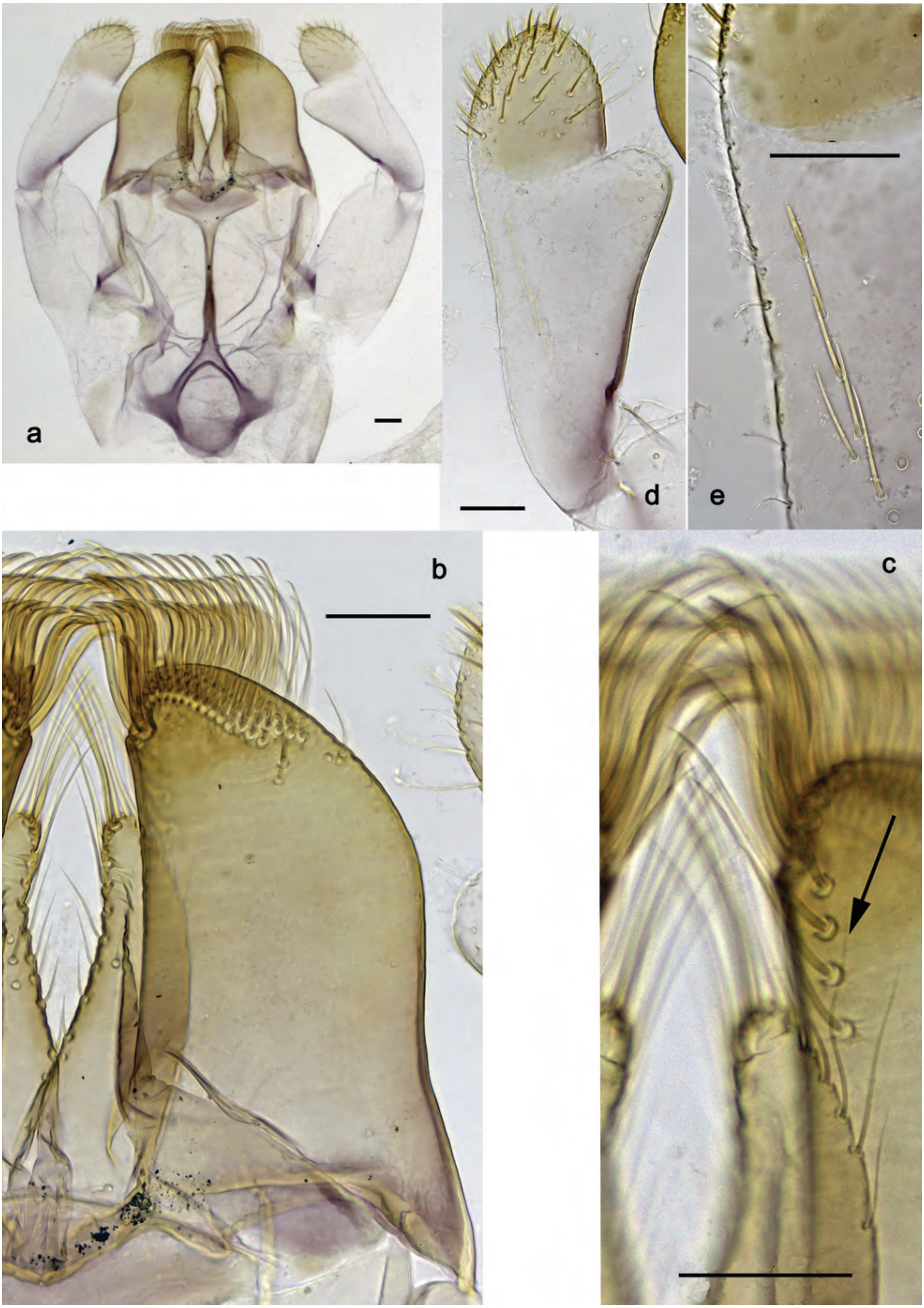


Figure 4. *Labiobaetis amber* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

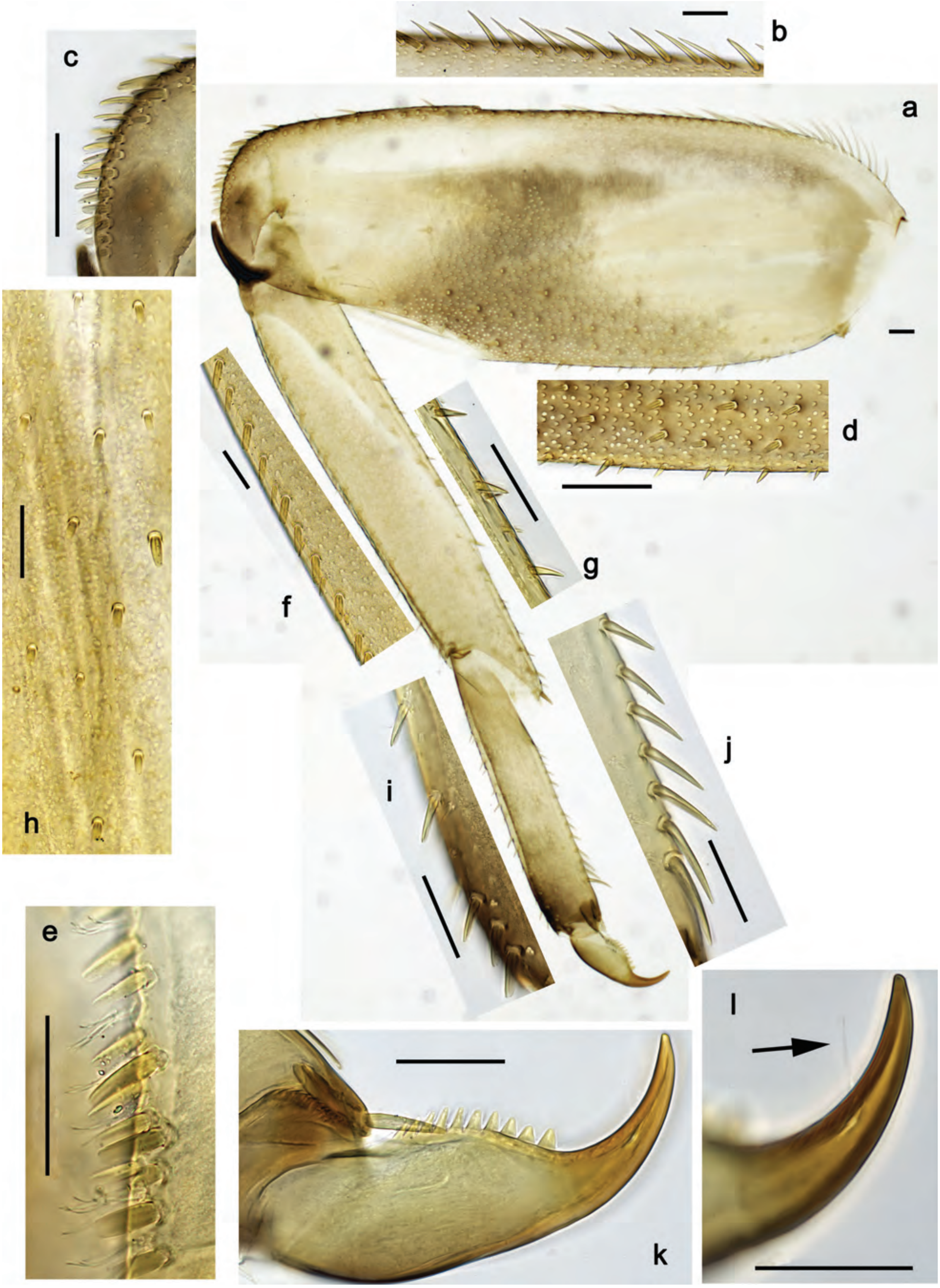


Figure 5. *Labiobaetis amber* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, apex; **d.** Fore femur, ventral margin; **e.** Fore femur, apex, posterior side; **f.** Fore tibia, dorsal margin; **g.** Fore tibia, ventral margin; **h.** Fore tibia, posterior surface; **i.** Fore tarsus, dorsal margin; **j.** Fore tarsus, ventral margin; **k.** Fore claw; **l.** Tip of fore claw. Scale bars: 50 µm.

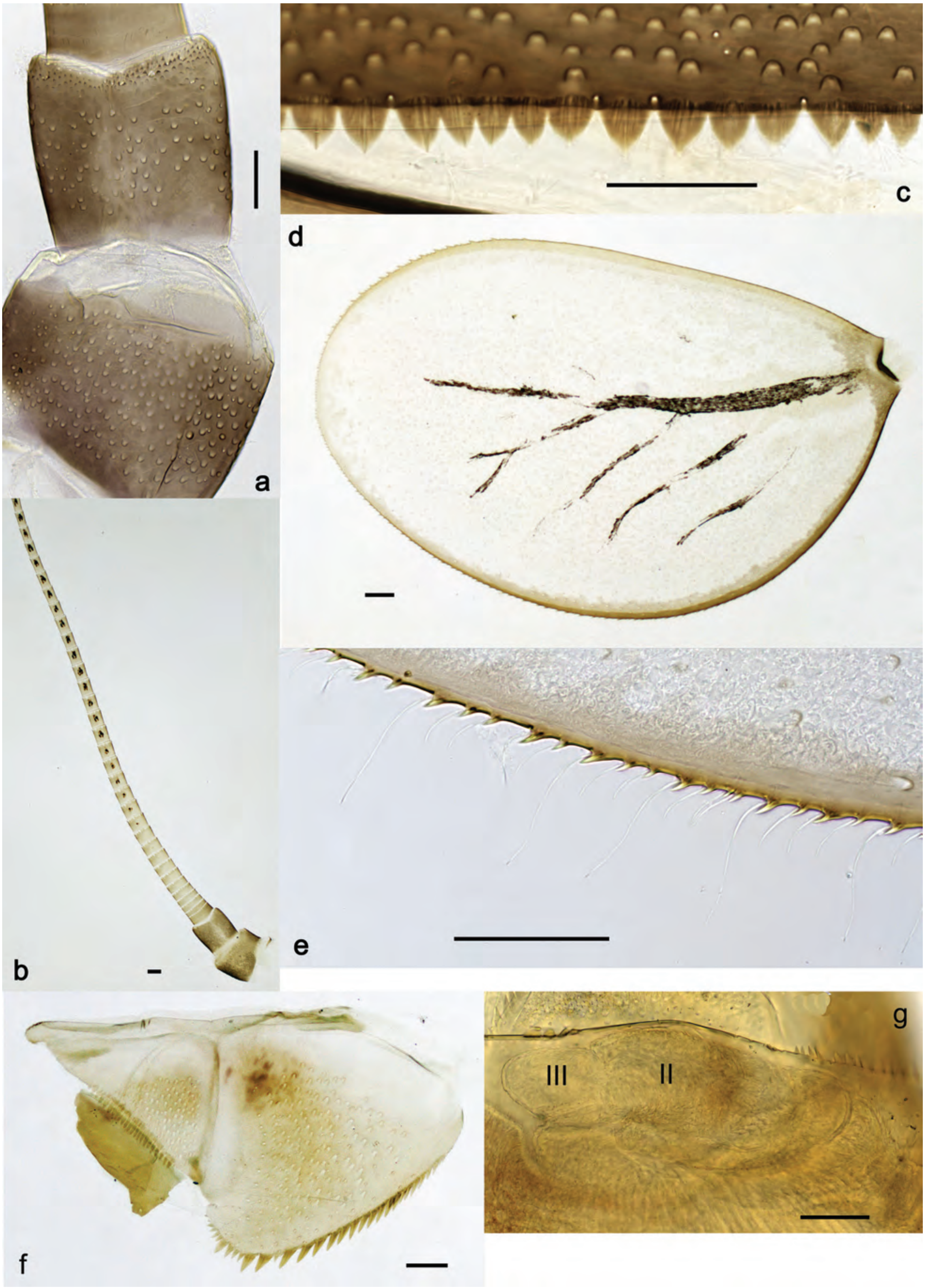


Figure 6. *Labiobaetis amber* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct; **g.** Larval protogonostylus (II, III: segments II and III). Scale bars: 50 µm.

Figure 7. *Labiobaetis amber* sp. nov., larva, distal part of fore claw with subapical setae; SEM picture. Scale bar: 20 µm.

Legs (Figs 5a–k, 7). Ratio of foreleg segments 1.4:1.0:0.6:0.2. ***Femur.*** Fore femur length ca. 2.7× maximum width, middle and hind femur less wide. Dorsal margin with a row of ca. 50 curved, spine-like setae; length of setae 0.16× maximum width of femur. Apex rounded, with many short, stout, lanceolate setae. Apex on posterior side with short, stout, apically truncate setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin, few such setae on surface of distomedial half; femoral patch reduced on fore and middle leg, well developed on hind leg. ***Tibia.*** Dorsal margin with row of medium, stout, apically rounded setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate setae along patellatibial suture. Posterior surface with short, stout, apically rounded, scattered setae. Patellatibial suture present on basal half. ***Tarsus.*** Dorsal margin with row of short, spine-like setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. ten denticles; distally pointed; with long, fine, transparent subapical seta on posterior side and short subapical seta on anterior side.

Abdominal terga (Fig. 6c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II–VII with triangular spines, mostly slightly wider than long; VIII–IX with spines becoming slenderer and longer.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 6d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V and ½ VI combined. Tergalius VII as long as length of segment VIII and ½ IX combined.

Paraproct (Fig. 6f). Distally not expanded, with ca. 33 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. With reference to Amber village, the type locality of the species.

Distribution. Indonesia, Papua Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 1200 m.

Type material. ***Holotype.*** INDONESIA • larva; Papua Prov., River Je, Loc. Arfak, East of Amber village; 01°10'59"S, 133°54'44"E; 1200 m; 16.vi.2016, leg. Sumoked and M. Balke; (BH 68); on slide; GBIFCH00763716; MZB. ***Paratypes.*** INDONESIA • 28 larvae; same data as holotype; 2 on slides; GBIFCH00763717, GBIFCH00592774; MZL; 23 in alcohol; GBIFCH00515646, GBIFCH00515647, GBIFCH00975600, GBIFCH00975607, GBIFCH00975712; MZL.

6. *Labiobaetis bilibil* sp. nov.

https://zoobank.org/0AC9992D-3D71-47B1-824D-81526F0B9C5D

Figs 8–13, 38

Diagnosis. Larva. Following combination of characters differentiates *L. bilibil* sp. nov. from other species of the group *petersorum*: A) labrum length 0.5× maximal width (Fig. 9a); B) both mandibles with row of minute denticles between prostheca and mola (Fig. 9e, h); C) labial palp segment II with extended, slightly hooked, distomedial protuberance; segment III conical (Fig. 10c); D) paraglossa dorsally with row of 2–4 long, spine-like setae near inner, distal margin (Fig. 10b); E) tibia with row of short and medium, stout, lanceolate, pointed setae on dorsal margin (Fig. 12a, e); posterior surface scattered with short, lanceolate setae (Fig. 12g); F) claw with ca. eight denticles (Fig. 12k); G) posterior margin of abdominal tergum IV with triangular, pointed spines, longer than wide (Fig. 13c).

Description. Larva (Figs 8–13). Body length 8.8–9.5 mm. Cerci: broken. Paracercus: ca. 0.4× body length. Antenna: approx. 2.5× as long as head length.

Cuticular colouration (Fig. 8a, b). Head, thorax and abdomen dorsally brown, with pattern as in Fig. 8a. Forewing pads light brown with dark brown and grey stripes; abdominal terga II–IV and VII–VIII darker. Thorax ventrally grey; abdominal sternum I grey, II–V beige and VI–X light brown to brown. Legs brown with brighter areas, femur with elongate proxomedial and distodorsal blanks. Caudalii light brown.

Hypodermal colouration (Fig. 13b). Antenna with dark brown dots in middle part of flagellum.

Antenna (Fig. 13a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 9a, b). Sub-rectangular, length 0.5× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. ten long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 9c–e). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles,

Figure 8. *Labiobaetis bilibil* sp. nov., larva habitus:; **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, with row of minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 9f–h). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with row of minute denticles. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 10a). Lingua longer as superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally slightly expanded. Superlinguae distolaterally protruding; lateral margins angulate; fine, long, simple setae along distal margin.

Maxilla (Fig. 10b–d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. eight long, simple setae. Maxillary palp approx. as long as length of galea-lacinia; 2-segmented; palp segment II approx. as long and much narrower as segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically slightly pointed, constricted.

Labium (Fig. 11a–d). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. seven spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area and one short, simple seta in anteromedial area; dorsally with 2–4 long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with elongate, slightly hooked distomedial protuberance; distomedial protuberance 0.6× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. five spine-like setae near outer margin. Segment III conical; length approx. width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 12a–k). Ratio of foreleg segments 1.6:1.0:0.7:0.2. ***Femur.*** Fore femur length ca. 2.3× maximum width, middle and hind femur less wide. Dorsal margin with a row of ca. 55 curved, spine-like setae, in proximal part a partial 2nd row; length of setae 0.13× maximum width of femur. Apex rounded, with many short, stout, spine-like, pointed setae. Apex on posterior side with short, stout, apically pointed setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin, few such setae on surface of distomedial half; femoral patch reduced on fore and middle leg, well developed on hind leg. ***Tibia.*** Dorsal margin with row of short and medium, stout, lanceolate, pointed setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae.

Anterior surface with short, stout, lanceolate, pointed setae mostly along patellatibial suture. Posterior surface with short, stout, apically rounded, scattered setae. Patellatibial suture present on basal 4/5 area. ***Tarsus.*** Dorsal margin with row of short, spine-like setae. Ventral margin with row of curved, spine-like setae increasing in length distally, and row of short, spine-like setae near ventral margin. Claw with one row of ca. eight denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

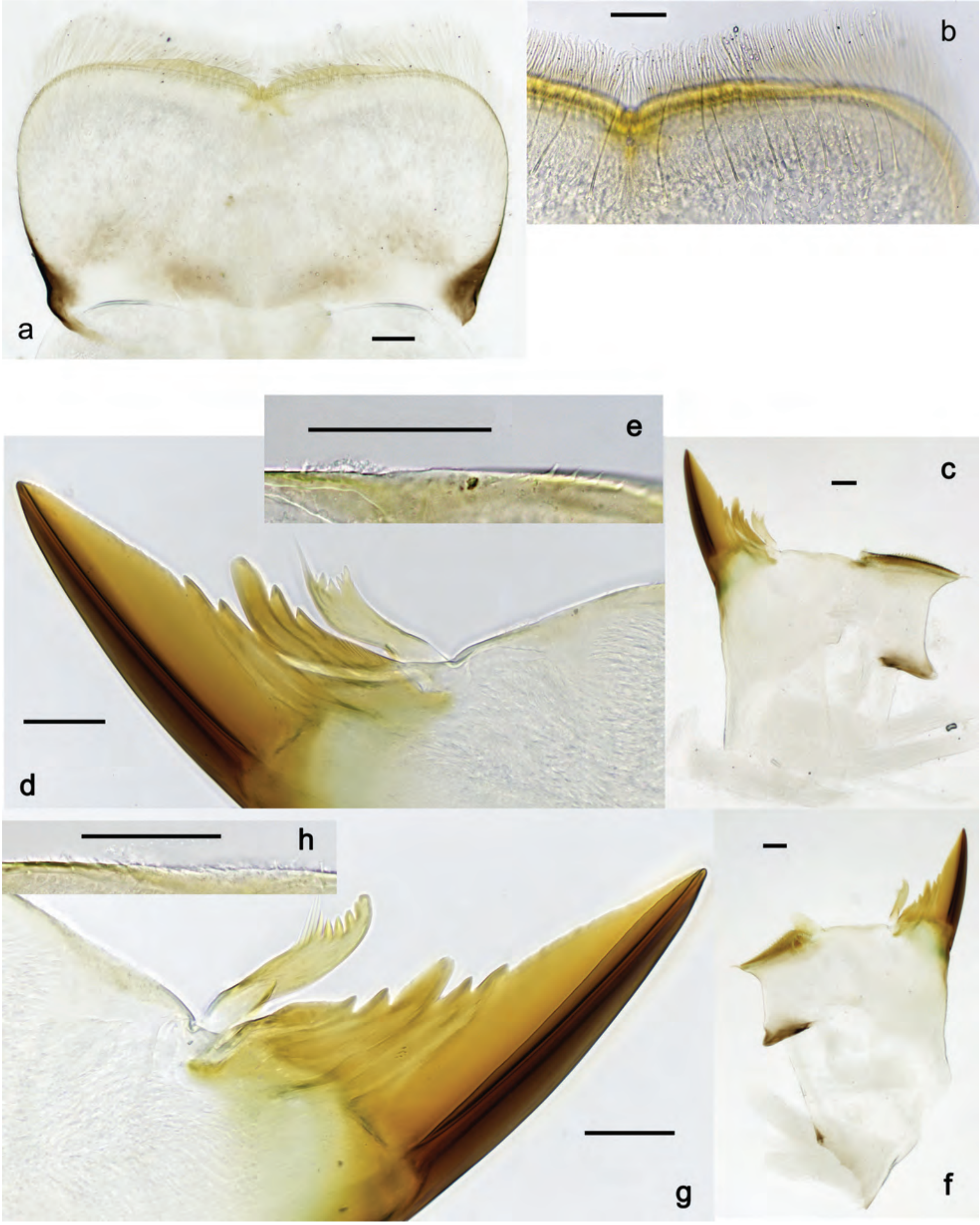


Figure 9. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e.** Right mandible, margin between prostheca and mola; **f, g.** Left mandible; **h.** Left mandible, margin between prostheca and mola. Scale bars: 50 µm.

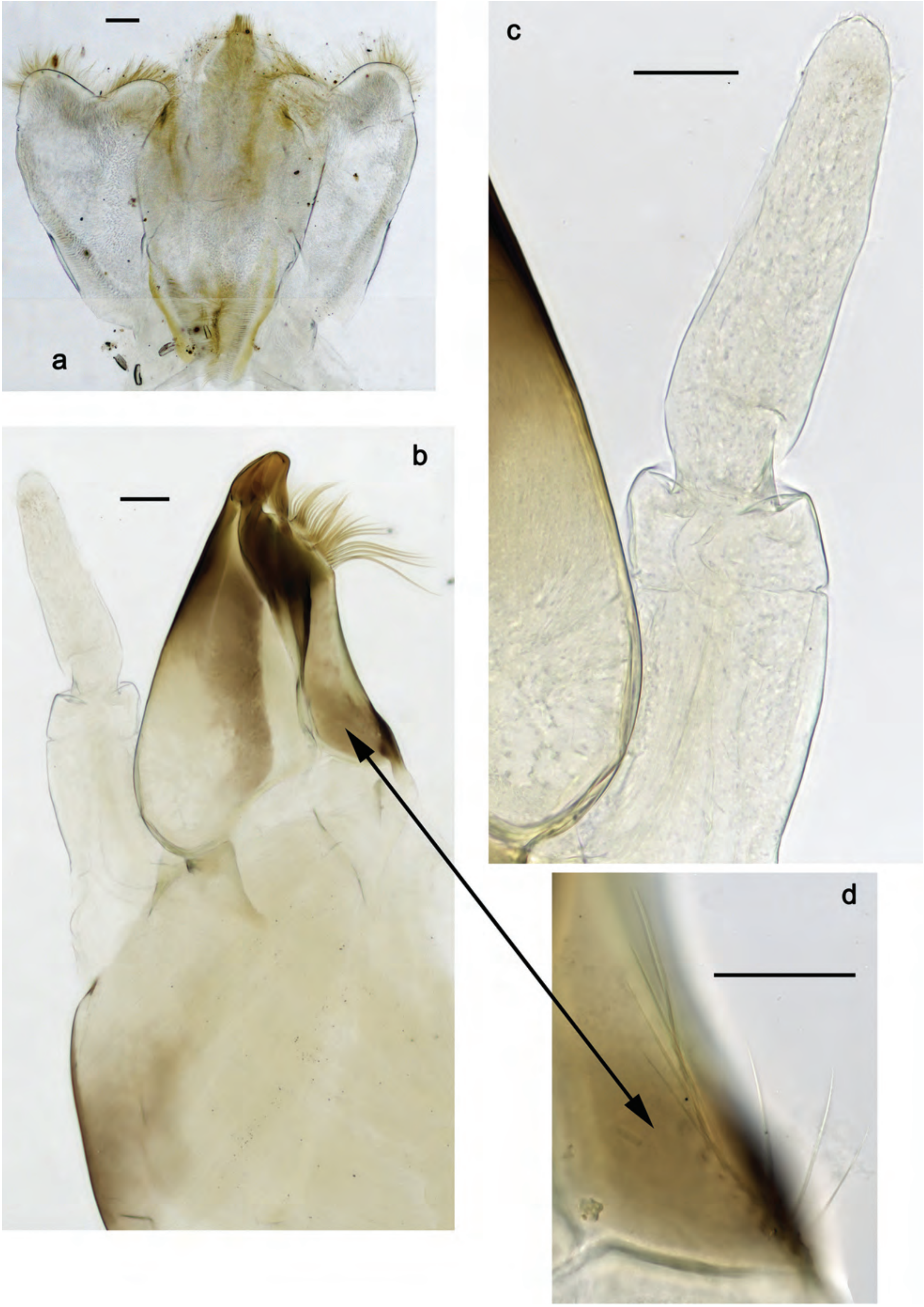


Figure 10. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

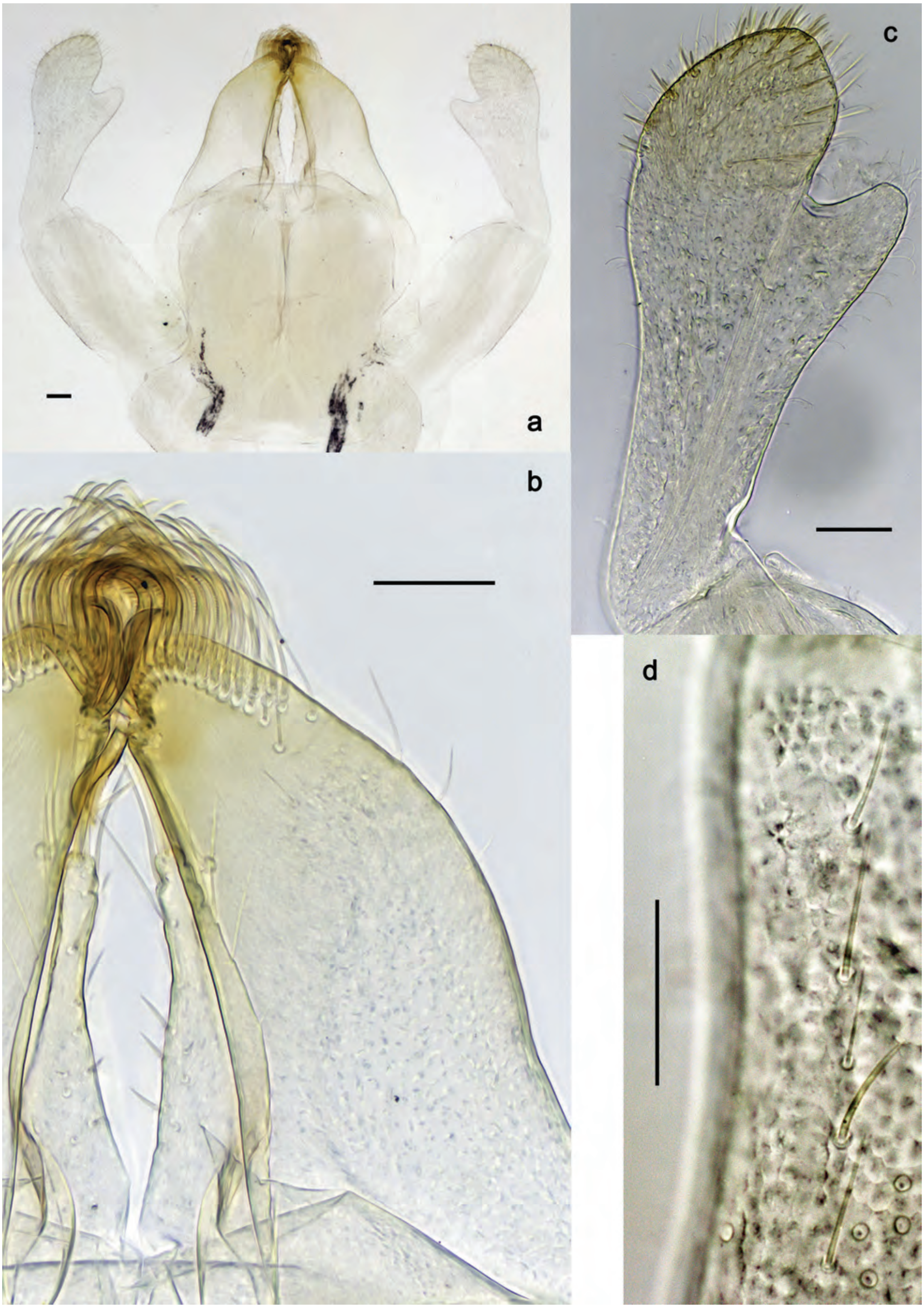


Figure 11. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Labial palp, ventral focus; **d.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

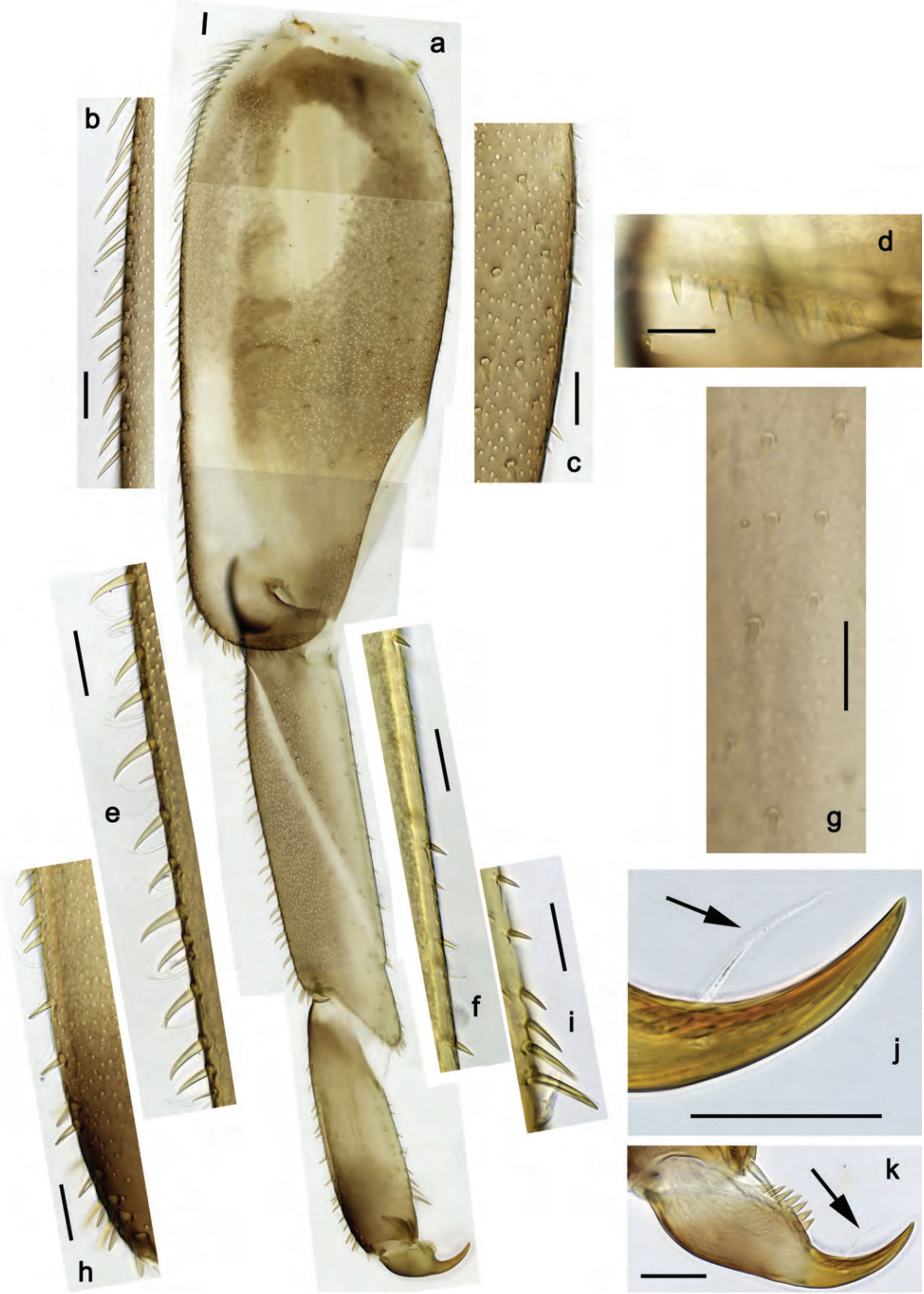


Figure 12. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tibia, ventral margin; **g.** Fore tibia, posterior surface; **h.** Fore tarsus, dorsal margin; **i.** Fore tarsus, ventral margin; **j.** Tip of fore claw; **k.** Fore claw. Scale bars: 50 µm.

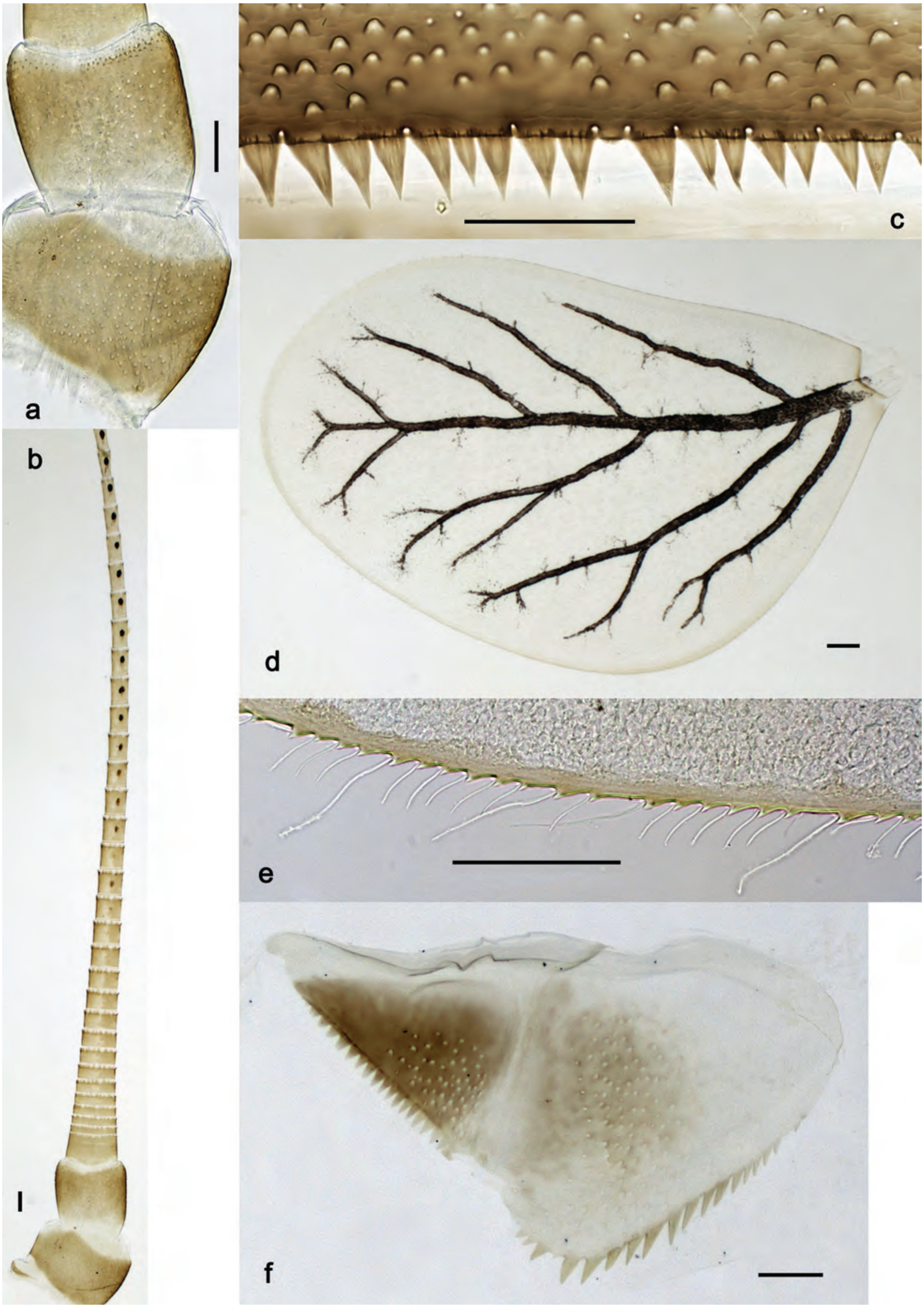


Figure 13. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct. Scale bars: 50 µm.

Abdominal terga (Fig. 13c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II–IX with triangular, sharply pointed spines, longer than wide.

Abdominal sterna. Posterior margin of sterna: I–V smooth, without spines; VI–IX with small, triangular spines.

Tergalii (Fig. 13d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V and VI combined. Tergalius VII as long as length of segments VIII and ½ IX combined.

Paraproct (Fig. 6f). Distally not expanded, with ca. 21 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to the indigenous Bilibil people of the Madang region, where the type locality is.

Distribution. Papua New Guinea (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 350 m.

Type material. *Holotype*. PAPUA NEW GUINEA • larva; Madang Prov., Adalbert Mts., Sewan; 04°41'01"S, 145°26'55"E, 350 m; 03.v.2006; leg. M. Balke and Manaono; (PNG 50); on slide; GBIFCH00592772; ZSM. ***Paratypes*.** PAPUA NEW GUINEA • 19 larvae; same data as holotype; 4 on slides; GBIFCH00592571, GBIFCH00592572, GBIFCH00592573, GBIFCH00763602; MZL; 15 in alcohol; GBIFCH00515641, GBIFCH00515642, GBIFCH00975601, GBIFCH00975616, GBIFCH00975711; MZL.

7. *Labiobaetis kinibeli* sp. nov.

https://zoobank.org/4E9B39F3-B746-46E9-8F06-8439008961F6

Figs 14–19, 38

Diagnosis. Larva. Following combination of characters differentiates *L. kinibeli* sp. nov. from other species of the group *petersorum*: A) labrum length 0.55× maximal width (Fig. 15a); B) both mandibles with row of minute denticles between prostheca and mola; subtriangular process of left mandible with minute denticles on basal outer margin (Fig. 15e, h, i); C) labial palp segment II with thumb-like, apically rounded distomedial protuberance; segment III slightly pentagonal (Fig. 17d); D) paraglossa dorsally with row of four long, spine-like setae near inner, distal margin (Fig. 17c); E) fore tibia with two rows of short, stout, lanceolate, pointed setae on dorsal margin (Fig. 18a, e); posterior surface without scattered, stout setae; F) claw with ca. eight denticles (Fig. 12k); G) posterior margin of abdominal tergum IV with triangular spines, mostly slightly wider than long (Fig. 19c).

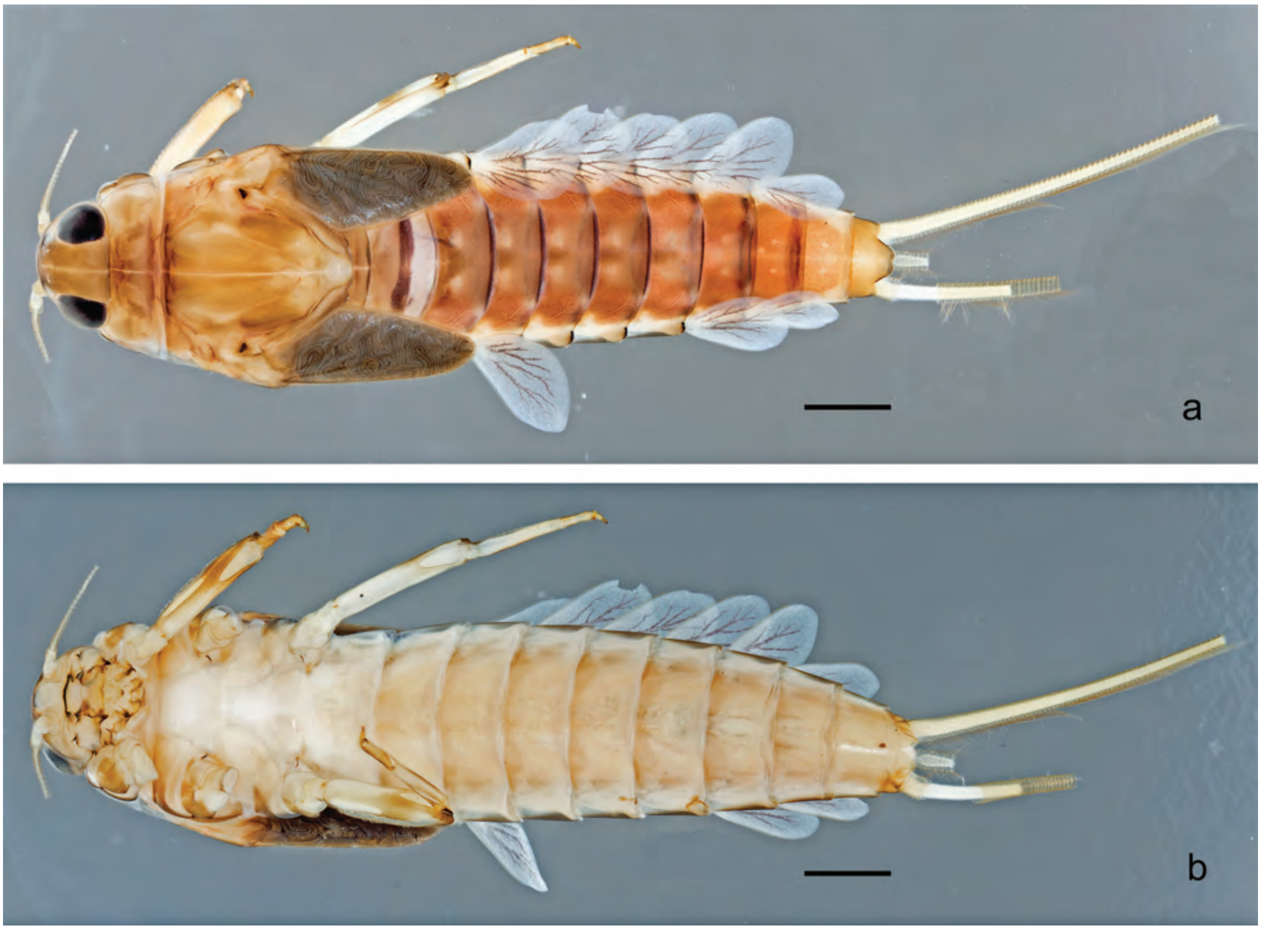


Figure 14. *Labiobaetis kinibeli* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

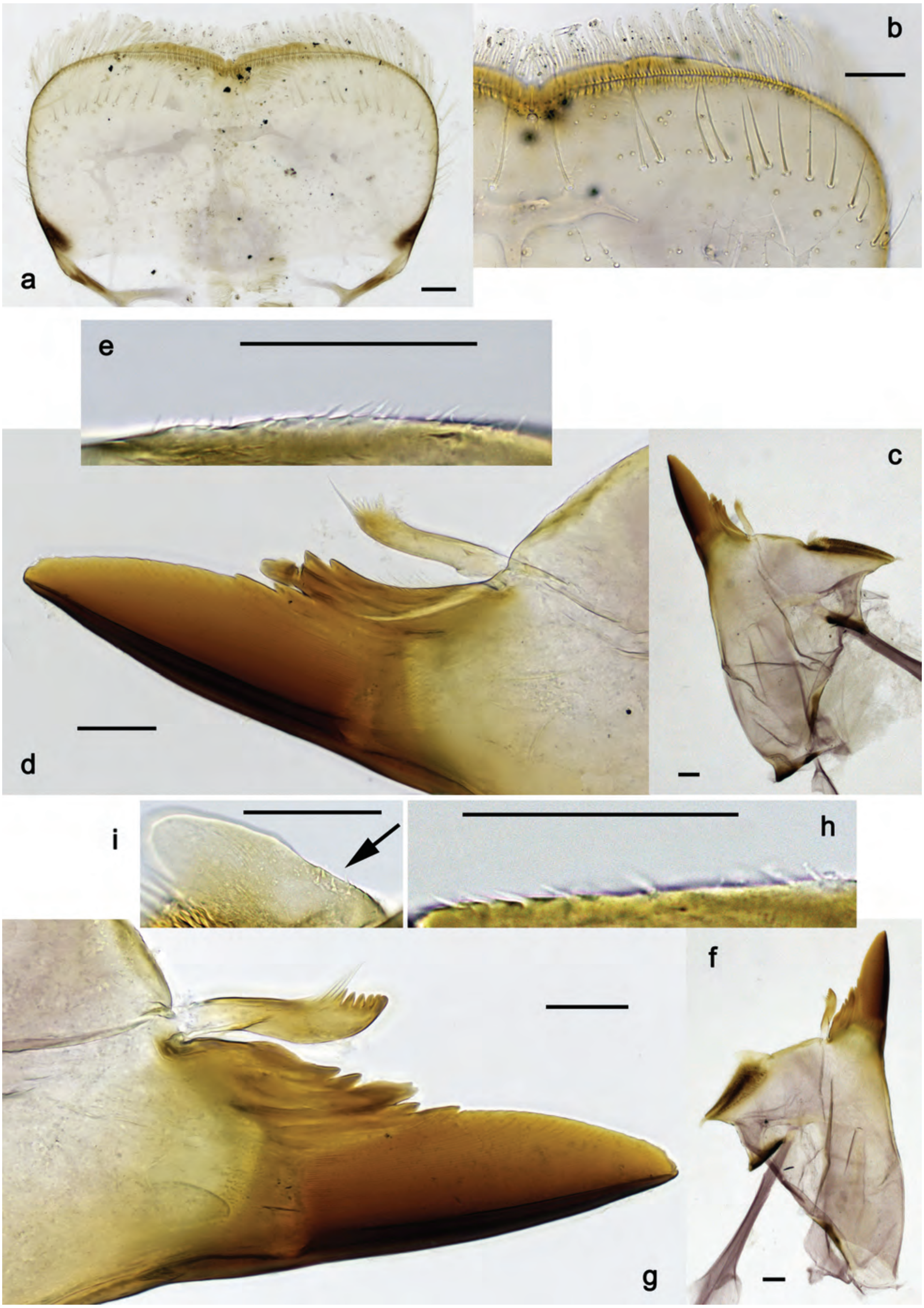


Figure 15. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e.** Right mandible, margin between prostheca and mola; **f, g.** Left mandible; **h.** Left mandible, margin between prostheca and mola; **i.** Left mandible, subtriangular process. Scale bars: 50 µm.

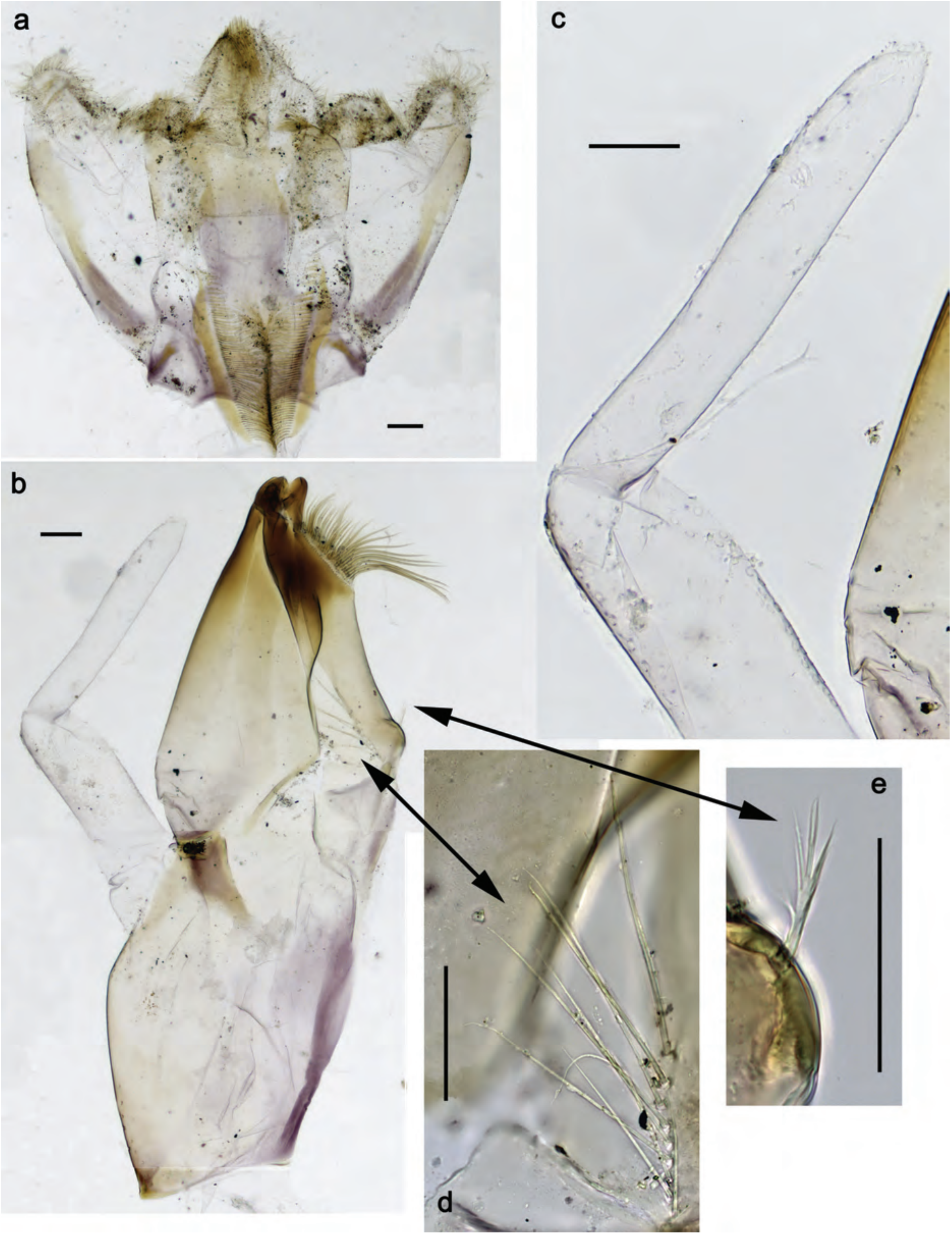


Figure 16. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d, e.** Sections of maxilla. Scale bars: 50 µm.

Description. Larva (Figs 14–19). Body length 7.6–8.5 mm. Cerci: ca. 2/3 of body length. Paracercus: ca. 0.8× cerci length. Antenna: approx. 2.5× as long as head length.

Cuticular colouration (Fig. 14a, b). Head, thorax and abdomen dorsally reddish-brown. Abdominal terga IX–X brighter. Thorax ventrally off-white; abdominal sterna light reddish-brown. Legs brown with, femur with elongate proxomedial and distodorsal blanks. Caudalii light brown.

***Hypodermal colouration*.** Antenna with dark brown dots in middle part of flagellum (Fig. 19b). Abdominal intersegmental membranes with dark purple-brown anterior margins (Fig. 14a).

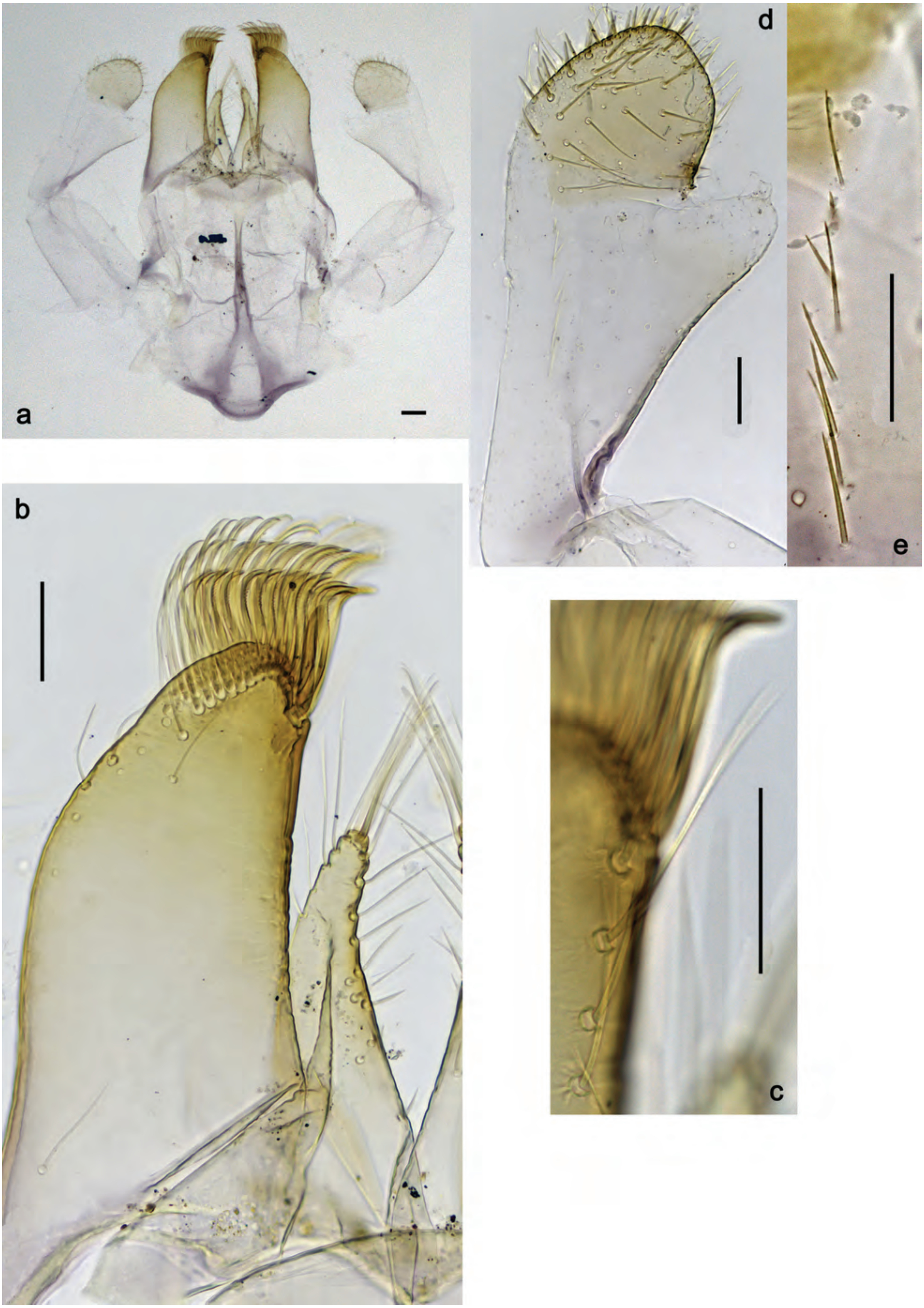


Figure 17. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

Figure 18. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tarsus, dorsal margin; **g.** Fore claw. Scale bars: 50 µm.

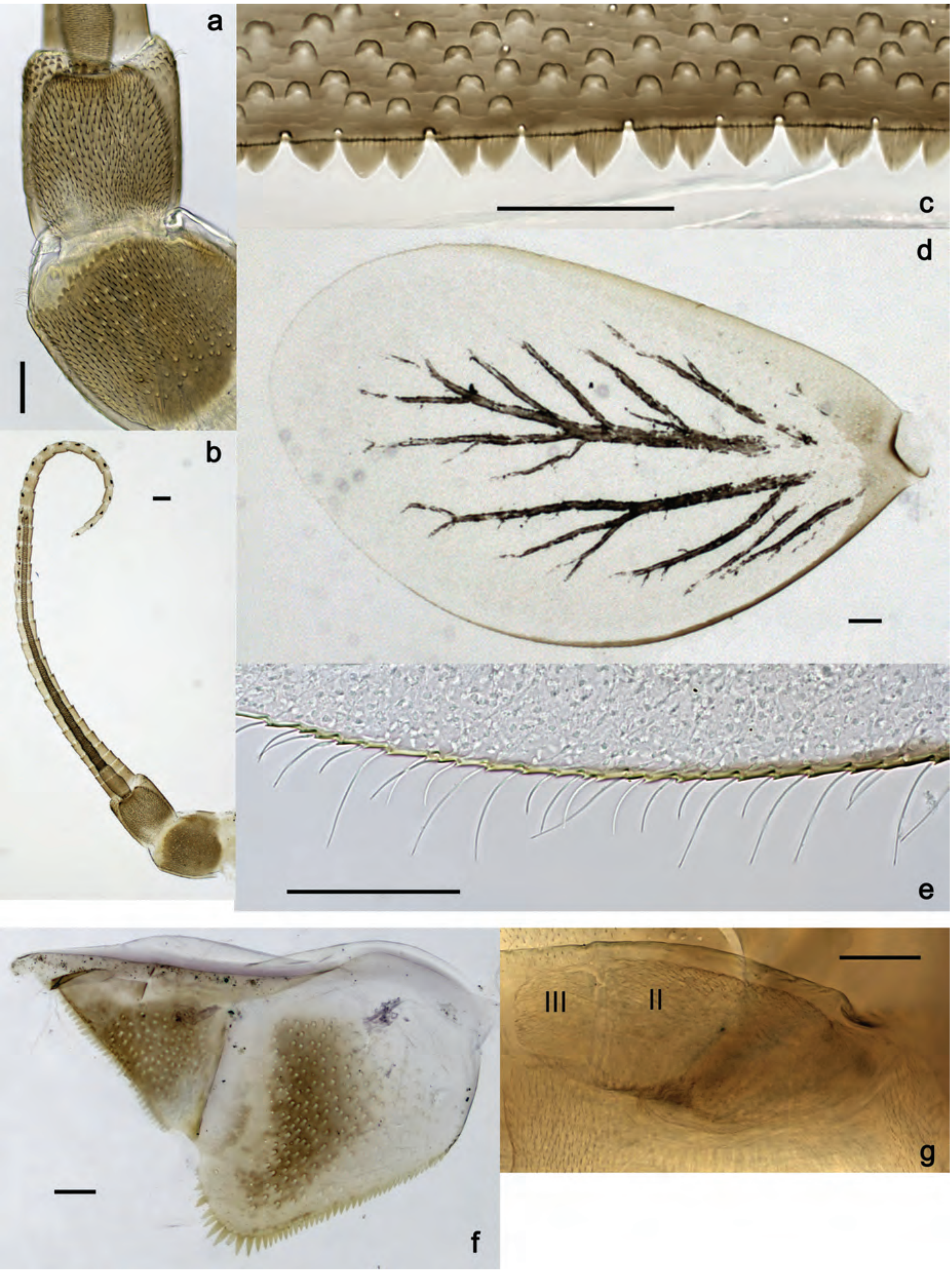


Figure 19. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct; **g.** Larval protogonostylus (II, III: segments II and III). Scale bars: 50 µm.

Antenna (Fig. 19a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 15a, b). Sub-rectangular, length 0.55× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. 13 long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 15c–e). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles, inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, with row of minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 15f–i). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with row of minute denticles. Subtriangular process above level of area between prostheca and mola, basally on outer margin with minute denticles Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 16a). Lingua longer as superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 16b–e). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. eight long, simple setae. Maxillary palp approx. as long as length of galea-lacinia; 2-segmented; palp segment II approx. 1.2× as long as segment I, and much narrower; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 17a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. nine spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area and one short, simple seta in anteromedial area; dorsally with row of four long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with thumb-like, apically rounded, distomedial protuberance; distomedial protuberance 0.5× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. eight spine-like setae near outer margin. Segment III slightly pentagonal; length approx. 0.9× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 18a–g). Ratio of foreleg segments 1.4:1.0:0.5:0.2. ***Femur.*** Fore femur length ca. 2.5× maximum width, middle and hind femur less wide. Dorsal margin with row of ca. 43 curved, spine-like setae; length of setae 0.13× maximum width of femur. Apex rounded, with many short, stout, spine-like, pointed setae. Apex on posterior side with short, stout, apically pointed setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; femoral patch absent on fore leg, rudimentary on middle leg, and reduced on hind leg. ***Tibia.*** Dorsal margin of fore leg with two rows of short, stout, lanceolate, pointed setae, 2nd row poorly developed on middle leg and only one row on hind leg. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae in distal part and along patellatibial suture. Posterior surface without stout setae in dorsal half, some stout setae in ventral half along patellatibial suture. Patellatibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with row of short, spine-like setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. eight denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

Abdominal terga (Fig. 19c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II with rudimentary, rounded spines; III–VI with triangular spines, mostly slightly wider than long; VII–IX with triangular spines, longer than wide; mostly 2–3 spines basally fused.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 19d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V and VI combined. Tergalius VII as long as length of segments VIII and 3/4 IX combined.

Paraproct (Fig. 19f). Distally not expanded, with ca. 53 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to the successful collector of the specimens, Mr. Kinibel (Papua New Guinea).

Distribution. Papua New Guinea (Fig. 38a).

Biological aspects. The specimens were collected at altitudes between 900 m–2000 m, partly together with *Labiobaetis gindroi* Kaltenbach & Gattolliat, 2018 and *Labiobaetis rutschmannae* Kaltenbach & Gattolliat, 2018.

Type material. *Holotype.* PAPUA NEW GUINEA • larva; Western Highlands Prov., Lugup River; 05°17'14"S, 144°28'13"E; 1700 m; 04.iii.2007; leg. Kinibel; (PNG 143); on slide; GBIFCH00975628; ZSM. ***Paratypes.*** PAPUA NEW GUINEA • 6 larvae; same data as holotype; 1 on slide; GBIFCH00975609; MZL; 5 in alcohol; GBIFCH00515639, GBIFCH00975665, GBIFCH00975667; MZL • 1 larva; Central Prov., Tapini, Loloipa River; near 08°20'31"S, 146°59'49"E; 940 m; 31.x.2007; leg. Kinibel; (PNG 163); on slide; GBIFCH00829887; MZL • 3 larvae; Western Highlands Prov., Simbai; 05°15'10"S, 144°32'49"E; 2000 m; 28.ii.2007; leg. Kinibel; (PNG 136); 1 on slide; GBIFCH00975632; MZL; 2 in alcohol; GBIFCH00515633; MZL • 2 larvae; Western Highlands, Simbai; 05°15'52"S, 144°32'43"E; 1800–2000 m; 26.ii.2007; leg. Kinibel; (PNG 134); 1 in alcohol; GBIFCH00975760; 1 on slide; GBIFCH00763775; MZL.

8. *Labiobaetis nabire* sp. nov.

https://zoobank.org/9CCF94C8-B0BD-499D-93DA-BA6CC143420A
Figs 20–25, 38

Diagnosis. Larva. Following combination of characters differentiates *L. nabire* sp. nov. from other species of the group *petersorum*: A) labrum length 0.6× maximal width (Fig. 21a); B) both mandibles with smooth margin between prostheca and mola (Fig. 21c, e); C) labial palp segment II with thumb-like, distomedial protuberance, distal margin of protuberance slightly concave; segment III oblong (Fig. 23d); D) paraglossa dorsally with two long, spine-like setae near inner, distal margin (Fig. 23c); E) tibia with row of short, stout, apically rounded setae on dorsal margin (Fig. 24e); posterior surface without scattered, stout setae; F) claw with ca. nine denticles (Fig. 24g); G) posterior margin of abdominal tergum IV with triangular spines, mostly slightly wider than long (Fig. 25c); H) legs with hypodermal, oblong, orange-brown spot medially on posterior side of femur (Fig. 20a).

Description. Larva (Figs 20–25). Body length 6.3–7.2 mm. Cerci: nearly as long as body length. Paracercus: ca. 0.5× cerci length. Antenna: approx. 2.5× as long as head length.

Cuticular colouration (Fig. 20a, b). Head, thorax and abdomen dorsally grey-brown, with pattern as in Fig. 20a. Abdominal terga VI, IX and partly X brighter; I–IX laterally with bright marks. Thorax and abdomen ventrally off-white. Legs with different shades of grey and brown as in Fig. 20b; femur with elongate proxomedial and distodorsal blanks. Caudalii grey-brown.

***Hypodermal colouration*.** Antenna with dark brown dots in middle part of flagellum (Fig. 25b). Abdominal intersegmental membranes in distal part of abdomen with dark brown anterior margins (Fig. 20a). Femora on posterior side with medial, oblong, orange-brown spots (Fig. 20a).

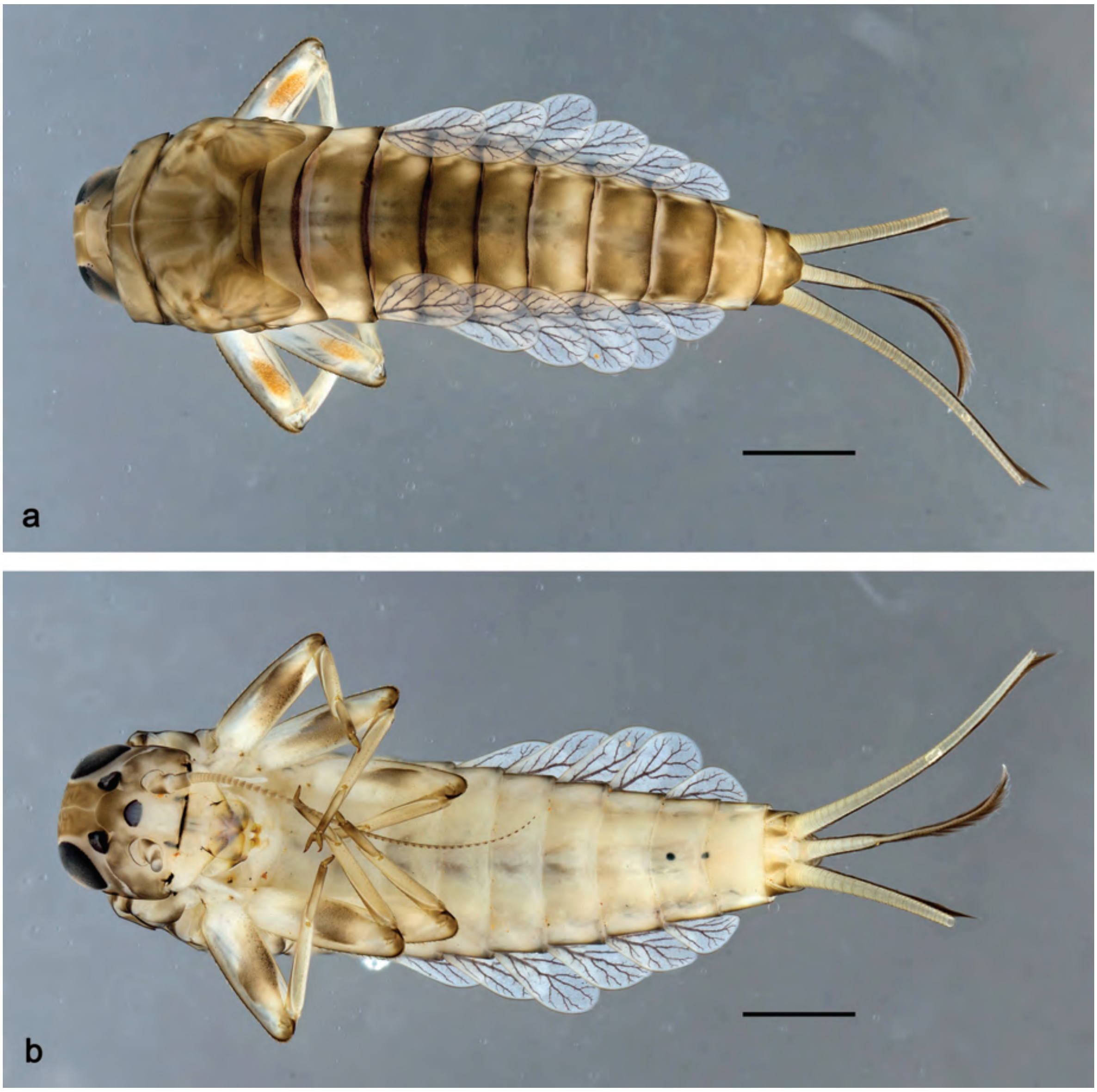


Figure 20. *Labiobaetis nabire* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

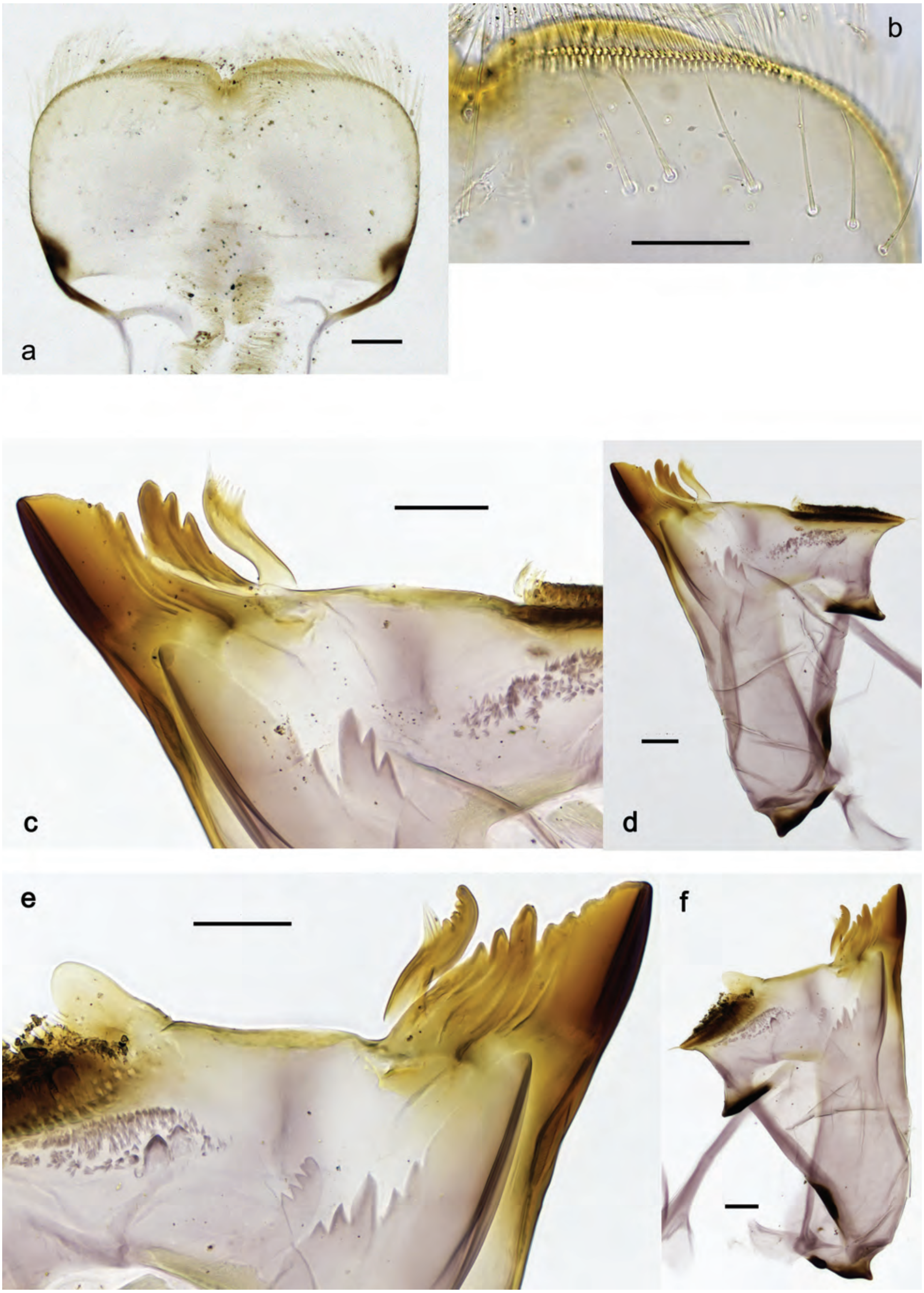


Figure 21. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e, f.** Left mandible. Scale bars: 50 µm.

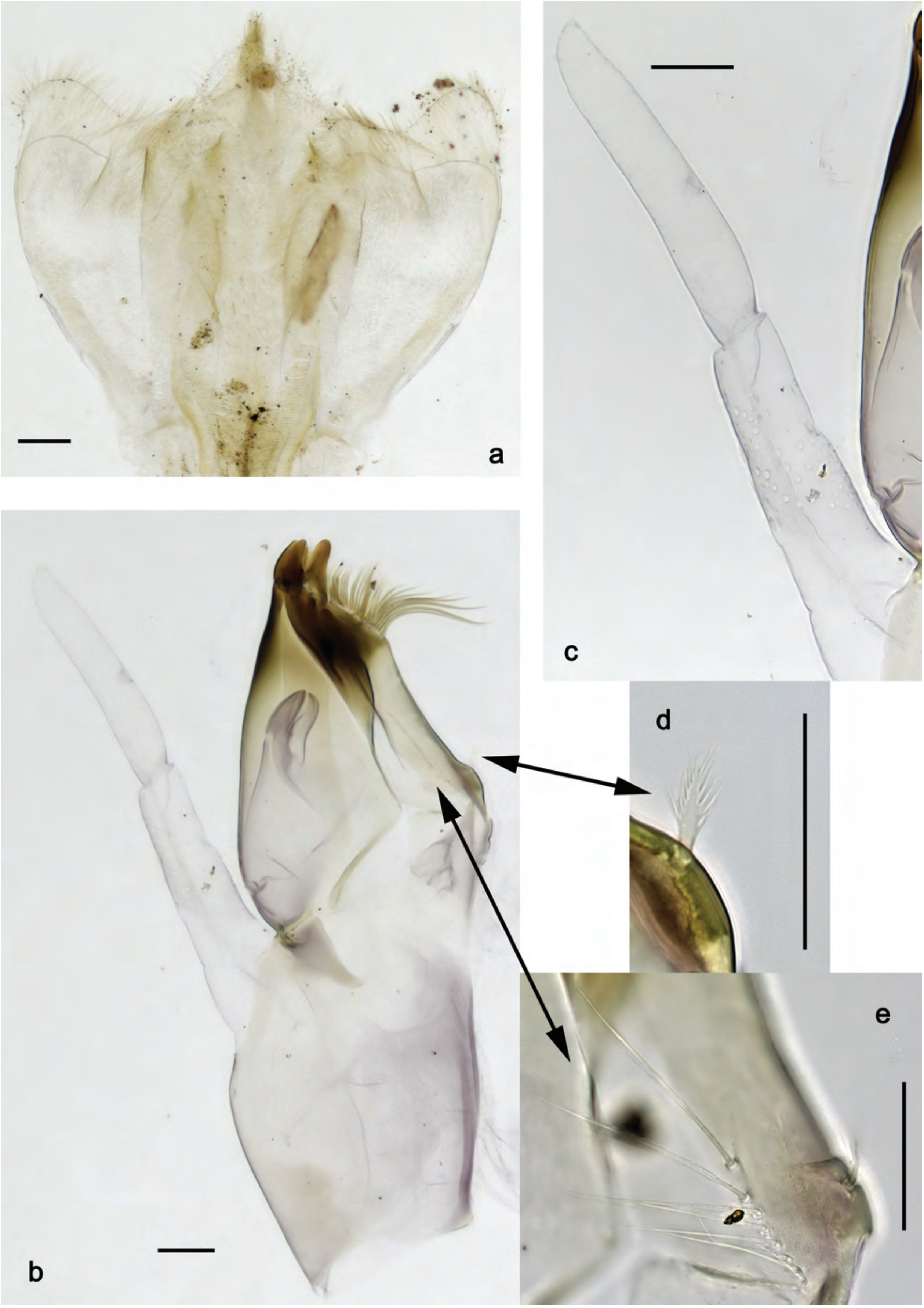


Figure 22. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d, e.** Sections of maxilla. Scale bars: 50 µm.

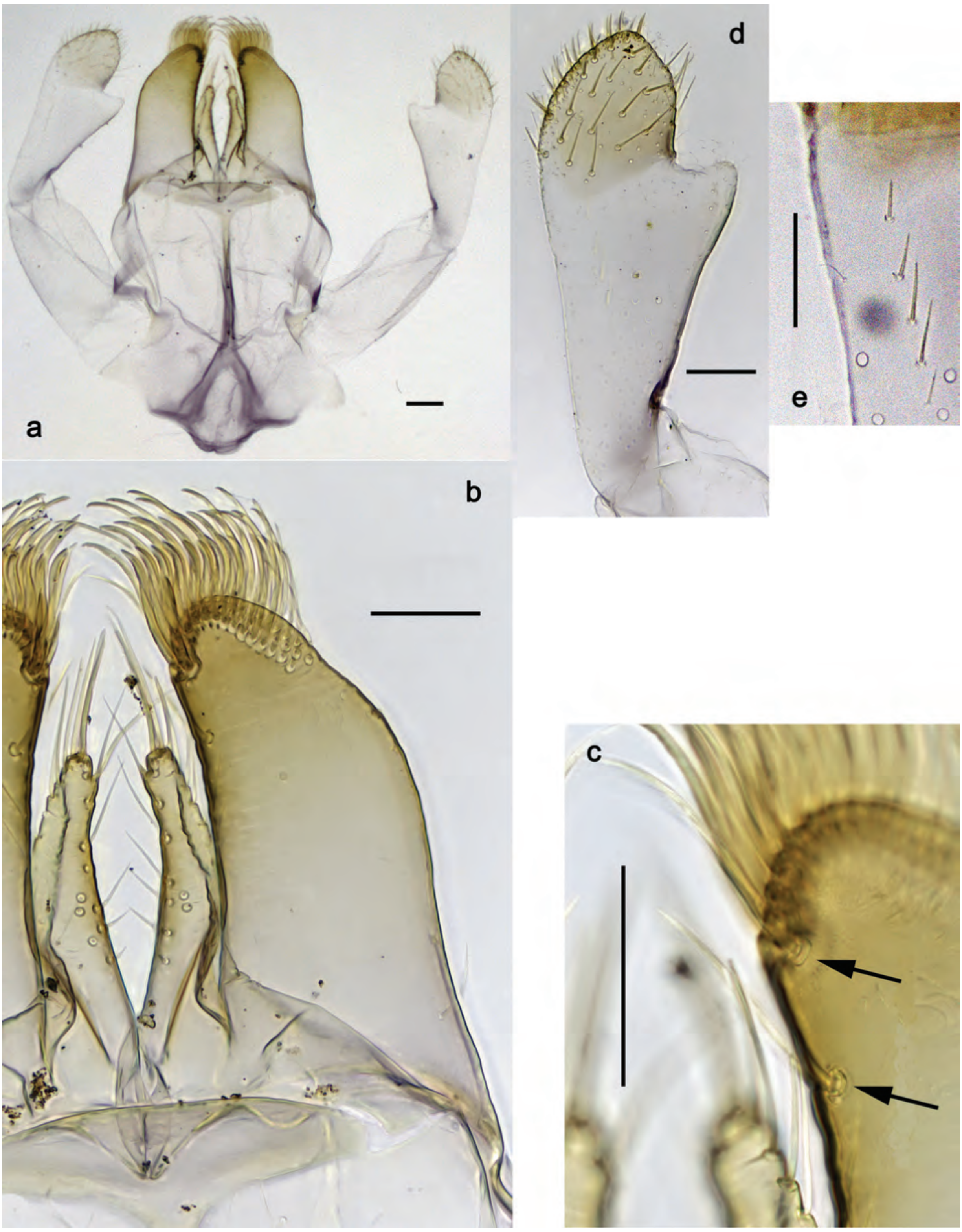


Figure 23. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

Antenna (Fig. 25a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 21a, b). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. eight long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 21c, d). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with four denticles,

Figure 24. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tarsus, dorsal margin; **g.** Fore claw; **h.** Tip of fore claw. Scale bars: 50 µm.

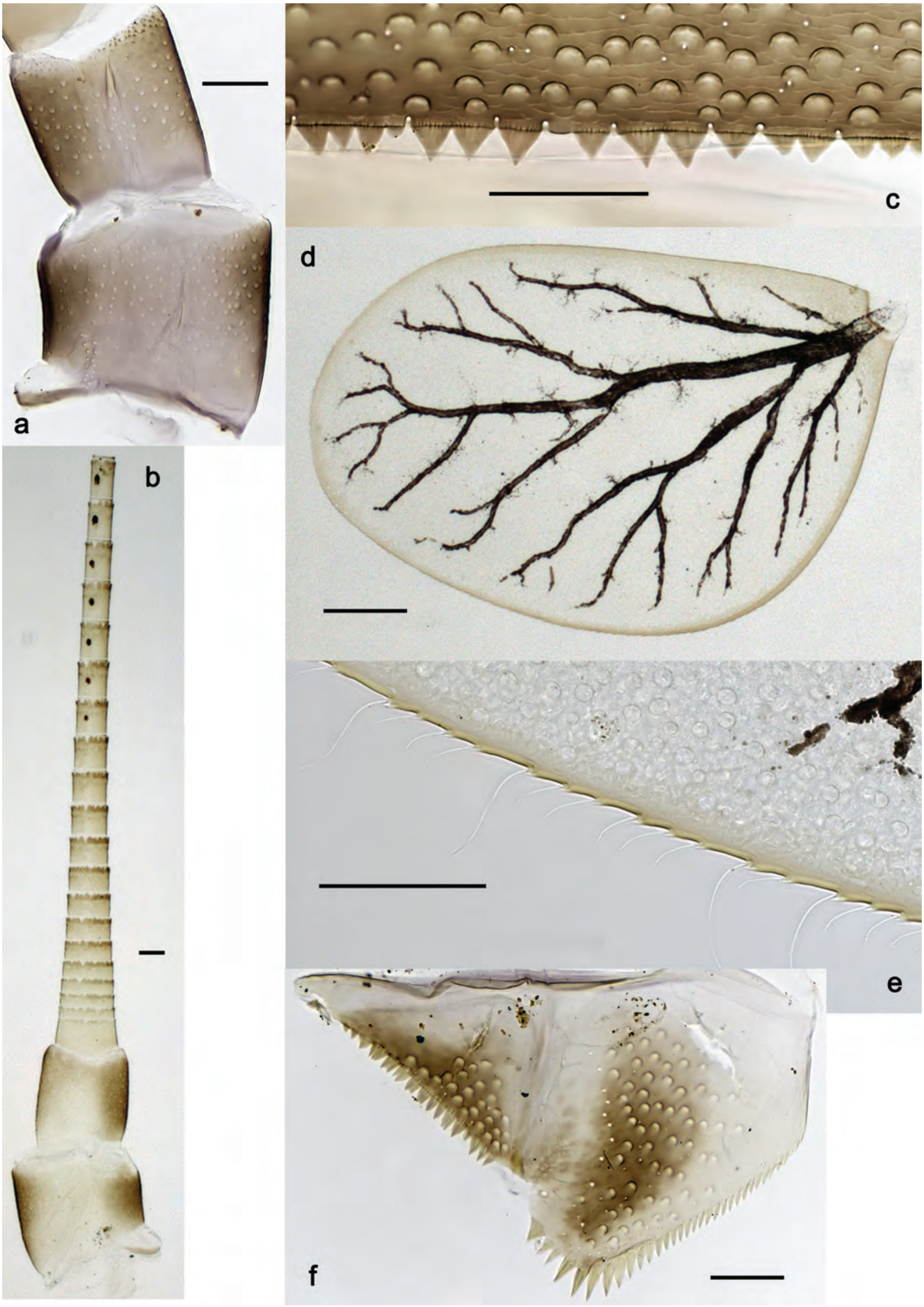


Figure 25. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct. Scale bars: 50 µm.

inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, smooth, without denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 21e, f). Incisor and kinetodontium fused. Incisor with four denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, smooth, without denticles. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 22a). Lingua longer than superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 22b–e). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. eight long, simple setae. Maxillary palp approx. as long as length of galea-lacinia; 2-segmented; palp segment II approx. as long as segment I, and narrower; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 23a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. seven spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area; dorsally with two long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with thumb-like, distomedial protuberance; distal margin of protuberance slightly concave; distomedial protuberance 0.5× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. five spine-like setae near outer margin. Segment III oblong; length approx. width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 24a–h). Ratio of foreleg segments 1.3:1.0:0.6:0.2. ***Femur.*** Fore femur length ca. 2.5× maximum width, middle and hind femur slightly less wide. Dorsal margin with row of ca. 25 short to medium, curved, spine-like, apically rounded setae; length of setae 0.13× maximum width of femur. Apex rounded, with many short, stout, apically rounded setae. Apex on posterior side with short, stout, apically rounded setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; femoral patch rudimentary on fore and middle leg, reduced on hind leg. ***Tibia.*** Dorsal margin with row of short, stout, apically rounded setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae along patellatibial suture. Posterior surface with very few stout setae. Patellatibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with row of short, apically rounded setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. nine denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

Abdominal terga (Fig. 25c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II–III with poorly developed spines; IV–V with triangular spines, mostly slightly wider than long; VI–IX with triangular spines, longer than wide.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 25d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V, VI and 1/3 VII combined. Tergalius VII as long as length of segments VIII and 1/3 IX combined.

Paraproct (Fig. 25f). Distally not expanded, with ca. 33 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Referring to the type locality in Nabire Regency, Central Papua Prov, Indonesia.

Distribution. Indonesia, Central Papua Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 774 m, together with *Labiobaetis papuaensis* Kaltenbach & Gattolliat, 2018.

Type material. *Holotype.* INDONESIA • larva; Papua Prov., Road Nabire-Enarotali KM 55; 03°29'48"S, 135°43'53"E; 774 m; 22.x.2011; leg. M. Balke; (PAP09); on slide; GBIFCH00980888; ZSM. ***Paratypes.*** INDONESIA • 11 larvae; same data as holotype; 3 on slides; GBIFCH00592568, GBIFCH00592569, GBIFCH00980889; MZL; 8 in alcohol; GBIFCH00975588, GBIFCH00975615; MZL.

9. *Labiobaetis simbuensis* sp. nov.

https://zoobank.org/B1E53880-E581-4F58-863F-32CA0910B01A

Figs 26–31, 38

Diagnosis. Larva. Following combination of characters differentiates *L. simbuensis* sp. nov. from other species of the group *petersorum*: A) labrum length 0.6× maximal width (Fig. 27a); B) both mandibles with row of minute denticles on margin between prostheca and mola (Fig. 27d, e, g h); C) labial palp segment II with small, thumb-like, hooked distomedial protuberance; segment III oblong (Fig. 29d); D) paraglossa dorsally with three long, spine-like setae near inner, distal margin (Fig. 29c);

Figure 26. *Labiobaetis simbuensis* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

E) tibia with row of short, spine-like setae on dorsal margin (Fig. 30a, e); posterior surface of tibia without scattered, stout setae; F) claw with ca. nine denticles (Fig. 30i); G) posterior margin of abdominal tergum IV with triangular or rounded spines, wider than long (Fig. 31c).

Description. Larva (Figs 26–31). Body length 4.7–6.1 mm. Caudalii: broken. Antenna: broken.

Cuticular colouration (Fig. 26a, b). Head, thorax and abdomen dorsally light brown. Head, thorax and abdomen ventrally beige. Legs light brown. Caudalii beige.

Hypodermal colouration. Antenna without dark brown dots on flagellum (Fig. 31b).

Antenna (Fig. 31a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 27a, b). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. seven long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 27c, d). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles, inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, with row of minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 27f–i). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with row of minute denticles. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 28a). Lingua much longer than superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally slightly protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 28b–d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of

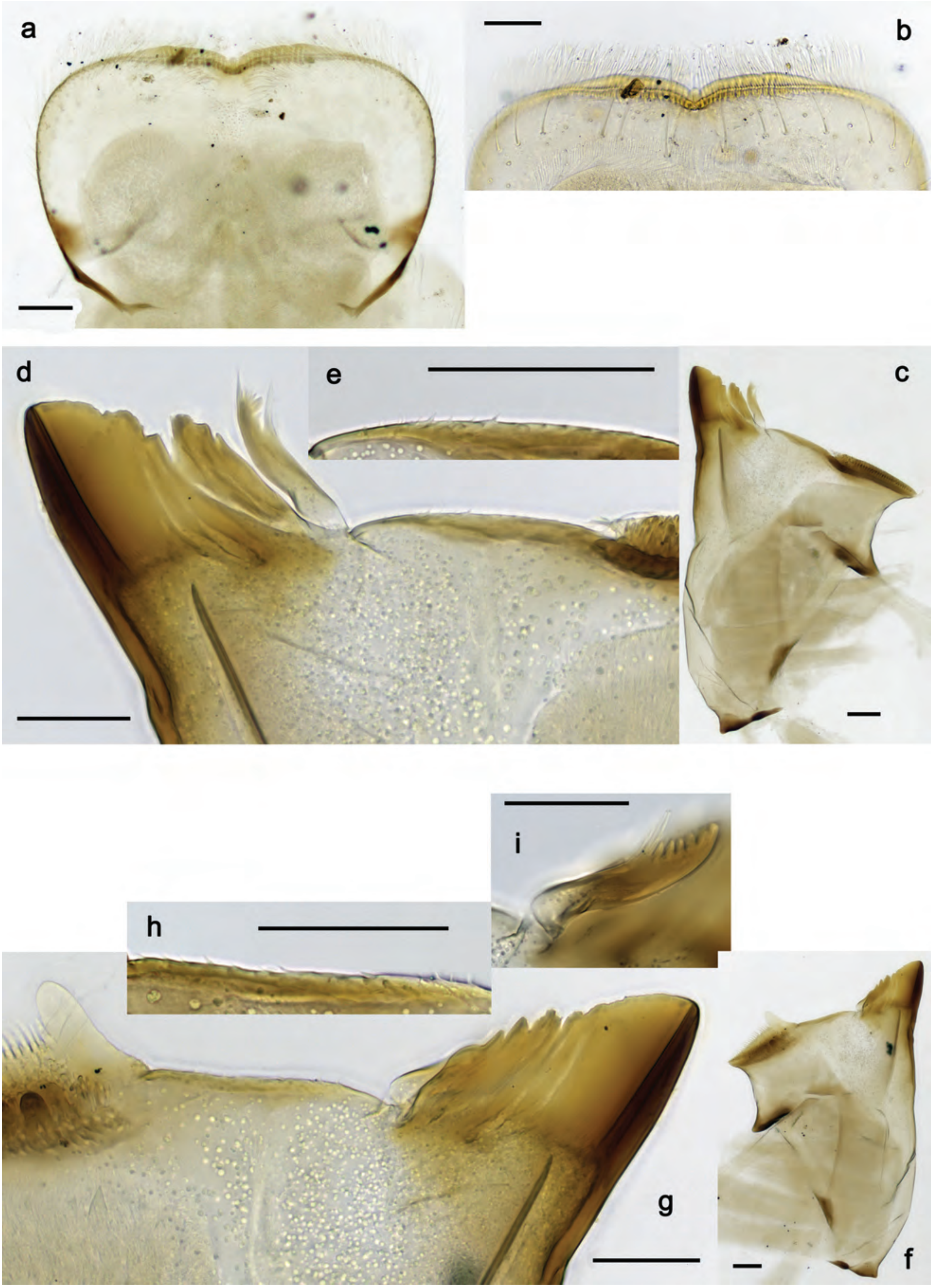


Figure 27. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e.** Right mandible, margin between prostheca and mola; **f, g.** Left mandible; **h.** Left mandible, margin between prostheca and mola; **i.** Left prostheca. Scale bars: 50 µm.

Figure 28. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

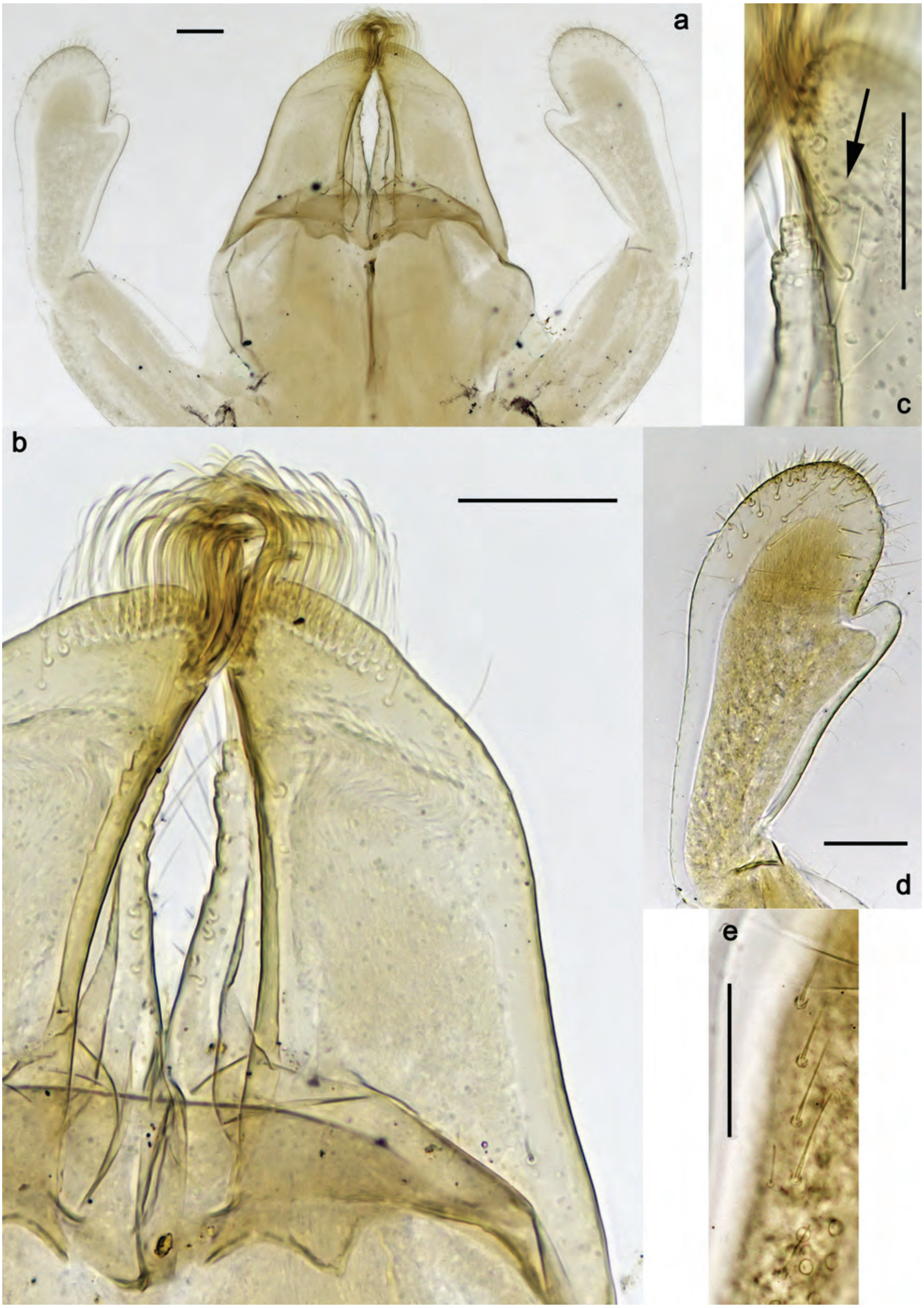


Figure 29. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

Figure 30. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tibia, ventral margin; **g.** Fore tarsus, dorsal margin; **h.** Fore tarsus, ventral margin; **i.** Fore claw. Scale bars: 50 µm.

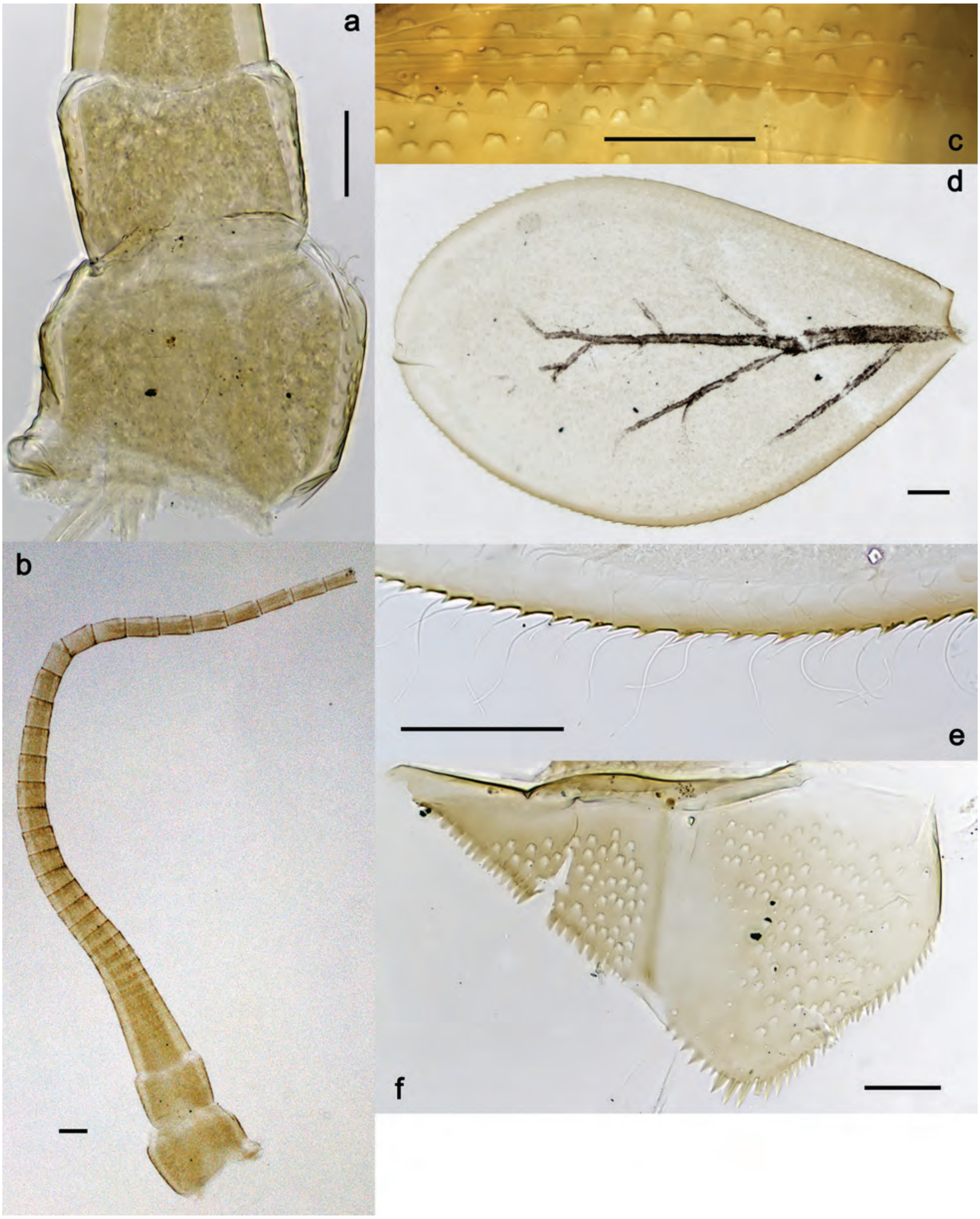


Figure 31. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct. Scale bars: 50 µm.

setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. seven long, simple setae. Maxillary palp slightly longer than length of galea-lacinia; 2-segmented; palp segment II 1.5× as long as segment I, slightly narrower; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 29a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. eight spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. four spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area; dorsally with three long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with small, thumb-like, hooked distomedial protuberance; distomedial protuberance 0.3× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. five spine-like setae near outer margin. Segment III oblong; length approx. width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 30a–i). Ratio of foreleg segments 1.5:1.0:0.6:0.2. ***Femur***. Fore femur very wide, length ca. 2.2× maximum width, middle and hind femur less wide. Dorsal margin with row of ca. 26 long, curved, spine-like setae, and some short spine-like setae in between; length of setae 0.17× maximum width of femur. Apex rounded, with medium, spine-like, pointed setae. Apex on posterior side with short, stout, pointed setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; femoral patch absent on fore leg, rudimentary on middle leg and hind leg. ***Tibia***. Dorsal margin with row of short, spine-like, pointed setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae along patellatibial suture. Posterior surface without stout setae. Patellatibial suture present on basal 2/3 area. ***Tarsus***. Dorsal margin with one or few short, stout setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. nine denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

Abdominal terga (Fig. 31c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I–II smooth, without spines; III–V with triangular or rounded spines, wider than long; VI–IX with triangular spines, mostly wider than long.

Abdominal sterna. Unknown.

Tergalii (Fig. 31d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V, VI and 1/3 VII combined.

Paraproct (Fig. 31f). Distally not expanded, with ca. 35 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Referring to the type locality in Simbu Prov., Papua New Guinea.

Distribution. Papua New Guinea, Simbu Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 2350 m, together with *Labiobaetis wilhelmensis* Kaltenbach & Gattolliat, 2018 and *Labiobaetis gladius* Kaltenbach & Gattolliat, 2018.

Type material. *Holotype*. PAPUA NEW GUINEA • larva; Simbu Prov., Mt. Wilhelm, Pindaunde Creek, S5, oria. 6; 05°49'57"S, 145°06'08"E; 2350 m; 18.viii.1999; leg. L. Cizek; on slide; GBIFCH00592493; MZL. ***Paratype*.** PAPUA NEW GUINEA • 1 larva; same data as holotype; on slide; GBIFCH00975591; MZL.

Labiobaetis vitilis group of species

(diagnosis slightly enhanced from Kaltenbach and Gattolliat 2018)

Following combination of characters: A) antennal scape without distolateral process (Fig. 37a); B) labrum dorsally with submarginal arc of simple setae; C) maxillary palp without distolateral excavation (Fig. 34c); D) labial palp segment II with short thumb-like distomedial protuberance, segment III rather long (Fig. 35d); E) anterior surface of femur medially usually with stout setae (Fig. 36a, d); F) hind protoptera absent; G) tergalii present on abdominal segments II–VII.

The *L. vitilis* group is known from New Guinea only, including the following species:

Labiobaetis vitilis (Lugo-Ortiz & McCafferty, 1999)
Labiobaetis altus Kaltenbach & Gattolliat, 2018
Labiobaetis gindroi Kaltenbach & Gattolliat, 2018
Labiobaetis paravitilis Kaltenbach & Gattolliat, 2018
Labiobaetis wilhelmensis Kaltenbach & Gattolliat, 2018
Labiobaetis kokoda sp. nov.

10. *Labiobaetis kokoda* sp. nov.

https://zoobank.org/91E672B7-A49D-4490-9D3F-6A2B92FD41EA
Figs 32–38

Diagnosis. Larva. Following combination of characters differentiates *L. kokoda* sp. nov. from other species of *Labiobaetis*: A) labrum length 0.7× maximal width; dorsal submarginal arc of setae consisting of one plus 3–5 simple setae, 1st and 2nd setae after submedian seta closely together (Fig. 33a–c); B) incisor and kinetodontium of right mandible with four and three denticles; margin between prostheca and mola slightly convex, smooth (Fig. 33d, e); C) incisor and kinetodontium of left mandible with three and three denticles; margin between prostheca and mola almost straight, smooth (Fig. 33f, g); D) hypopharynx with well-developed medial tuft of stout setae (Fig. 34a); E) maxillary palp longer than galea-lacinia; segment II without distolateral excavation, apically pointed, constricted (Fig. 34b, c); F) labial palp segment II with thumb-like, distomedial protuberance; segment III oblong (Fig. 35a, d); G) femur dorsally with row of ca. 12 long, spine-like setae on margin; several such setae additionally in partial 2nd row near margin (Fig. 36a, b); H) claw with ca. 14 denticles (Fig. 36i); I) posterior margin of abdominal tergum IV with triangular or rounded spines, wider than long (Fig. 37c); J) antennal scape without distolateral process (Fig. 37a).

Figure 32. *Labiobaetis kokoda* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

Description. Larva (Figs 32–37). Body length ca. 3 mm (immature). Cerci: broken. Paracercus ca. 0.4× body length. Antenna ca. 2.5× head length.

Cuticular colouration (Fig. 32a, b). Antenna light brown, darker at distal margins of segments. Head, thorax and abdomen dorsally brown, with pattern as in Fig. 32a; abdominal terga I, V and IX–X brighter. Head, thorax and abdomen ventrally light brown; abdominal sterna VI–VIII darker, IX–X brighter. Legs light brown, darker along dorsal margins of tibia and tarsus, femur medially and apically darker. Caudalii light brown.

Antenna (Fig. 37a) with scape and pedicel sub-cylindrical, without distolateral process at scape. Pedicel distally with triangular scales.

Labrum (Fig. 33a–c). Sub-rectangular, length 0.7× maximum width. Distal margin with deep medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of 3–5 long, simple setae, 1st and 2nd seta after submedian seta closely together. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 33d, e). Incisor and kinetodontium fused. Incisor with four denticles; kinetodontium with three denticles, inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola slightly convex, smooth. Tuft of setae at apex of mola present.

Left mandible (Fig. 33f, g). Incisor and kinetodontium fused. Incisor with three denticles; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola almost straight, smooth. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 34a). Lingua slightly longer than superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally slightly expanded. Superlinguae distolaterally slightly protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 34b–d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. six long, simple setae. Maxillary palp ca. 1.1× length of galea-lacinia; 2-segmented; palp segment II subequal in length to segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically slightly pointed, constricted.

Figure 33. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Labrum; **b, c.** Sections of labrum, dorsal focus; **d, e.** Right mandible; **f, g.** Left mandible. Scale bars: 50 µm.

Labium (Fig. 35a–e). Glossa basally broad, narrowing toward apex; shorter than paraglossa; inner margin with ca. six spine-like seta; apex with two long and one medium robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area; ventrally ca. four medium, fine, simple setae in anteromedial area; dorsally with five long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with thumb-like, distomedial protuberance; distomedial protuberance 0.4× width of base of segment III; ventral surface with

Figure 34. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

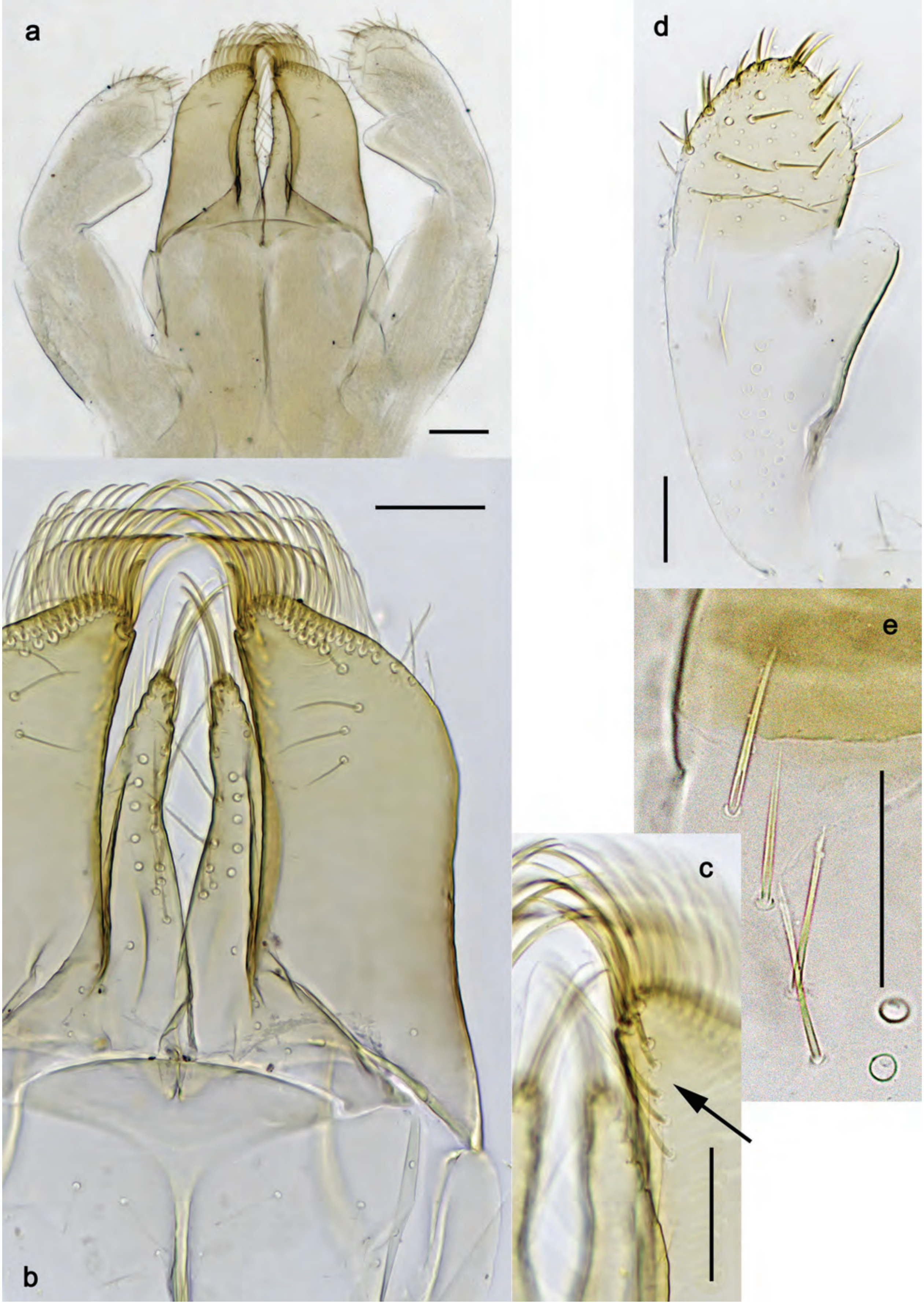


Figure 35. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Labium; **b.** Glossa, paraglossa and mentum, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

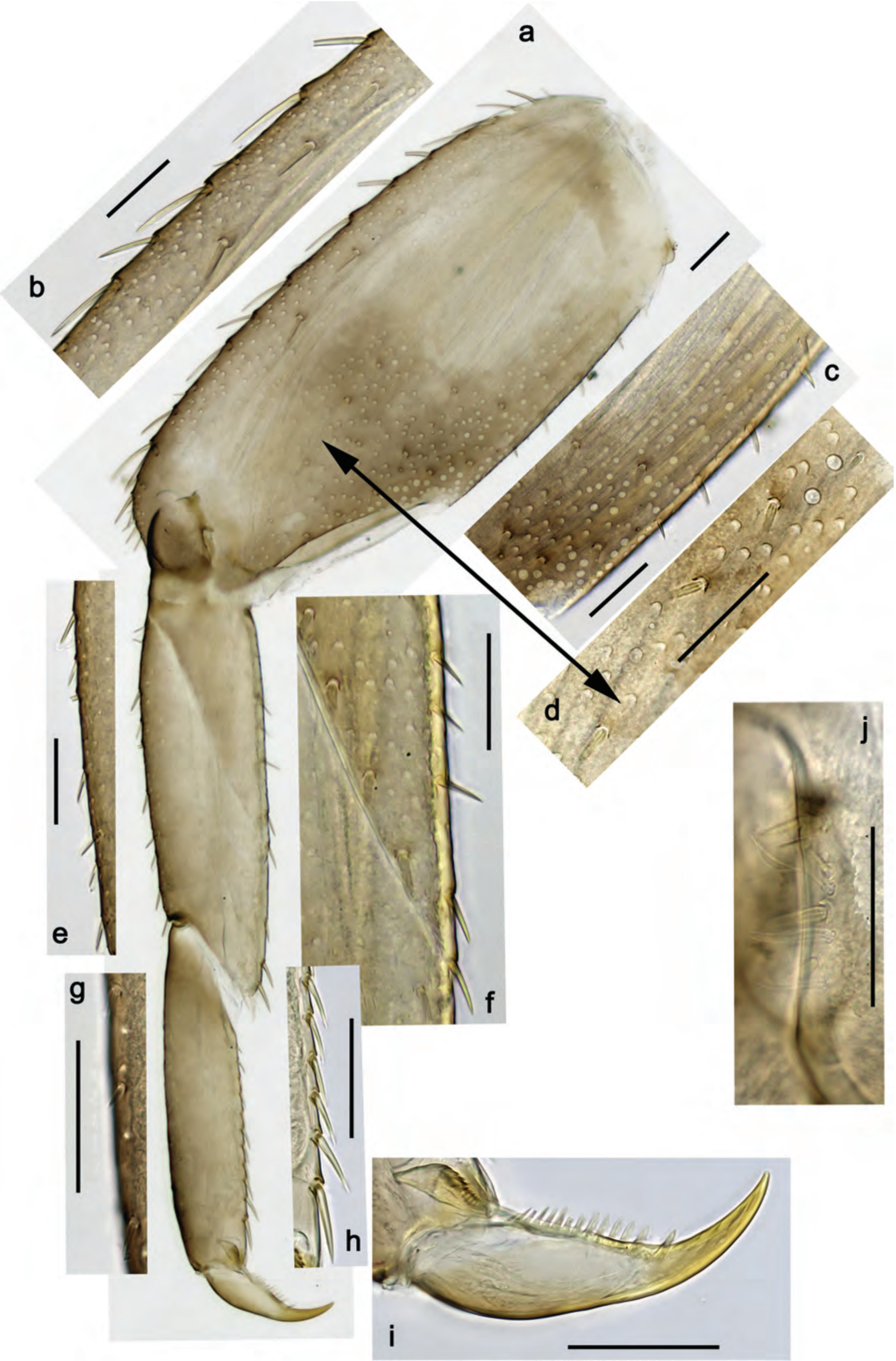


Figure 36. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, setae on distomedial surface; **e.** Fore tibia, dorsal margin; **f.** Fore tibia, ventral margin; **g.** Fore tarsus, dorsal margin; **h.** Fore tarsus, ventral margin; **i.** Fore claw; **j.** Fore femur, apex, posterior side. Scale bars: 50 µm.

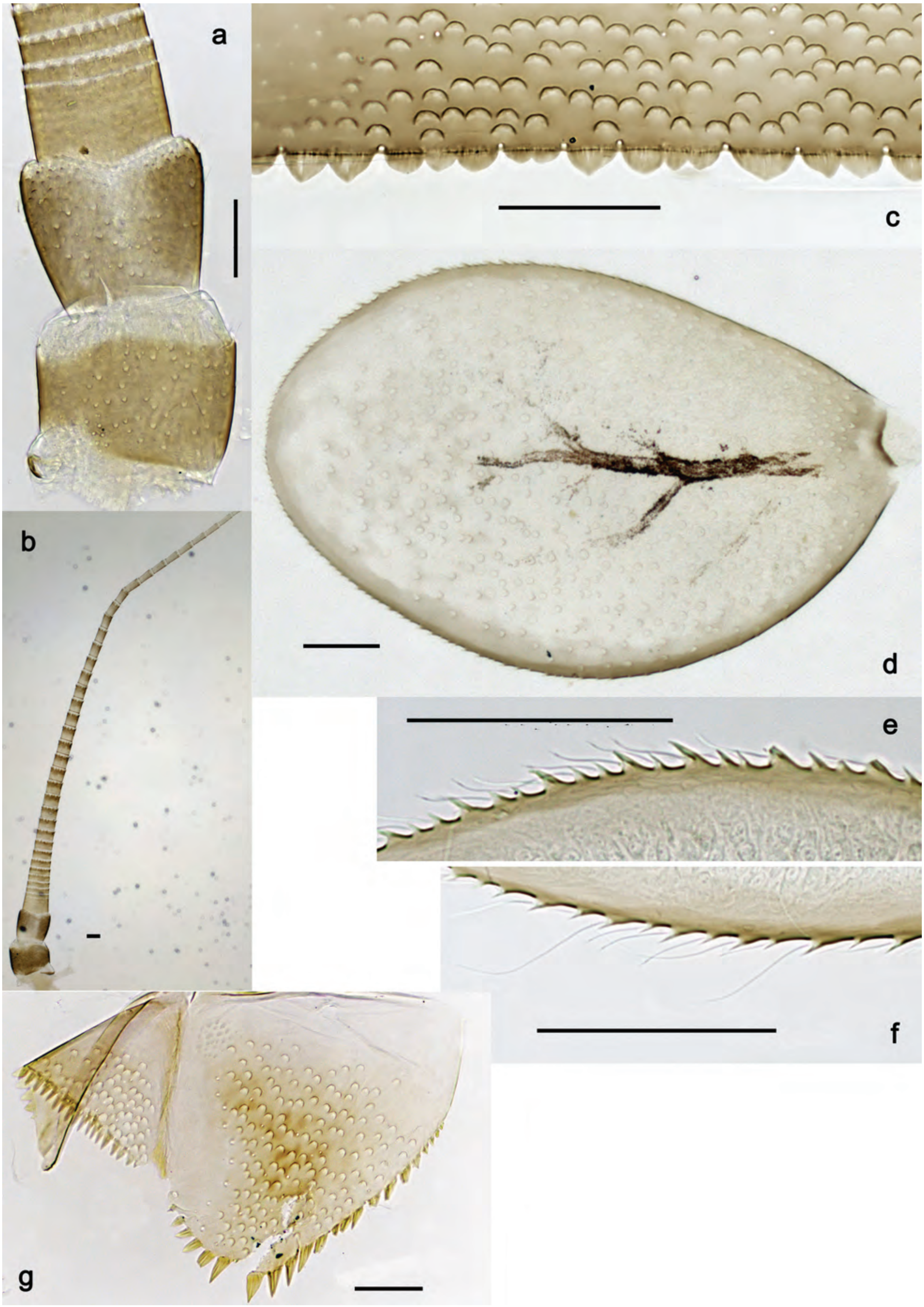


Figure 37. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Costal margin of tergalius IV; **f.** Anal margin of tergalius IV; **g.** Paraproct. Scale bars: 50 µm.

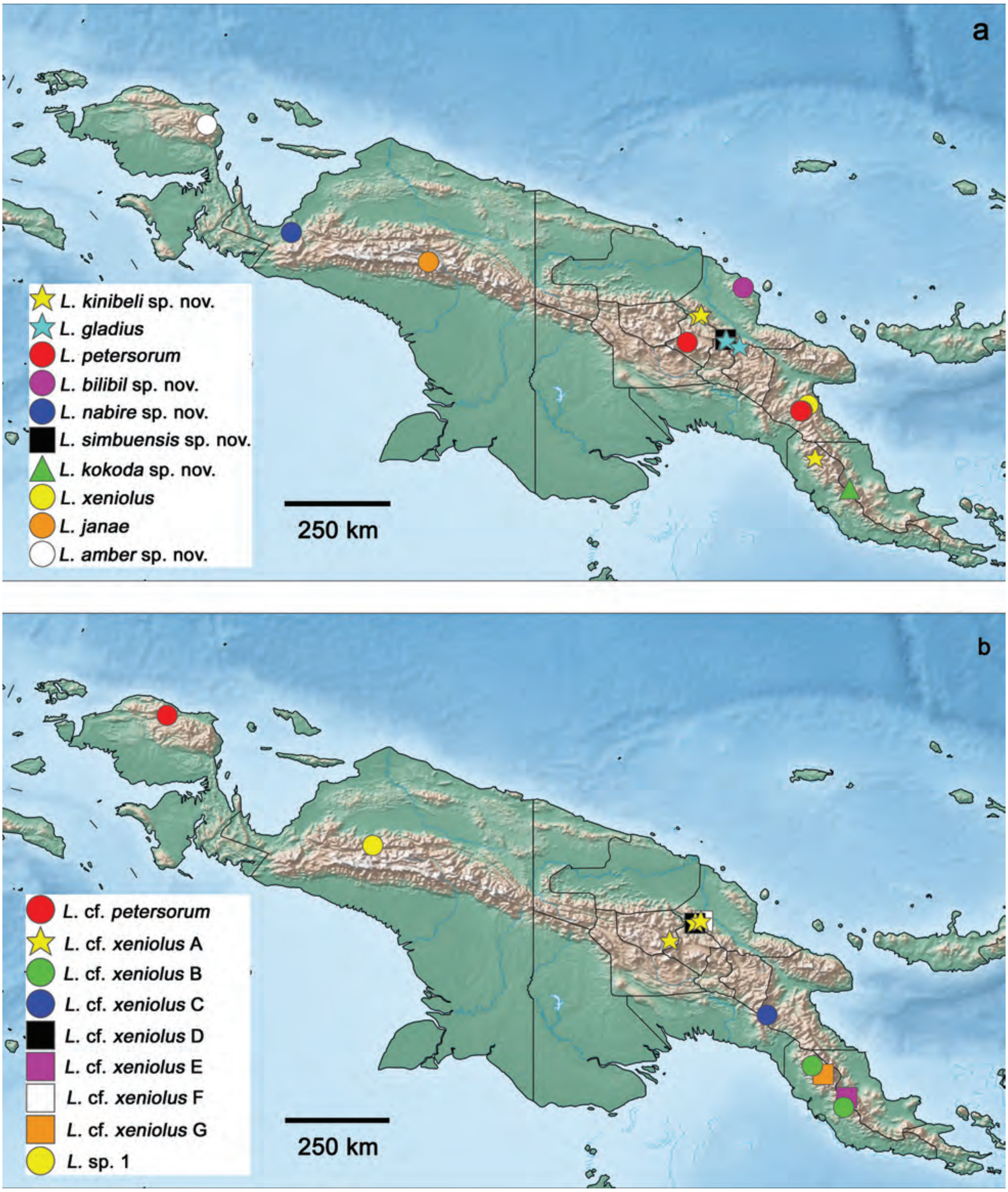


Figure 38. Distribution of species treated in this study: **a.** Species of group *petersorum* and *L. kokoda* sp. nov.; **b.** MOTUs of group *petersorum*, not described in this study.

short, fine, simple setae; dorsally with row of ca. four spine-like setae near outer margin. Segment III oblong; length ca. 1.1× width; ventrally covered with short to medium, spine-like, simple setae and short, fine, simple setae. Mentum ventrally with medium fine, simple setae scattered on distal part of surface.

Hind protoptera absent.

Legs (Fig. 36a–j). Ratio of foreleg segments 1.5:1.0:0.8:0.3. ***Femur.*** Femur very wide, length ca. 2.3× maximum width. Dorsal margin with row of ca. 12 long, curved, spine-like setae, and some additional spine-like setae in partial 2nd row near margin; length of setae 0.2× maximum width of femur. Apex rounded, with a pair of long, spine-like setae and several medium, spine-like setae. Apex on posterior side with few short, stout, setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; several of such setae on distomedial surface. Femoral patch rudimentary on fore and middle legs, reduced on hind leg. ***Tibia.*** Dorsal margin with row of short, spine-like, pointed setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae along patellatibial suture. Posterior surface without stout setae. Patellatibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with few short, stout setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. 14 denticles; distally pointed; without subapical seta on.

Abdominal terga (Fig. 37c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II with rounded spines, much wider than long; III–VI with triangular or rounded spines, wider than long; VII–IX with triangular spines, longer than wide.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 37d–f). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Costal margin with alternating larger and smaller denticles. Tracheae not reaching inner and outer margins. Tergalius IV as long as length of segments V and VI combined.

Paraproct (Fig. 31f). Distally slightly expanded, with ca. 22 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Referring to the Kokoda Trek in Central Prov. of Papua New Guinea, along which the specimens were collected.

Distribution. Papua New Guinea, Central Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 1390 m, together with *Labiobaetis lobatus* Kaltenbach & Gattolliat, 2018 and other species of *Labiobaetis*.

Type material. *Holotype.* PAPUA NEW GUINEA • larva; Central Prov., Kokoda Trek; 09°00'20"S, 147°44'15"E; 1390 m; i.2008; leg. Posman; (PNG 173); on slide; GBIFCH00975629; ZSM. ***Paratypes.*** PAPUA NEW GUINEA • 2 larvae; same data as holotype; on slides; GBIFCH00592683, GBIFCH00592684; MZL.

Genetics

The COI data set was >99.5% complete and included 36% of parsimony informative sites. The missing data almost exclusively resulted from a single sequence (GBIFCH00465182) that lacked 5’ end. Pairwise COI distances across all sequences ranged from 0 to 23.3%. The overall mean p-distance within MOTUs was 1.4% (mean range 0–3.9%), and the overall mean p-distance between MOTUs was 18.7% (mean range 8.6%–23.2%). The maximum p-distance within all MOTUs ranged from 0 (*L. kinibeli* sp. nov.) to 5.5% (*L.* cf. *xeniolus* A), whereas it ranged from 0 (*L. kinibeli* sp. nov.) to 0.2% (*L. nabire* sp. nov.) when only considering newly described species. The minimum distance between all MOTUs ranged from 8.5% (*L. nabire* sp. nov.–*L.* sp. 1) to 23.2% (*L. janae*–*L.* cf. *xeniolus* E), whereas it ranged from 16.1% (*L. kinibeli* sp. nov.–*L. nabire* sp. nov.) to 21.7% (*L. amber* sp. nov.–*L. nabire* sp. nov.) when only considering newly described species. The four sequences of *L. kinibeli* sp. nov. were grouped in a well-supported monophyletic clade, supported as distinct MOTU in the ASAP, PTP and GMYC species delimitation analyses (Fig. 39). Similarly, the two sequences of *L. nabire* sp. nov. were grouped in a well-supported monophyletic clade, supported as distinct MOTU in all species delimitation analyses. *Labiobaetis amber* sp. nov., *L. bilibil* sp. nov. and *L. kokoda* sp. nov., each represented by a single COI sequence, were also supported as distinct MOTUs in all analyses. The three species delimitation methods were also congruent for the other MOTUs, except for *L.* cf. *xeniolus* A and B that were each split into 2 MOTUs according to ASAP and PTP (*L.* cf. *xeniolus* A) or PTP (*L.* cf. *xeniolus* B) methods.

Key to the species of the *Labiobaetis petersorum* group (larvae)

1 Labial palp segment III very short, conical (0.2×–0.3× length of segment II); paraproct with poorly developed marginal spines (Lugo-Ortiz et al. 1999: figs 109, 115)........ *L. xeniolus*

– Labial palp segment III longer (at least 0.4×, usually 0.6× length of segment II) (Figs 4d); paraproct with marginal spines normally developed (Fig. 6f)........ 2

2 Paraproct with obvious expansion of distal margin (Kaltenbach and Gattolliat 2018: fig. 20e)........ *L. janae*

– Paraproct without expansion of distal margin (Fig. 6f)........ 3

3 Dorsal margin of femur with ca. 25 spine-like setae (Fig. 24a)........ 4

– Dorsal margin of femur with ca. 37 to >50 spine-like setae (Fig. 12a)........ 5

4 Dorsal margin of femur with short to medium, spine-like setae (Fig. 24a, b); femur with medial, orange-brown spot on posterior side (Fig. 20a); tibia dorsal margin with row of short, apically rounded setae (Fig. 24e)........ *L. nabire* sp. nov.

– Dorsal margin of femur with long, spine-like setae (Fig. 30a, b); femur without orange-brown spot (Fig. 26a); tibia dorsal margin with row of medium pointed setae (Fig. 30e)........ *L. simbuensis* sp. nov.

5 Labrum very wide (length 0.5× width) (Fig. 9a); labial palp segment II with elongate, slightly hooked, distomedial protuberance (Fig. 11c); posterior margin of abdominal tergum IV with triangular, sharply pointed spines, longer than wide (Fig. 13c)........ *L. bilibil* sp. nov.

– Not this combination of characters........ 6

6 Tibia dorsal margin with two rows of short, stout setae (Fig. 18e); margin between prostheca and mola of both mandibles with minute denticles, subtriangular process with minute denticles at base (Fig. 15e, h, i); posterior margin of abdominal tergum IV with triangular spines, slightly wider than long (Fig. 19c) .... *L. kinibeli* sp. nov.

– Not this combination of characters 7

7 Labial palp segment III rather short (0.4× length of segment II) (Fig. 4d); posterior margin of abdominal tergum IV with triangular spines, slightly wider than long (6c)..*L. amber* sp. nov.

– Labial palp segment III long (0.6× length of segment II) (Kaltenbach and Gattolliat 2018: fig. 17h); spines at posterior margin of abdominal tergum IV of different shape... 8

8 Labial palp segment III oblong, segment II with broad, thumb-like protuberance; posterior margin of abdominal tergum IV with rounded spines, wider than long (Kaltenbach and Gattolliat 2018: figs 17h, 18c)................................*L. gladius*

– Labial palp segment III slightly pentagonal, segment II with rather small, thumb-like protuberance, distal margin of protuberance slightly concave; posterior margin of abdominal tergum IV with triangular, pointed spines, longer than wide (Kaltenbach and Gattolliat 2018: fig. 16c, d) ....*L. petersorum*

Table 2. GPS coordinates of locations of examined specimens.

Species	Country	Location	Coordinates
L. petersorum	Papua New Guinea	Morobe Prov.	07°20'14"S, 146°42'57"E
			07°20'05"S, 146°41'05"E
			05°51'29"S, 144°14'35"E
L. xeniolus	Papua New Guinea	Morobe Prov.	07°12'28"S, 146°50'41"E
L. gladius	Papua New Guinea	Simbu Prov.	05°49'58"S, 145°06'08"E
			05°48'03"S, 145°04'09"E
			05°49'02"S, 145°05'16"E
		Western Highlands Prov.	05°15'52"S, 144°32'43"E
		Easterm Highlands Prov.	05°56'48"S, 145°22'14"E
L. janae	Indonesia	Papua Prov.	04°07'46"S, 138°40'46"E
L. amber sp. nov.	Indonesia	Papua Barat Prov.	01°10'59"S, 133°54'44"E
L. bilibil sp. nov.	Papua New Guinea	Madang Prov.	04°41'01"S, 145°26'55'E
L. kinibeli sp. nov.	Papua New Guinea	Central Prov.	08°20'31"S, 146°59'49"E
		Western Highlands Prov.	05°17'14"S, 144°28'13"E
		Western Highlands Prov.	05°15'10"S, 144°32'49"E
		Western Highlands Prov.	05°15'52"S, 144°32'43"E
L. nabire sp. nov.	Indonesia	Papua Prov.	03°29'48"S, 135°43'53"E
L. simbuensis sp. nov.	Papua New Guinea	Simbu Prov.	05°48'03"S, 145°04'09"E
L. cf. *petersorum*	Indonesia	Papua Barat Prov.	00°47'02"S, 133°04'20"E
L. cf. *xeniolus* A	Papua New Guinea	Enga Prov.	05°38'06"S, 143°55'20"E
		Western Highlands Prov.	05°14'50"S, 144°28'27"E
		Madang Prov.	05°12'42"S, 144°35'31"E
L. cf. *xeniolus* B	Papua New Guinea	Central Prov.	08°20'31"S, 146°59'49"E
		Central Prov.	09°14'20"S, 147°40'32"E
L. cf. *xeniolus* C	Papua New Guinea	Morobe Prov.	07°14'49"S, 146°01'20"E
L. cf. *xeniolus* D	Papua New Guinea	Western Highlands Prov.	05°16'06"S, 144°27'52"E
L. cf. *xeniolus* E	Papua New Guinea	Central Prov.	09°01'57"S, 147°44'27"E
L. cf. *xeniolus* F	Papua New Guinea	Madang Prov.	05°13'23"S, 144°37'17"E
		Madang Prov.	05°13'20"S, 144°37'37"E
L. cf. *xeniolus* G	Papua New Guinea	Central Prov.	08°31'35"S, 147°14'06"E
L. sp. 1	Indonesia	Papua Prov.	03°35'17"S, 137°30'41"E
L. kokoda sp. nov.	Papua New Guinea	Central Prov.	09°00'20"S, 147°44'15"E

Discussion

Assignment to *Labiobaetis*

For the assignment of the new species to *Labiobaetis* we refer to Kluge and Novikova (2014), Müller-Liebenau (1984) and McCafferty and Waltz (1995). *Labiobaetis* is characterized by a number of characters, some of which are not found in other taxa (Kluge and Novikova 2014): antennal scape sometimes with a distolateral process (Kaltenbach et al. 2020: fig. 2h); maxillary palp two segmented with excavation at inner distolateral margin of segment II, excavation may be poorly developed or absent (Kaltenbach et al. 2020: fig. 2n–p); labium with paraglossae widened and glossae diminished; labial palp segment II with distomedial protuberance (Fig. 4d). All these characters vary and may be secondarily lost (Kluge and Novikova 2014). The concept of *Labiobaetis* is also based on additional characters, summarized and discussed in Kaltenbach and Gattolliat (2018, 2019).

Labiobaetis petersorum group

The morphological groups within *Labiobaetis* are primarily a working tool, but could also serve as a basis for future studies on the generic delimitation and phylogeny of this genus. The inclusion of nuclear gene sequences may prove that some are natural groups.

Five of the new species, *L. amber* sp. nov., *L. bilibil* sp. nov., *L. kinibeli* sp. nov., *L. nabire* sp. nov. and *L. simbuensis* sp. nov., belong to the group *petersorum* as originally defined in Kaltenbach and Gattolliat 2018: incisor of both mandibles with outermost denticle blade-like enlarged (Fig. 9d, g; in worn condition as Fig. 2d, f); labrum dorsally with submarginal arc of long, simple setae (Fig. 2b); labial palp segment II with rather short, rounded distomedial protuberance (Fig. 4d). The investigation of the new species and re-examination of type material of known species allowed to enhance the morphological characterisation of the group *petersorum* (see above).

Subapical setae

Re-examination of type material of *L. gladius* and *L. janae* revealed the presence of a long, fine subapical setae on the claws, as it is usually the case in the group *petersorum*. They are not mentioned or figured in the original description. These subapical setae seem to break easily or to stick along the posterior side of the claw and therefore, may be difficult to see. The subapical setae of the group *petersorum* are inserted on posterior side of the claw, in anterior position (between distalmost denticle and tip of the claw). On anterior side, there is a short subapical seta (*L. amber* sp. nov.; Fig. 7). *Labiobaetis petersorum* seems to be an exception for this character, as subapical setae were originally not described or figured and were also not detected during an earlier re-examination of a paratype by the authors (without specifically looking for this character). Additionally, *L.* cf. *petersorum* from a very distant location compared to the type locality, which has all characters of *L. petersorum*, is also missing subapical setae. The original description of *L. xeniolus* does also not mention or figure subapical setae, nor were they discovered during a re-examination of two paratypes based on stacking videos of fore claws. Other legs were not embedded in these paratype slides. However, this study revealed several MOTUs with the same larval morphology than *L. xeniolus*, and they all have subapical setae.

Two other species of *Labiobaetis*, which are not part of the group *petersorum* are known to have subapical setae, *L. catadupa* Kaltenbach & Gattolliat, 2021 from Borneo and *L. toraja* Kaltenbach & Gattolliat, 2021 from Sulawesi (both are forming the group *catadupa*). In both cases, their position is as usually on posterior side, but in posterior position (at or close to the distalmost denticle; “posterior seta” according to Kluge and Novikova 2014: 11; Kaltenbach and Gattolliat 2021: fig. 4a, b).

One single, long subapical seta or one on each side of the claw were also described from other genera of Baetidae (see discussion and citations in Kaltenbach and Gattolliat 2021). The genus *Philibaetis* Kaltenbach & Gattolliat, 2021 has two or more subapical setae on posterior side of the claw, which also exists in a few other genera of Baetidae (see discussion and citations in Kaltenbach et al. 2021b).

Mandibles with blade-like incisors

The most obvious character present in all species of *Labiobaetis* group *petersorum* is the incisors with blade-like enlarged outermost denticles on both mandibles. This character was also observed in other genera of Baetidae, and is most probably a convergence: e.g. *Branchiobaetis* Kaltenbach, Kluge & Gattolliat, 2022; *Philibaetis* Kaltenbach & Gattolliat, 2021; Liebebiella Waltz & McCafferty, 1987; and *Baetis* Leach, 1815 (Müller-Liebenau 1982, 1984; Müller-Liebenau and Hubbard 1985; Kaltenbach et al 2021b, 2022b). Interestingly, this character is usually combined with a wide, sub-rectangular labrum with a well-developed, dorsal, submarginal arc of long, simple setae. It could be a co-adaptation of both characters to a specific way of alimentation like scraping (Sartori and Brittain 2015). Further studies are necessary to explore this possibility in the future. However, *Baetis collinus* Müller-Liebenau & Hubbard, 1985 is an exception with a rather narrow labrum (Müller-Liebenau and Hubbard 1985: fig. 4a, e).

Genetics

The five newly described species included in the genetic investigations are highly supported by our CO1-based analyses. The minimum p-distance between MOTUs of 8.5% (distance between *L. nabire* sp. nov. and *L.* sp. 1) is far beyond the generally accepted threshold of 3% divergence for mayflies (e.g., Ball et al. 2005; Kjærstad et al. 2012; Gattolliat et al. 2015), and all three species delimitation analyses are congruent and support their species status, despite a very limited intraspecies diversity. *L. bilibil* sp. nov. and *L.* cf. *petersorum* are supported as related to each other (Fig. 39) and the morphology is supporting this as well: both have long, sharply pointed spines at posterior margins of abdominal terga; similar setation of the legs; and a similar shape of labial palps segments II and III. The main differences are the shape of the labrum (length ca. 0.6× width in *L.* cf. *petersorum* and 0.5× in *L. bilibil* sp. nov.), the shape of the tarsus (slender in *L.* cf. *petersorum*, relativ short and wide in *L. bilibil* sp. nov.) and the subapical setae (absent in *L.* cf. *petersorum*, present in *L. bilibil* sp. nov.). Other relations are supported between *L. janae* and *L. kinibeli* sp. nov. and between *L. nabire* sp. nov. and *L.* sp.1 (Fig. 39). In the first case, the larval morphology is not showing further evidence, and in the second case, there are morphological similarities of *L.* sp. 1 with both *L. nabire* sp. nov. and *L. kinibeli* sp. nov. However, most species of the group *petersorum* are morphologically close and we are mostly lacking characters to recognise and support subgroups inside this group.

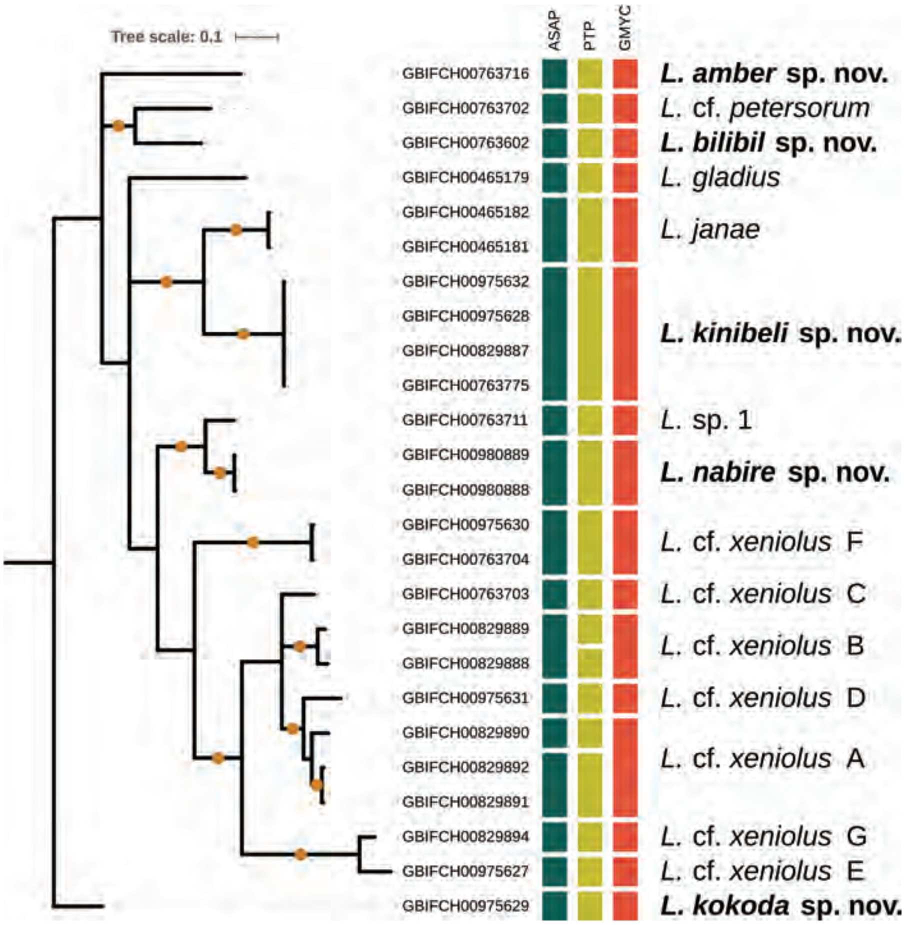


Figure 39. Bayesian majority-rule consensus tree reconstructed from the CO1 data set. Coloured vertical boxes indicate species delimitation hypothesis (MOTUs) according to the ASAP, PTP and GMYC methods. Tips are labelled according to Table 1. For each GMYC-based MOTU, the corresponding species name (where available) is provided, with newly described species specified in bold. Circles on branches indicate Bayesian posterior probabilities > 0.9.

Interestingly, the seven *L.* cf. *xeniolus* MOTUs are integrated in the same clade (although without a strong support), suggesting a potentially cryptic species complex that requires further investigation. We recommend that future studies include more populations to increase the amount of intraspecies diversity within the *L.* cf. *xeniolus* complex, as well as information from the nuclear genome to complement the classic COI-based approach.

Taking into account the extreme biodiversity in New Guinea, the rather poor collection activities in the past, with many still unexplored regions, and the obvious richness of *Labiobaetis* on this island, we have to expect many more new species with further collections in the future.

Acknowledgements

We sincerely thank Michael Balke (Zoologische Staatssammlung München, ZSM/SNSB) and his local team in New Guinea for the collection of most of this precious material. A part of it is the result of a long-term capacity building program between SNSB-Zoologische Staatssammlung and Cenderawasih University (UNCEN). We are also thankful to the late Tomáš Soldán (Institute of Entomology, Biology Centre CAS, České Budějovice) for the allocation of material from New Guinea to the Muséum Cantonal des Sciences Naturelles in Lausanne (MZL) and to Lukáš Čížek (Institute of Entomology, Biology Centre CAS, České Budějovice), the collector of this part of the material. Further, we are appreciative to Luke Jacobus and Christopher Charles Wirth (Purdue University, Columbus), who helped us with information and photos of type material from New Guinea, and we are grateful to Nadir Alvarez (Muséum Cantonal des Sciences Naturelles, Lausanne, MZL) for his interest and support for our projects, to Céline Stoffel and Marion Podolak (MZL) for their support with lab work and preparation of the COI barcodes, and to Antonio Mucciolo (University Lausanne, UNIL) for the SEM picture. Finally, we are thankful to the reviewers for their valuable comments and corrections.

References

Allison A (2010) New Guinea, Biology. In: Gillespie RG, Clague DA (Eds) Encyclopedia of islands, University of California Press, Berkeley, Los Angeles, London, 652–659. https://doi.org/10.1525/9780520943728-157

Ball SL, Hebert PDN, Burian SK, Webb JM (2005) Biological identifications of mayflies (Ephemeroptera) using DNA barcodes. Journal of the North American Benthological Society 24: 508–524. https://doi.org/10.1899/04-142.1

Barber-James HM, Sartori M, Gattolliat J-L, Webb J (2013) World checklist of freshwater Ephemeroptera species. http://fada.biodiversity.be/group/show/35

Chakrabarty P, Warren M, Page LM, Baldwin CC (2013) GenSeq: An updated nomenclature and ranking for genetic sequences from type and non-type sources. Zookeys 346: 29–41. https://doi.org/10.3897/zookeys.346.5753

Chesters D (2013) collapsetypes.pl. [computer software available at] http://sourceforge.net/projects/collapsetypes/

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature methods 9(8): 772–772. https://doi.org/10.1038/nmeth.2109

Ezard T, Fujisawa T, Barraclough TG (2021) SPLITS: SPecies' LImits by Threshold Statistics. R-package version 1.0-20/r56. https://R-Forge.R-project.org/projects/splits/

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from divers metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299. http://www.mbari.org/staff/vrijen/PDFS/Folmer_94MMBB.pdf

Fujisawa T, Barraclough TG (2013) Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent approach: a revised method and evaluation on simulated data sets. Systematic Biology 62(5): 707–724. https://doi.org/10.1093/sysbio/syt033

Gattolliat J-L, Cavallo E, Vuataz L, Sartori M (2015) DNA barcoding of Corsican mayflies (Ephemeroptera) with implications on biogeography, systematics and biodiversity. Arthropod Systematics & Phylogeny 73(1): 3–18.

Hurvich CM, Tsai C L (1989) Regression and time series model selection in small samples. Biometrika 76(2): 297–307. https://doi.org/10.1093/biomet/76.2.297

Hubbard MD (1995) Towards a standard methodology for the description of mayflies (Ephemeroptera). In: Corkum LD, Ciborowski JJH (Eds) Current directions in research on Ephemeroptera. Canadian Scholar's Press, Toronto, 361–369.

Jacobus LM, Macadam CR, Sartori M (2019) Mayflies (Ephemeroptera) and their contributions to ecosystem services. Insects 10: 1–26. https://doi.org/10.3390/insects10060170

Kaltenbach T, Gattolliat J-L (2018) The incredible diversity of *Labiobaetis* Novikova & Kluge in New Guinea revealed by integrative taxonomy (Ephemeroptera, Baetidae). ZooKeys 804: 1–136. https://doi.org/10.3897/zookeys.804.28988

Kaltenbach T, Gattolliat J-L (2019) The tremendous diversity of *Labiobaetis* Novikova & Kluge in Indonesia (Ephemeroptera, Baetidae). ZooKeys 895: 1–117. https://doi.org/10.3897/zookeys.895.38576

Kaltenbach T, Gattolliat J-L (2020) *Labiobaetis* Novikova & Kluge in Borneo (Ephemeroptera, Baetidae). ZooKeys 914: 43–79. https://doi.org/10.3897/zookeys.914.47067

Kaltenbach T, Gattolliat J-L (2021) New species of *Labiobaetis* Novikova & Kluge from Southeast Asia and New Guinea (Ephemeroptera, Baetidae). ZooKeys 1067: 159–208. https://doi.org/10.3897/zookeys.1067.72251

Kaltenbach T, Garces JM, Gattolliat J-L (2020) The success story of *Labiobaetis* Novikova & Kluge in the Philippines (Ephemeroptera, Baetidae), with description of 18 new species. ZooKeys 1002: 1–114. https://doi.org/10.3897/zookeys.1002.58017

Kaltenbach T, Garces J, Gattolliat J-L (2021b) *Philibaetis* gen. nov., a new genus from the Philippines (Ephemeroptera, Baetidae). Deutsche Entomologische Zeitschrift 68: 1–20. https://doi.org/10.3897/dez.68.59462

Kaltenbach T, Garces J, Gattolliat J-L (2022a) First contribution to *Labiobaetis* Novikova & Kluge in Cambodia (Ephemeroptera, Baetidae), with description of two new species. ZooKeys 1123: 63–81. https://doi.org/10.3897/zookeys.1123.90308

Kaltenbach T, Kluge NJ, Gattolliat J-L (2022b) A widespread new genus of Baetidae (Baetidae, Ephemeroptera) from Southeast Asia. ZooKeys 1135: 1–59. https://doi.org/10.3897/zookeys.1135.93800

Kaltenbach T, Surbakti S, Kluge NJ, Gattolliat J-L, Sartori M, Balke M (2021a) Discovery of a new mayfly species (Ephemeroptera, Baetidae) near Cenderawasih University campus in Papua, Indonesia. Treubia 48: 37–54. https://doi.org/10.14203/treubia.v48i1.4020

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in bioinformatics 20(4): 1160–1166. https://doi.org/10.1093/bib/bbx108

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16: 111–120. https://doi.org/10.1007/BF01731581

Kjærstad G, Webb JM, Ekrem T (2012) A review of the Ephemeroptera of Finnmark–DNA barcodes identify Holarctic relations. Norwegian Journal of Entomology 59(2): 182–195.

Kluge NJ (2004) The phylogenetic system of Ephemeroptera. Academic Publishers, Dordrecht, 442 pp. https://doi.org/10.1007/978-94-007-0872-3

Kluge NJ (2005) Larval/pupal leg transformation and a new diagnosis for the taxon Metabola Burmeister, 1832 = Oligoneoptera Martynov, 1923. Russian Entomological Journal 13: 189–229.

Kluge NJ, Novikova EA (2014) Systematics of *Indobaetis* Müller-Liebenau & Morihara 1982, and related implications for some other Baetidae genera (Ephemeroptera). Zootaxa 3835: 209–236. https://doi.org/10.11646/zootaxa.3835.2.3

Kluge N, Sivaruban T, Srinivasan P, Barathy S, Isack R (2023) Diagnosis, variability, distribution and systematic position of *Labiobaetis pulchellus* (Müller-Liebenau & Hubbard 1985) (Ephemeroptera, Baetidae, Baetis s. l.). Zootaxa 5264: 94–108. https://doi.org/10.11646/zootaxa.5264.1.6

Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A (2019) RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35(21): 4453–4455. https://doi.org/10.1093/bioinformatics/btz305

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35(6): 1547. https://doi.org/10.1093/molbev/msy096

Letunic I, Bork P (2021) Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. Nucleic acids research 49(W1): W293–W296. https://doi.org/10.1093/nar/gkab301

Lugo-Ortiz CR, McCafferty WP, Waltz RD (1999) Definition and reorganization of the genus *Pseudocloeon* (Ephemeroptera: Baetidae) with new species descriptions and combinations. Transactions of the American Entomological Society 125: 1–37.

McCafferty WP, Waltz RD (1995) *Labiobaetis* (Ephemeroptera: Baetidae): new status, new North American species, and related new genus. Entomological News 106: 19–28.

Monaghan MT, Wild R, Elliot M, Fujisawa T, Balke M, Inward DJ, Vogler AP (2009) Accelerated species inventory on Madagascar using coalescent-based models of species delineation. Systematic biology 58(3): 298–311. https://doi.org/10.1093/sysbio/syp027

Müller-Liebenau I (1982) New species of the family Baetidae from the Philippines (Insecta, Ephemeroptera). Archiv für Hydrobiologie 94: 70–82.

Müller-Liebenau I (1984) New genera and species of the family Baetidae from West-Malaysia (River Gombak) (Insecta: Ephemeroptera). Spixiana 7: 253–284.

Müller-Liebenau I, Hubbard MD (1985) Baetidae from Sri Lanka with some general remarks on the Baetidae of the Oriental Region (Insecta: Ephemeroptera). Florida Entomologist 68: 537–561. https://doi.org/10.2307/3494855

Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Daniel PD, Hazell S, Kamoun S, William DS, Vogler AP (2006) Sequence-Based Species Delimitation for the DNA Taxonomy of Undescribed Insects, Systematic Biology 55: 595–609. https://doi.org/10.1080/10635150600852011

Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery 643 for primary species delimitation. Molecular Ecology 21: 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Puillandre N, Brouillet S, Achaz G (2020) ASAP: assemble species by automatic partitioning. Molecular Ecology Resources 21(2): 609–620. https://doi.org/10.1111/1755-0998.13281

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic biology 67(5): 901–904. https://doi.org/10.1093/sysbio/syy032

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna, Larget S, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Sanger F, Nicklen S, Coulson AR (1977) DNA sequencing with chain-terminating inhibitors. Proceedings of the National Academy of Sciences U.S.A. 74: 5463–5467. https://doi.org/10.1073/pnas.74.12.5463

Sartori M, Brittain JE (2015) Order Ephemeroptera. In: Thorp J, Rogers DC (Eds) Ecology and general biology: Thorp and Corvich's Freshwater Invertebrates. Academic Press, 873–891. https://doi.org/10.1016/B978-0-12-385026-3.00034-6

Shi W, Tong X (2014) The genus *Labiobaetis* (Ephemeroptera: Baetidae) in China, with description of a new species. Zootaxa 3815: 397–408. https://doi.org/10.11646/zootaxa.3815.3.5

Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. [Retrieved from] https://www.simplemappr.net [Accessed March 03, 2021]

Srivathsan A, Meier R (2012) On the inappropriate use of Kimura-2-parameter (K2P) divergences in the DNA-barcoding literature. Cladistics 28(2): 190–194. https://doi.org/10.1111/j.1096-0031.2011.00370.x

Stecher G, Tamura K, Kumar S (2020) Molecular evolutionary genetics analysis (MEGA) for macOS. Molecular Biology and Evolution 37(4): 1237–1239. https://doi.org/10.1093/molbev/msz312

Suchard MA, Lemey P, Baele G, Ayres DL, Drummond AJ, Rambaut A (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10 Virus Evolution 4, vey016. https://doi.org/10.1093/ve/vey016

Talavera G, Dincă V, Vila R (2013) Factors affecting species delimitations with the GMYC model: insights from a butterfly survey. Methods in Ecology and Evolution 4(12): 1101–1110. https://doi.org/10.1111/2041-210X.12107

Tofilski A (2018) DKey software for editing and browsing dichotomous keys. ZooKeys 735: 131–140. https://doi.org/10.3897/zookeys.735.21412

Toussaint EFA, Sagata K, Surbakti S, Hendrich L, Balke M (2013) Australasian sky islands act as a diversity pump facilitating peripheral speciation and complex reversal from narrow endemic to widespread ecological supertramp. Ecology and Evolution 3: 1031–1049. https://doi.org/10.1002/ece3.517

Toussaint EA, Hall R, Monaghan MT, Sagata K, Ibalim S, Shaverdo HV, Vogler AP, Pons J, Balke M (2014) The towering orogeny of New Guinea as a trigger for arthropod megadiversity. Nature Communications 5: 4001–4010. https://doi.org/10.1038/ncomms5001

Vuataz L, Sartori M, Wagner A, Monaghan MT (2011) Toward a DNA taxonomy of Alpine *Rhithrogena* (Ephemeroptera: Heptagenidae) using a mixed Yule-Coalescent Analysis of mitochondrial and nuclear DNA. PLoS ONE 6: 1–11. https://doi.org/10.1371/journal.pone.0019728

Waterhouse AM, Procter JB, Martin DMA, Clamp M, Barton GJ (2009) Jalview Version 2 —a multiple sequence alignment editor and analysis workbench. Bioinformatics 25: 1189–1191. https://doi.org/10.1093/bioinformatics/btp033

Wickham H (2011) The split-apply-combine strategy for data analysis. Journal of Statistical Software 40(1): 1–29. https://doi.org/10.18637/jss.v040.i01

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29(22): 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

Alpine Entomology 7 2023, 135–141 | DOI 10.3897/alpento.7.107649

PENSOFT.

Alpine
Entomology

Are yellow dung flies domesticated cow dung specialists?

Wolf U. Blanckenhorn[1], Dieter Burkhard[2]

1 *Department of Evolutionary Biology & Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland*
2 *Kantonsschule Heerbrugg, Fachgruppen Biologie & Informatik, Karl-Völker-Str. 11, CH-9435 Heerbrugg, Switzerland*

https://zoobank.org/DE3B8274-1D97-404F-B805-27A58CC50356

Corresponding author: Wolf U. Blanckenhorn (Wolf.Blanckenhorn@ieu.uzh.ch)

Academic editor: Inon Scharf ♦ **Received** 7 June 2023 ♦ **Accepted** 7 August 2023 ♦ **Published** 18 August 2023

Abstract

The theory of niche differentiation implies some extent of specialization of species with regard to key resources, notably food. Coprophagous (dung-eating) insect larvae play a critical role in the decomposition of livestock dung in modern and traditional agricultural grasslands. The yellow dung fly (*Scathophaga stercoraria* L.; Diptera: Scathophagidae) is one of the largest, most common and abundant dung decomposers on pastures in cold-temperate regions across the entire northern hemisphere. As this fly is often associated with domesticated cattle or dairy cows, which are commonly kept for human nutrition worldwide (beef, milk, cheese, etc.), it is sometimes suspected to be a cow dung specialist. However, yellow dung flies are regularly active on and around other dung types, and must have reproduced on dung of wild vertebrates before the domestication of cattle. We therefore experimentally studied the performance of yellow dung fly larvae on dung of various large domestic vs. wild mammals (cow, horse, wild boar, red deer) in the laboratory in Switzerland. Larval performance in terms of juvenile survival, egg-to-adult development time, growth rate, and final adult body size, the major life history indicators of individual reproductive success, did not vary greatly among the various dung types tested. Thus, yellow dung flies can successfully reproduce on multiple types of mammal (vertebrate) dung, wild and domestic, and are therefore dung generalists rather than specialists. We conclude that yellow dung flies are common in European low- and highlands because they could plastically shift to dung of common herbivorous livestock after their domestication without losing the ability to reproduce on dung of common wild mammals.

Key Words

Behavioral Ecology, body size, coprophagy, development, Diptera, domestication, dung, food niche, insect, larval food manipulation, livestock dung, *Scathophaga stercoraria*, specialist-generalist, survival

Introduction

According to the theory of niche differentiation, species inhabiting the same ecological niche should not be able to coexist in the long term (Abrams 1987; Holt 2009). This implies some extent of specialization of species with regard to their key resources, notably food. In the long term, physiological adaptations facilitating efficient nutrient acquisition are expected to evolve, which ultimately drive niche differentiation. Nevertheless, in nature multiple species often live in the same habitat, feeding on roughly the same resource. A prominent example is the coprophagous (i.e. dung-eating) insect community, consisting mainly of beetles and flies that inhabit and decompose vertebrate, often domesticated livestock dung (Hammer 1941; Holter 1979; Hanski and Cambefort 1991; Skidmore 1991; Lumaret et al. 1992; Rohner et al. 2015; Laux et al. 2019). These species essentially all compete for the same types of resources, although there are consumers, predators and parasitoids, some of which are considered dung specialists, others generalists (Hanski and Cambefort 1991; Skidmore 1991; Pont and Meier 2002; Jochmann and Blanckenhorn 2016). Whereas a generalist of this community can thrive on the dung of various different vertebrates, any specialist may only exploit the dung of a single vertebrate (e.g. cow or human dung). In practice this will be a continuum, however.

Coprophagous insect larvae play a critical role in the decomposition of vertebrate dung, which in turn is crucial for nutrient cycling in managed agricultural grasslands in many parts of the world (Skidmore 1991; Jochmann et al. 2011; Adler et al. 2016; Floate 2023). As a prominent example, the introduction of livestock for farming in many new areas of the world (for instance in Australia) led to the subsequent introduction of dung organisms from other parts of the world (e.g. *Onthophagus* dung beetles from southern Europe) to biocontrol the proliferating excrements, which were not broken down because a co-evolved dung fauna was lacking (Bornemissza 1960, 1976). Nonetheless, to date it is not clear precisely which nutrients are taken up and digested by the various dung feeding insects (plant matter, inorganic components, fungi or bacteria growing on the dung, fluid components, etc.: Lumaret 1995; Holter 2016). Regardless, many of these nutritional components may be alike for particular classes of vertebrate dung depending on the food of the producers, i.e. herbivores vs. carnivores vs. omnivores, so that not only the fibrous content of the dung, but even the microbiome of these animals ending up in their dung might be sufficiently similar (Shukla et al. 2016). One could therefore hypothesize *a priori* that coprophagous insects more likely are generalists rather than extreme dung specialists (Holter 2016; Laux et al. 2019). This, in turn, could facilitate their broader geographic distribution, especially if they can thrive on the dung of common and ubiquitous livestock species such as cattle, sheep, horses, etc.

The yellow dung fly (*Scathophaga stercoraria* L.; Diptera: Scathophagidae) is one of the largest (approaching the size of honey bees) and most abundant dung decomposers on livestock (especially cattle) pastures in cold-temperate regions across the entire northern hemisphere (Hammer 1941; Stone et al. 1965; Gorodkov 1984; Blume 1985; Skidmore 1991; Papp 1992; Bernasconi et al. 2010; Blanckenhorn et al. 2010, 2018). Unlike most insects, which are most common when and where it is warm, this fly actually prefers cooler climates, as it invaded arctic regions in the Old and New Worlds as well as higher altitude habitats in warmer regions, for instance the Alps (Vockeroth 1987; Sigurjónsdóttir and Snorrason 1995; Blanckenhorn 1997; Šifner 2008; Blanckenhorn et al. 2018). In Switzerland this species is omnipresent, likely related to the high density of cows for milk, cheese but also beef production as well as other livestock, which range from low to high altitude pastures in the Alps up to ca. 2000 m beyond the treeline (Kraushaar et al. 2002). Yellow dung flies depend on the availability of fresh vertebrate dung, into which females lay their eggs and which the larvae consume and thereby recycle, eventually pupating in the ground close to a dung pat. Adult flies lick nectar from flowers for energy but additionally require small insect prey to reproduce (nutritional anautogeny: Foster 1967; Gibbons 1980; Blanckenhorn et al. 2007, 2010; Kaufmann et al. 2013). Reproduction consequently also happens around the (fresh) dung pat, and especially the mating behaviour of yellow dung flies has been studied intensively over the past decades (Parker 1970; Parker et al. 2020; Blanckenhorn 2021). Male flies therefore abound on and around cow dung pats to mate with incoming females. Females only come to the dung when they have eggs ready to be laid, and otherwise spend most of their time foraging for prey and nectar in the vegetation surrounding a pasture to avoid continuous harassment by males (Parker et al. 2020).

From its common link with domesticated cattle worldwide, the yellow dung fly has been implicitly suggested to be a cow dung specialist, but this has not yet been confirmed (Blanckenhorn et al. 2001). Blanckenhorn (2009) further raised the more general hypothesis that this fly’s wide range may be a consequence of its documented extensive phenotypic plasticity in various life history and behavioural traits, supposedly mediating dung generalism. Yellow dung flies are regularly active on and around other dung types of common herbivores such as sheep or horses (Cotterell 1920; Hirschberger and Degro 1996), and they must have reproduced on dung of wild vertebrates before the domestication of cattle. Contrary to some other coprophagous insect groups (e.g. dung beetles and sepsid flies: Holter 2016; Laux et al. 2019), the success of yellow dung fly larvae on diverse dung types has so far not been studied systematically in detail. We therefore here provide a comparative assessment in the laboratory of how well the offspring of yellow dung flies perform in dung of various large domestic vs. wild mammals: cow, horse, wild boar, red deer. The precise composition of the dung in terms of bacteria and fungi, its consistency, dryness, particle size and specific nutrients knowingly affects the performance of yellow dung fly larvae in terms of juvenile survival, egg-to-adult development time, growth rate, and final adult body size, the major life history indicators of individual reproductive success (Frank et al. 2017; e.g. Amano 1983). Differentiation along these traits may therefore be used as a surrogate for reproductive fitness, and hence the degree of adaptation and specialisation to any particular dung type of any given coprophagous species, yellow dung flies in particular here (Blanckenhorn 2009).

Thus, if yellow dung flies are indeed herbivore and as such mainly cow dung specialists, then they should perform exclusively, or more likely at least better on that type of dung; that is, they should survive best, develop and grow fastest, and produce largest individuals when raised in cow dung. And if they are secondarily, i.e. evolutionarily recently adapted to and therefore specialized on domesticated livestock, they should perform better on livestock than wild mammal dung. We investigated this by raising yellow dung fly larvae on dung of domesticated cow (herbivore), domesticated horse (herbivore), wild boar (omnivore), and wild red deer (herbivore) in the laboratory.

Material and methods

General rearing methods

We used dung from four large mammals common in Switzerland to raise yellow dung fly larvae from our existing laboratory stock to adulthood in standard common-garden laboratory conditions (given below). Laboratory flies had been originally caught in Fehraltorf, Switzerland (47°23'N, 8°44'E), and maintained subsequently on defrosted cow dung for several generations in climate chambers. Cow and horse dung was collected from farms near Zürich, wild boar dung from Wildpark Langenberg, and red deer dung from Tierpark Goldau (both in Switzerland). In all cases, freshly collected dung from many individuals was mixed thoroughly and subsequently frozen at -80 °C for at least 2 weeks to kill all arthropods therein. Yellow dung flies had previously been raised already on sheep dung by Hirschberger and Degro (1996), and dung of carnivores was not tested since *S. stercoraria* had not been observed on their faeces.

Larval performance on different dung types

To obtain test individuals for the experiment, single-held yellow dung fly females were allowed to copulate with a random male in a 100 ml glass vial containing water, sugar and *Drosophila* prey as nutrients, at room temperature of roughly 22 °C. The females (total N = 26) could lay a clutch of eggs into a smear of cow dung on a filter paper. Using a split-brood design, typically n = 10 of these eggs were then transferred with a small layer of the original dung smear into a small plastic container with overabundant (>2 g/egg; Amano 1983) dung of any of the 4 dung types, in which the larvae could subsequently develop and eventually emerge as adult flies in a climate chamber set at 19 °C, 60% relative humidity, and 13 h light period.

We scored survivorship as the proportion of individuals (of both sexes) that emerged from the typically 10 eggs transferred, their sex-specific egg-to-adult development time, and measured the length of their hind tibia as a reliable index of final structural adult body size (size data unfortunately missing for red deer dung). Linearized growth rate was crudely calculated as hind tibia length (in mm) divided by development time (in days; Blanckenhorn 2009). All life history variables were analyzed separately in SPSS V29 with generalized linear models (survival with binomial errors, all others with normal errors), entering dung type and fly sex (plus their interaction) as fixed factors and the mother's identity (i.e. family) as random factor because related sibling individuals of both sexes emerged from each clutch.

Results

Larval performance on different dung

Larva-to-adult survival did not vary significantly among the 4 different dung types ($\text{Chi}^2 = 5.58$; P > 0.15), hovering around an overall mean of 80% (±2.4% (SE), ±11.2% (SD)), a typical value for cow dung (Table 1; Fig. 1). Survival was a little lower in boar dung (72.6±4.1% SE) and a bit higher in red deer dung (92.5±11.1% SE; Fig. 1); consequently there was also no overall difference between domestic (cow, horse) and wild mammals (boar, deer; planned comparison; P > 0.3). Juvenile survival in dung of the only omnivore tested (boar) appeared lower than overall survival in dung of herbivores (cow, horse, deer; planned comparison: P < 0.1), but omnivore dung remains unreplicated here.

Juvenile performance as measured by all other life history traits assessed varied significantly among the dung

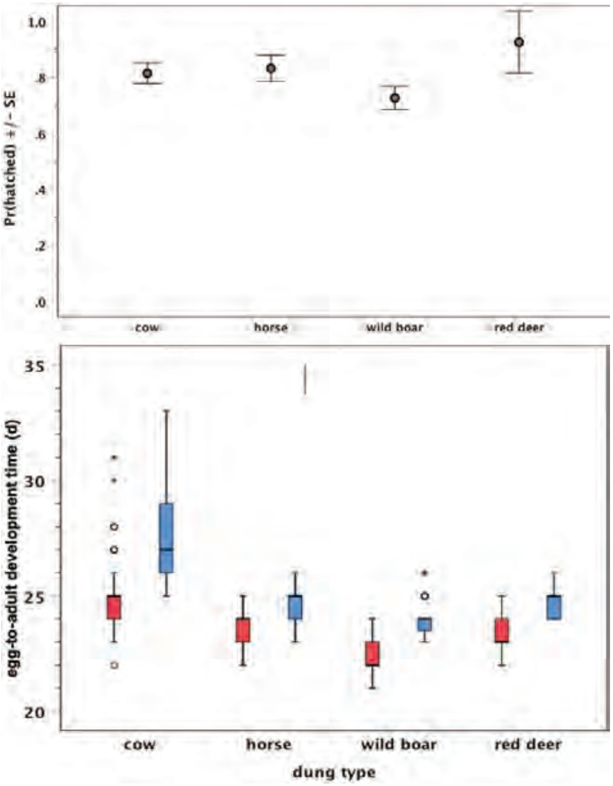


Figure 1. Mean proportion of emerged adults (± SE) on 4 types of mammal dung (top), and corresponding egg-to-adult development times of male (blue) and female (red) flies.

Table 1. Analysis of variance tables for the effects of 4 (3) dung types, sex, and their interaction on egg-to-adult development time, tibia length (body size), and linearized calculated growth rate, with family variation (i.e. clutch) removed as random effect (no size data for deer dung).

	development time				hind tibia length				growth rate		
	df	MS	F	P	df	MS	F	P	MS	F	P
dung type	3	359.66	437.84	<0.001	2	4.89	331.41	<0.001	0.008	200.68	<0.001
sex	1	231.01	281.22	<0.001	1	48.38	3281.17	<0.001	0.036	894.51	<0.001
sex * dung type	3	13.29	16.18	<0.001	2	0.59	40.38	<0.001	0.001	12.96	<0.001
family	25	5.82	7.09	<0.001	16	0.11	7.32	<0.001	0.00001	4.84	<0.001
error	407	0.821			342	0.015			0.00004		

types (Table 1). Egg-to-adult development time at 19 °C was longer in cow dung than all other dung types, and longer for the larger males than the females (the latter is well known in this species: Blanckenhorn 2009; Blanckenhorn et al. 2010; Fig. 1; Table 1). Body size varied somewhat among the dung types, being largest in cow dung, while growth rate was highest in boar dung (Fig. 2; missing data for red deer dung). The sex-by-dung type interaction was also highly significant for all performance variables assessed (Table 1; Figs 1, 2), which is typical in this species with strong sexual dimorphism (males larger) (Blanckenhorn 1998a, 2009; Blanckenhorn et al. 2010).

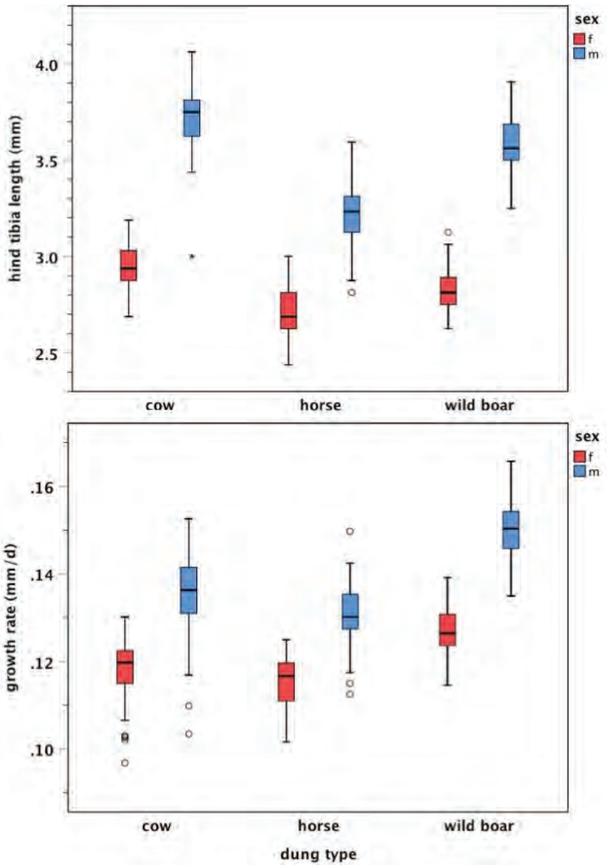


Figure 2. Box plots for hind tibia length (top) and linearized growth rate (tibia length/day) of yellow dung fly females (red) and males (blue) raised on three types of mammal dung.

Discussion

We here compared the life history performance of yellow dung fly larvae in overabundant dung of various large mammals, wild or domestic, in the laboratory to investigate presumed domestic cattle dung specialization of this species. In essence, we found some variation in juvenile survival, roughly between 73% and 93%, among the various dung types tested (cow, horse, wild boar, red deer). Nevertheless, the overall survival average of 80%±2.4% (SE) found here corresponds to the long-term average and range typically observed in the laboratory in unmanipulated cow dung (Blanckenhorn et al. 2010; Fig. 1). Although power analysis indicates that an increase in sample size by ca. 50% (from 65 to 100) would render the overall dung type variation in juvenile mortality obtained significant, with some pairwise comparisons also differing significantly (e.g. boar vs. red deer dung; Fig. 1), we judge this variation minor relative to that typically induced by other environmental stressors (dung limitation, heat, drought, etc.; Blanckenhorn 1998a, 2009) and, importantly, not in accordance with our tested main hypotheses specified in the Introduction.

The body size of emerged flies also varied somewhat among the various dung types (Table 1; Fig. 2), but again was well within the range of what is typically observed in the field or the laboratory at overabundant cow dung, and large in comparison to situations when dung (i.e. food) is limited (Amano 1983; Blanckenhorn 1998a; Blanckenhorn et al. 2010). Somewhat unexpectedly, juvenile development was longest in cow dung to however result in the largest adult flies, while flies emerged smallest in horse dung (Figs 1, 2). Probably the best indicator of success, growth rate – calculated crudely as tibia length increment per day of juvenile development – was fastest in wild boar dung, nevertheless resulting in relatively small adults (Fig. 2). That is, as observed before in cattle dung, growth and development varied flexibly in response to environmental factors, here dung type, so as to affect the life history of the species presumably in an adaptive manner, with recognized consequences for survival and reproduction (Blanckenhorn 1998a, 1999, 2009; Jann et al. 2000; D'Amico et al. 2001; Rohner et al. 2017). We therefore conclude that yellow dung fly juveniles grow and survive reasonably well in the dung of all vertebrates tested here.

As the amount of dung available was more than sufficient in all cases, i.e. not limited in terms of quantity, we here tested for physiological (digestive) responses of yellow dung fly larvae to presumed variation in dung quality mainly depending on the food and/or digestive system of the various mammals considered (in consistency, dryness, particle size, bacteria or fungi content, specific nutrients, etc.; Frank et al. 2017). For instance, the proportion of water (± SE) of the different dung types used was previously estimated as 0.81 (± 0.001) for typical cow, 0.77 (± 0.013) for horse, 0.69 (± 0.007) for red deer, and 0.71 (± 0.003) for wild boar dung ($P < 0.01$; Laux et al. 2019), which likely differentially affects the ability of dung fly larvae to move in and digest their food. We judge the typical variation between the sexes in growth trajectories (significant sex-by-dung type interactions in all performance variables in Table 1) of this species with strong sexual dimorphism (males larger) as mainly reflecting size scaling rather than differential physiological responses to the food source (Blanckenhorn 1998a, 2009; Rohner et al. 2017). It was already previously well documented for yellow dung flies that (cow) dung limitation, typically mediated by high intra- or inter-specific competition of larvae in the food resource, strongly reduces larval survival and final body size of the emerging adults (Amano 1983; Blanckenhorn 1998a, 1999, 2009; Jann et al. 2000; Blanckenhorn et al. 2010). The finer-scale variation in survival, growth, development and final body size obtained here (Figs 1, 2; Table 1) most likely reflects differences in dung consistency and the nutritional value of the dung microbiome of the various mammals tested, but this remains to be investigated further in detail.

At least in species whose immatures are poor dispersers, choice of oviposition site by the mothers plays an additional major role. A female's choice of oviposition site may be innate (Barron 2001; Dormont et al. 2010), but should generally evolve to maximize juvenile performance (Wiklund 1975; Fox and Czesak 2000; Forister 2004; Gómez Jiménez et al. 2014; Konig et al. 2016). In addition to dispersal ability, other factors, such as optimal foraging of gravid females (Forister et al. 2009), may lead to suboptimal outcomes. A next investigatory step would therefore be testing oviposition preferences of gravid females in choice experiments, which we would expect to correlate with the performance ranking indicated by the various life history traits tested here (Figs 1, 2; see e.g. Laux et al. 2019).

Most likely, our study signifies that yellow dung flies are opportunistic in their choice of dung depending on availability in their environment, given their good performance on many different types (qualities) of dung/food documented here (Holter 2016; Laux et al. 2019). Thus, flies may reproduce on deer or boar dung when in the forest, or alternatively on cow, horse or sheep (Hirschberger and Degro 1996) dung when in grasslands, readily switching between these habitats depending on site and weather (Blanckenhorn et al. 2001). In Swiss lowland pastures interspersed with agricultural areas and forests there may be more alternative livestock substrates available than in highland grasslands. While in the Alps cows and sheep abound up to the treeline at roughly 2000 m, wild animal dung (deer, ibex, mountain goat, some carnivores, etc.) should be relatively more abundant there, again permitting easy switching between various dung types. Longer winters shorten the growing season and extend winter diapause of dung fly pupae in the Alps, but should not strongly reduce fly mortality and population density (see Blanckenhorn 1998a, b). As yellow dung flies are cold-adapted in general (see Introduction), flexible oviposition substrate can explain the ubiquity of this species in low- and highland Europe unless temperatures become excessive (e.g. in the Mediterranean; Blanckenhorn et al. 2001, 2018; Scharf et al. 2010).

Even though we here tested merely a small subset of all dung types available in nature, we conclude that yellow dung flies can reproduce successfully on multiple types of mammal (vertebrate) dung, wild or domestic, herbivore or omnivore (and likely also carnivore). At least their reproductive fitness does not strongly deviate from that observed in cattle dung (summarized in Blanckenhorn 2009). Yellow dung flies are therefore probably rather dung generalists than specialists. This dung fly species is widespread presumably because they could plastically shift to dung of common herbivorous livestock species after their domestication, without losing the ability to reproduce on dung of common wild mammals (cf. Blanckenhorn et al. 2018). The yellow dung fly *Scathophaga stercoraria* thus definitely belongs to the minority of insect taxa that benefit from humanity's agricultural activities (e.g. Loboda et al. 2018), and which therefore are not of special conservation concern.

Acknowledgements

W.U.B thanks D.B. for resuscitating this study over 20 years later in a totally different context, as it had gone forgotten. This work was funded by the Zoological Museum of the University of Zurich and continuous grants from the Swiss National Science Foundation to W.U.B. In memory of Paul I. Ward, who died too early.

References

Abrams PA (1987) Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. Evolution 41: 651–661. https://doi.org/10.2307/2409267

Adler N, Bachmann J, Blanckenhorn WU, Floate KD, Jensen J, Römbke J (2016) Effects of ivermectin application on the diversity and function of dung and soil fauna: regulatory and scientific background information. Environmental Toxicology and Chemistry 35: 1914–1923. https://doi.org/10.1002/etc.3308

Amano K (1983) Studies on the intraspecific competition in dung breeding flies. I. Effects of larval density on the yellow dung fly. Japanese Journal of Sanitary Zoology 34: 165–175. https://doi.org/10.7601/mez.34.165

Barron AB (2001) The life and death of Hopkins' host-selection principle. Journal of Insect Behavior 14: 725–737. https://doi.org/10.1023/A:1013033332535

Bauerfeind SS, Sørensen JG, Loeschcke V, Berger D, Broder ED, Geiger M, Ferrari M, Blanckenhorn WU (2018) Geographic variation in responses of European yellow dung flies to thermal stress. Journal of Thermal Biology 73: 41–49. https://doi.org/10.1016/j.jtherbio.2018.01.002

Bernasconi MV, Berger D, Blanckenhorn WU (2010) Systematic ambiguity in the well-established model system insect *Scathophaga stercoraria* (Diptera: Scathophagidae): sister species *S. soror* revealed by molecular evidence. Zootaxa 2441: 27–40. https://doi.org/10.11646/zootaxa.2441.1.3

Blanckenhorn WU (1997) Altitudinal life history variation in the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea*. Oecologia 109: 342–352. https://doi.org/10.1007/s004420050092

Blanckenhorn WU (1998a) Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. Evolution 52: 1394–1407. https://doi.org/10.1111/j.1558-5646.1998.tb02021.x

Blanckenhorn WU (1998b) Altitudinal differentiation in the diapause response of two species of dung flies. Ecological Entomology 23: 1–8. https://doi.org/10.1046/j.1365-2311.1998.00098.x

Blanckenhorn WU (1999) Different growth responses to temperature and resource limitation in three fly species with similar life histories. Evolutionary Ecology 13: 395–409. https://doi.org/10.1023/A:1006741222586

Blanckenhorn WU (2009) Causes and consequences of phenotypic plasticity in body size: the case of the yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae). In: Whitman DW, Ananthakrishnan TN (Eds) Phenotypic Plasticity of Insects: Mechanism and Consequences. Science Publishers, Enfield, NH, USA, 369–422. https://doi.org/10.1201/b10201-11

Blanckenhorn WU (2021) Energetic underpinnings of yellow dung fly mating success in the field. Alpine Entomology 5: 61–67. https://doi.org/10.3897/alpento.5.68153

Blanckenhorn WU, Henseler C, Burkhard DU, Briegel H (2001) Summer decline in populations of the yellow dung fly: diapause or quiescence? Physiological Entomology 26: 260–265. https://doi.org/10.1046/j.0307-6962.2001.00245.x

Blanckenhorn WU, Fanti J, Reim C (2007) Size-dependent energy reserves, energy utilization and longevity in the yellow dung fly. Physiological Entomology 32: 372–381. https://doi.org/10.1111/j.1365-3032.2007.00589.x

Blanckenhorn WU, Pemberton AJ, Bussière LF, Roembke J, Floate KD (2010) Natural history and laboratory culture of the yellow dung fly, *Scathophaga stercoraria* (L.; Diptera: Scathophagidae). Journal of Insect Science 10: 1–17. https://doi.org/10.1673/031.010.1101

Blanckenhorn WU, Bauerfeind SS, Berger D, Davidowitz G, Fox CW, Guillaume F, Nakamura S, Nishimura K, Sasaki H, Stillwell CR, Tachi T, Schäfer MA (2018) Life history traits, but not body size, vary systematically along latitudinal gradients on three continents in the widespread yellow dung fly. Ecography 41: 2080–2091. https://doi.org/10.1111/ecog.03752

Blume RR (1985) A checklist, distributional record, and annotated bibliography of the insects associated with bovine droppings of pastures in America north of Mexico. Southwestern Entomologist Supplement 9: 1–54.

Bornemissza GF (1960) Could dung eating insects improve our pastures? Journal of the Australian Institute of Agricultural Science 26: 54–56.

Bornemissza GF (1976) The Australian dung beetle project 1965–1975. Australian Meat Research Committee Review 30: 1–30.

Cotterell GS (1920) The life history and habits of the yellow dung-fly (*Scathophaga stercoraria*): a possible blow-fly check. Proceedings of the Zoological Society London 1920: 629–647. https://doi.org/10.1111/j.1096-3642.1920.tb03245.x

D'Amico LJ, Davidowitz G, Nijhout HF (2001) The developmental and physiological basis of body size evolution in an insect. Proceedings of the Royal Society of London B 268: 1589–1593. https://doi.org/10.1098/rspb.2001.1698

Floate KD (2023) Cow patty critters: An introduction to the ecology, biology and identification of insects in cattle dung on Canadian pastures. Agriculture and Agrifood, Canada.

Forister ML (2004) Oviposition preference and larval performance within a diverging lineage of lycaenid butterflies. Ecological Entomology 29: 264–272. https://doi.org/10.1111/j.0307-6946.2004.00596.x

Forister ML, Nice CC, Fordyce JA, Gompert Z (2009) Host range evolution is not driven by the optimization of larval performance: the case of *Lycaeides melissa* (Lepidoptera: Lycaenidae) and the colonization of alfalfa. Oecologia 160: 551–561. https://doi.org/10.1007/s00442-009-1310-4

Foster W (1967) Hormone-mediated nutritional control of sexual behavior in male dung flies. Science 158: 1596–1597. https://doi.org/10.1126/science.158.3808.1596

Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45: 341–369. https://doi.org/10.1146/annurev.ento.45.1.341

Frank K, Brückner A, Hilpert A, Heethoff M, Bluthgen N (2017) Nutrient quality of vertebrate dung as a diet for dung beetles. Scientific Reports 7: 12141. https://doi.org/10.1038/s41598-017-12265-y

Dormont L, Jay-Robert P, Bessiere JM, Rapior S, Lumaret J-P (2010) Innate olfactory preferences in dung beetles. Journal of Experimental Biology 213: 3177–3186. https://doi.org/10.1242/jeb.040964

Gibbons DS (1980) Prey consumption, mating and egg production in *Scathophaga stercoraria* (Dipt., Scathophagidae) in the laboratory. Entomology Monthly Magazine 116: 25–32.

Gorodkov KB (1984) Scathophagidae. In: Soós A, Papp L (Eds) Catalogue of palaearctic diptera. Elsevier, Amsterdam, The Netherlands, 11–41.

Gómez Jiménez MI, Sarmiento CE, Díaz MF, Chautá A, Peraza A, Ramírez A, Poveda K (2014) Oviposition, larval preference, and larval performance in two polyphagous species: does the larva know best? Entomologia Experimentalis et Applicata 153: 24–33. https://doi.org/10.1111/eea.12225

Hammer O (1941) Biological and ecological investigations on flies associated with pasturing cattle and their excrements. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 105: 140–393.

Hanski I, Cambefort Y (1991) Dung Beetle Ecology. Princeton University Press, Princeton, New Jersey. https://doi.org/10.1515/9781400862092

Hirschberger P, Degro HN (1996) Oviposition of the dung beetlw *Aphodius ater* in relation to abundance of yellow dung fly larvae (*Scathophaga stercoraria*). Ecological Entomology 21: 352–357. https://doi.org/10.1046/j.1365-2311.1996.t01-1-00008.x

Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. PNAS 106: 19659–19665. https://doi.org/10.1073/pnas.0905137106

Holter P (1979) Effect of dung-beetles (*Aphodius* spp) and earthworms on the disappearance of cattle dung. Oikos 32: 393–402. https://doi.org/10.2307/3544751

Holter P (2016) Herbivore dung as food for dung beetles: elementary coprology for entomologists. Ecological Entomology 41: 367–377. https://doi.org/10.1111/een.12316

Jann P, Blanckenhorn WU, Ward PI (2000) Temporal and microspatial variation in the intensities of natural and sexual selection in the yellow dung fly *Scathophaga stercoraria*. Journal of Evolutionary Biology 13: 927–938. https://doi.org/10.1046/j.1420-9101.2000.00230.x

Jochmann R, Blanckenhorn WU (2016) Non-target effects of Ivermectin on trophic groups of the cow dung insect community replicated across an agricultural landscape. Basic and Applied Ecology 17: 291–299. https://doi.org/10.1016/j.baae.2016.01.001

Jochmann R, Lipkov E, Blanckenhorn WU (2016) A field test of the effect of spiked ivermectin concentrations on the biodiversity of coprophagous dung insects in Switzerland. Environmental Toxicology & Chemistry 35: 1947–1952. https://doi.org/10.1002/etc.3081

Kaufmann C, Reim C, Blanckenhorn WU (2013) Size-dependent insect flight energetics at different sugar supplies. Biological Journal of the Linnean Society 108: 565–578. https://doi.org/10.1111/j.1095-8312.2012.02042.x

Konig MAE, Wiklund C, Ehrlen J (2016) Butterfly oviposition preference is not related to larval performance on a polyploid herb. Ecology & Evolution 6: 2781–2789. https://doi.org/10.1002/ece3.2067

Kraushaar U, Goudet J, Blanckenhorn WU (2002) Geographic and altitudinal population genetic structure of two dung fly species with contrasting mobility and temperature preference. Heredity 89: 99–106. https://doi.org/10.1038/sj.hdy.6800097

Laux A, Wegmann A, Roy J, Gourgoulianni N, Blanckenhorn WU, Rohner PT (2019) The role of larval substrate specialization and female oviposition in mediating species diversity of closely-related sepsid flies (Diptera: Sepsidae). European Journal of Entomology 116: 75–84. https://doi.org/10.14411/eje.2019.008

Loboda S, Savage J, Buddle CM, Schmidt NM, Høye TT (2018) Declining diversity and abundance of High Arctic fly assemblages over two decades of rapid climate warming. Ecography 41: 265–277. https://doi.org/10.1111/ecog.02747

Lumaret J-P (1995) Desiccation rate of excrements: a selective pressure on dung beetles. In: Time Scales of Biological Responses to Water Constraints. The case of Mediterranean biota. In: Roy J, Aronson J, Di Castri F (Eds) SPB Academic Publishing, Amsterdam, The Netherlands, 105–118.

Lumaret J-P, Kadiri N, Bertrand M (1992) Changes in Resources: Consequences for the Dynamics of Dung Beetle Communities. Journal of Applied Ecology 29: 349–356. https://doi.org/10.2307/2404504

Papp L (1992) Fly communities in pasture dung - Some results and problems (Diptera). Acta Zoologica Hungarica 38: 7588.

Parker GA (1970) The reproductive behaviour and the nature of sexual selection in *Scathophaga stercoraria* L. (Diptera: Schathophagidae) I. Diurnal and seasonal changes in population density around the site of mating and oviposition. Journal of Animal Ecology 39: 185–204. https://doi.org/10.2307/2895

Pont AC, Meier R (2002) The Sepsidae (Diptera) of Europe. Fauna Entomologica Scandinavica 37: 1221. https://doi.org/10.1163/9789047401391

Rohner PT, Bächli G, Pollini Paltrinieri L, Duelli P, Obrist MK, Jochmann R, Blanckenhorn WU (2015) Distribution, diversity gradients and Rapoport's elevational rule in the black scavenger flies of the Swiss Alps (Diptera: Sepsidae). Insect Conservation and Diversity 8: 367–376. https://doi.org/10.1111/icad.12114

Rohner PT, Blanckenhorn WU, Schäfer MA (2017) Critical weight mediates sex-specific body size plasticity and sexual dimorphism in the yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae). Evolution & Development 19: 147–156. https://doi.org/10.1111/ede.12223

Scharf I, Bauerfeind SS, Blanckenhorn WU, Schäfer MA (2010) Effects of maternal and offspring environmental conditions on growth, development and diapause in latitudinal yellow dung fly populations. Climate Research 43: 115–125. https://doi.org/10.3354/cr00907

Shukla SP, Sanders JG, Byrne MJ, Pierce NE (2016) Gut microbiota of dung beetles correspond to dietary specializations of adults and larvae. Molecular Ecology 25: 6092–6106. https://doi.org/10.1111/mec.13901

Šifner F (2008) Catalogue of the Scathophagidae flies of the Palaearctic region (Diptera: Scathophagidae), with notes on taxonomy and faunistics. Acta Entomologica Musei Nationalis Pragae 48: 111–196.

Sigurjónsdóttir H, Snorrason SS (1995) Distribution of male yellow dungflies around oviposition sites: the effect of body size. Ecological Entomology 20: 84–90. https://doi.org/10.1111/j.1365-2311.1995.tb00432.x

Simmons LW, Parker GA, Hosken DJ (2020) Evolutionary insight from a humble fly: sperm competition and the yellow dung fly. Philosophical Transactions of the Royal Society B 375: 20200062. https://doi.org/10.1098/rstb.2020.0062

Skidmore P (1991) Insects of the British Cow-dung Community, Vol. 21. Aids to Identification in Difficult Groups of Animals and Plants. Field Studies Council, Shrewsbury, UK.

Stone A, Sabrosky CW, Wirth WW, Foote RH, Coulson JR (1965) A catalogue of the Diptera of America north of Mexico. U.S. Department of Agriculture, Washington, DC.

Vockeroth JR (1987) Scathophagidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (Eds) Manual of Nearctic Diptera, Volume 2. Agriculture Canada Monograph 28, 1085–1097.

Wiklund C (1975) The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. Oecologia 18: 185–197. https://doi.org/10.1007/BF00345421

Supplementary material 1

Data file corresponding to the submitted paper

Authors: Wolf U. Blanckenhorn, Dieter Burkhard

Data type: xslx

Explanation note: Individual trait values for male and female yellow dung flies: developmental duration, tibia length, growth rate.

Link: https://doi.org/10.3897/alpento.7.107649.suppl1

Alpine Entomology 7 2023, 143–152 | DOI 10.3897/alpento.7.109562

PENSOFT.
Alpine Entomology

First report of *Cloeon vanharteni* Gattolliat & Sartori, 2008 (Baetidae, Ephemeroptera) in the Maghreb

Mokhtar Benlasri[1], Laurent Vuataz[2,3], Jean-Luc Gattolliat[2,3], Arne J. Beermann[4,5], Heribert Leßner[4], Majida El Alami El Moutaouakil[6], Mohamed Ghamizi[1], Elisabeth Berger[7]

1 *Museum of Natural History, University Cadi Ayyad, Faculty of Science Semlalia, Marrakech, Morocco*
2 *Muséum Cantonal des Sciences Naturelles, Palais de Rumine, Place Riponne 6, CH-1005, Lausanne, Switzerland*
3 *Department of Ecology and Evolution, Biophore, University of Lausanne, CH-1015 Lausanne, Switzerland*
4 *University of Duisburg-Essen, Aquatic Ecosystem Research, Universitaetsstr. 5, 45141 Essen, Germany*
5 *University of Duisburg-Essen, Centre for Water and Environmental Research (ZWU), Universitaetsstr. 3, 45141 Essen, Germany*
6 *Université Abdelmalek Essaâdi, Faculté des Sciences, Département de Biologie, Laboratoire Ecologie, Systématique et Conservation de la Biodiversité (LESCB), Unité de Recherche Labellisée CNRST N°18. B.P.2121, Tétouan 93002, Morocco*
7 *RPTU – University of Kaiserslautern-Landau, iES Institute for Environmental Sciences, Landau, Germany*

https://zoobank.org/DADC69BF-EB06-4655-9ECB-F9EDE595D5B1

Corresponding author: Mokhtar Benlasri (benlasri@gmail.com)

Academic editor: Dávid Murányi ♦ **Received** 14 July 2023 ♦ **Accepted** 17 September 2023 ♦ **Published** 26 September 2023

Abstract

Cloeon vanharteni Gattolliat & Sartori, 2008 was newly discovered in the framework of our study of Ephemeroptera in the Draa basin, located in the southern region of the High Atlas in Morocco. This discovery is rather unexpected as the species was never reported outside the Arabian Peninsula and Levant; it is thus the first record for the Maghreb. The identification was based on morphological evidence and confirmed by the mitochondrial COI barcode.

Key Words

COI, Drâa basin, Distribution, Mayflies, Morocco

Introduction

Morocco by its geographical position in the northwest of Africa is part of the Maghreb (region that includes five countries in North Africa: Morocco, Algeria, Tunisia, Libya, and Mauritania). Research on macroinvertebrates and Ephemeroptera in the Maghreb has primarily focused on Morocco, Algeria, and Tunisia, while comparatively less research has been conducted in Libya and Mauritania (Gattolliat et al. 2023). In Morocco, the studies of Ephemeroptera began with the work of Lestage and Kimmins (Lestage 1925; Kimmins 1938), that were then taken up by Navás (1929), and following these studies, a first faunistic list of ten species was established (Gattolliat et al. 2023). After a period of interruption, the study of mayflies resumed in the late 1970s , with the work of Dakki (1978) and then Dakki and El Agbani (1983), who completed this list with 16 additional species, resulting in a total of 26 species distributed in the different Moroccan regions (Gattolliat et al. 2023).

Starting in the 1980s, several hydrobiological studies were conducted in the different Moroccan rivers (Dakki and Giudicelli 1979; Dakki and Thomas 1986; Thomas and Bouzidi 1986; Ouahsine and Lavandier 1988; Qninba et al. 1988; Vitte and Thomas 1988; Vitte 1991; El Alami et al. 2000; El Bazi et al. 2017; Khadri et al. 2017; Mabrouki et al. 2017), which has allowed to further enrich the species list for Morocco and led to the discovery of species new to science, considerably increasing the list of Ephemeroptera species in Morocco.

The most recent compilation of Ephemeroptera species in Morocco was carried out by El Alami et al. (2022b) who established a list of 54 species belonging to 26 genera and 10 families distributed as follows: The Rif with 37 species, the Middle Atlas with 31 species, the High Atlas with 30 species, Eastern Morocco with 24 species, and finally the Central Plateau with 19 species. In this list, there are 18 species currently considered endemic to Morocco and nine endemic to the Maghreb region (El Alami et al. 2022b). Finally, the recent description of *Prosopistoma maroccanum* El Alami, Benlasri & Sartori, 2022 from the northern slope of the High Atlas (El Alami et al. 2022a) and *Centroptilum alamiae* Kaltenbach, Vuataz & Gattolliat, 2022 from the Rif (Kaltenbach et al. 2022) has increased the number of mayfly species in Morocco to 56. However, none of these studies focused on the south of Morocco.

Morocco is characterized by four mountain ranges: the Rif, which borders the Mediterranean in the north and extends to the Atlantic coast, and the Atlas Mountains in the center of the country, which extend on a southwest-northeast axis to the Algerian border in the northeast. The Atlas Mountain is divided into three chains: the Middle Atlas, the High Atlas, and the Anti-Atlas.

Depending on the part of Morocco, the climate varies between Mediterranean and Atlantic. It presents a dry and hot season from May to September, and a cold season from October to April (Houssni et al. 2020); indeed, the mountain chains separate vast regions that are part of very differentiated climatic zones. The north of the country is characterized by a Mediterranean climate, while the areas located in the south of Morocco and southeast of the Atlas Mountains are marked by a Saharan climate. The presence of the sea attenuates the temperature differences, moderates the seasons, and increases the humidity of the air in the coastal regions. The mountainous regions benefit from a sub-humid to humid climate (Bouaicha and Benabdelfadel 2010). The rainfall is marked by strong annual and decennial variability.

During an ongoing project investigating benthic macroinvertebrates in the southern Draa basin, our sampling revealed the presence of *Cloeon* larvae that morphologically and genetically differ from members of the *Cloeon* group *dipterum* previously documented from Morocco. Further analysis proved that the larvae unambiguously belong to *Cloeon vanharteni* Gattolliat & Sartori, 2008. This unexpected observation was confined to a single salty stream. This species was originally described from the United Arab Emirates (UAE hereafter; Gattolliat and Sartori 2008). It was then reported in the Middle East in Israel and the Palestinian Authority in arid and semi-arid areas (Yanai et al. 2020), in running water habitats, and in brackish ponds in Jordan (Alhejoj et al. 2020, 2023). In the Maghreb countries however, it has never been reported. Therefore, the aim of the present paper is to provide detailed morphological characteristics of the species, to compare the COI barcode of the Moroccan population with other populations and species, and to discuss its ecology and biogeographic distribution.

Material and method

As part of the study of macroinvertebrates in the Draa basin, the first author sampled 17 sites from multiple streams throughout the basin (Fig. 1) that differ in altitude, temperature and conductivity (Benlasri et al. 2022). The Draa basin is located between the southern slopes of the High Atlas Mountains in Morocco and extends southwards into the Sahara. It is divided into three sub-basins: the Upper, Middle, and Lower Draa (Fig. 1). The sub-basin of the Upper Draa is the drainage area of Atlas Mountains feeding the Mansour Eddehbi reservoir. Here we focus on three sampling sites in the west zone of the Upper Draa basin: Ounilla 1, a left tributary of Oued El Maleh which is not salty; Ounilla 2, a salty right tributary of Oued El Maleh with a high conductivity, which hosted specimens of *Cloeon vanharteni*; Oued El Maleh, referred to as the “salty stream” in Arabic, characterized by a lower flow and temperate water (Fig. 2, Table 1). Sampling was conducted in March and June 2022 using a 0.20 m × 0.25 m Surber sampler with a mesh size of 500 µm. To ensure comprehensive collection of macroinvertebrates, twenty spots covering all microhabitats were sampled within each site. Water conductivity was measured using WTW MultiLine® Multi 3510 IDS device. The samples were placed in tubes with 96% alcohol and sorted in the laboratory under a binocular magnifier to separate and identify species.

To complement our morphological investigations, we sequenced a 658 bp fragment of the mitochondrial gene cytochrome oxidase subunit 1 (COI hereafter) for two specimens of *Cloeon vanharteni* (one from our newly discovered site in Morocco and the other from Israel), three specimens of *Cloeon peregrinator* Gattolliat & Sartori, 2008 and one specimen of *Procloeon stagnicola* Soldán & Thomas, 1983 (all from Morocco). The *Cloeon peregrinator* sequences were chosen for comparison, as this species represents the only other genetically confirmed lineage of this genus in Morocco (El Alami et al. 2022a, Gattolliat et al. 2023). The *Procloeon stagnicola* sequence was used as the outgroup (Table 3). Sanger sequencing procedures were carried out at three locations: Duisburg-Essen, Germany using standard protocols (Suppl. material 1); Lausanne, Switzerland; and Tel Aviv, Israel. In Lausanne and Tel Aviv, the non-destructive DNA extraction method from Vuataz. (Vuataz et al. 2011) was used. Polymerase Chain Reaction (PCR) and sequencing were conducted according to the methodology described by El Alami (El Alami et al. 2022a) for Lausanne, and by Yanai (Yanai et al. 2018) for Tel Aviv. To augment our molecular dataset, we downloaded all COI sequences associated with *Cloeon vanharteni* available on the GenBank database as of June 8, 2023, resulting in three additional records from Israel (Yanai et al. 2020), for a total of nine sequences in our COI dataset. All sequences were aligned using MAFFT (Katoh et al. 2019) with default settings as implemented in Jalview 2.11.2.6 (Waterhouse et al.

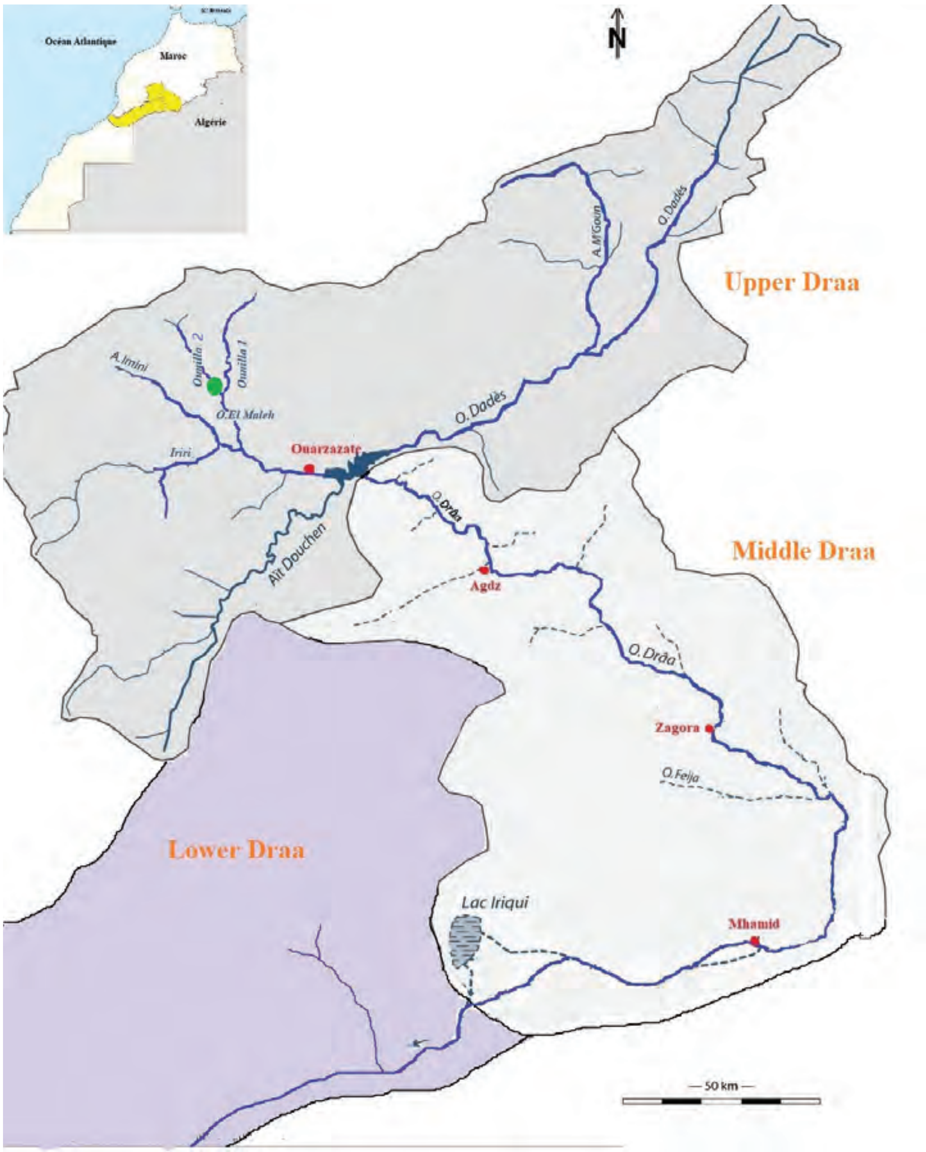


Figure 1. The 17 sampling sites in Draa basin with the location of the site hosting *Cloeon vanharteni* in the west zone of the Upper Draa basin (green dot).

Table 1. Location and collection dates of study sites, with water conductivity specified.

Site Name	Coordinates Latitude, Longitude	Alt (m)	Date	Conductivity [µS/cm]	Water temperature °C
Ounilla 2 salty	31,09406, -7,148652	1318	12/03/2022	19330	22.3
			26/06/2022	19660	33.7
Ounilla 1 fresh	31,094021, -7,14659	1311	12/03/2022	3890	18.3
			26/06/2022	2590	30.3
Oued El Maleh	31,011, -7,10006	1229	12/03/2022	10570	17.1
			26/06/2022	12100	24.3

2009). The number of parsimony-informative sites of the alignment was calculated in Mega 10.2.4 (Kumar et al. 2018; Stecher et al. 2020).

To explore and visualize the COI evolutionary divergence, we employed both pairwise genetic distances and gene tree approaches. COI pairwise distances were calculated using the dist.dna function from the ape 5.7-1 package (Paradis and Schliep 2019) in R 4.3.0 (R Core team 2023), selecting the raw model and the pairwise. deletion option, corresponding to uncorrected p-distances (see Srivathsan and Meier 2012) with missing data removed in a pairwise way. Mean, minimum and maximum distances within and between species were calculated using the ddply function from the plyr 1.8.8 package (Wickham 2011). We also applied the species delimitation method ASAP (Assemble Species by

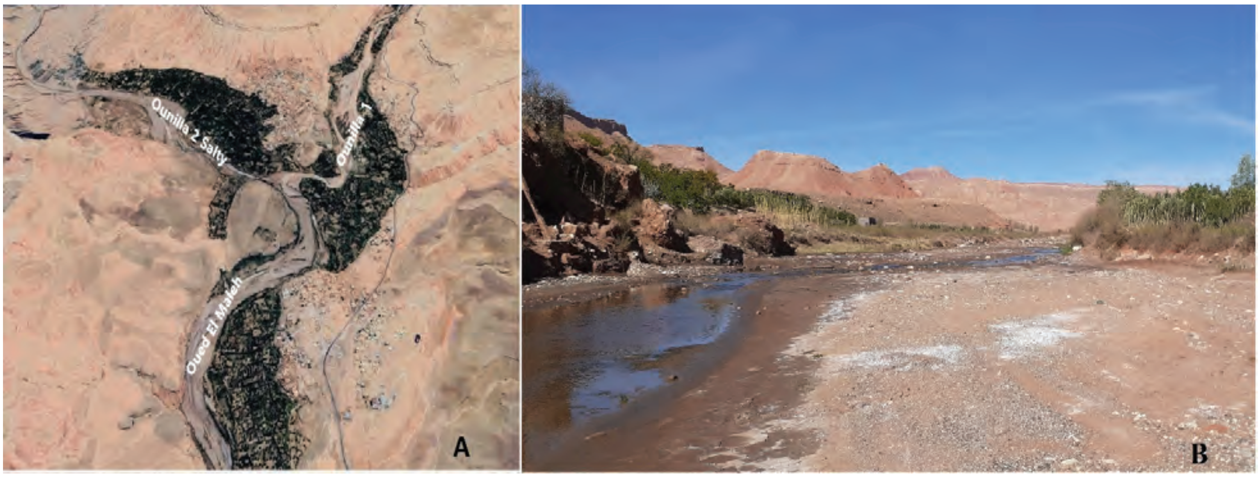


Figure 2. Photographic views of the study sites. **A.** Aerial view of the three study sites (from google Earth); **B.** downstream view of Ounilla 2 salty site.

Automatic Partitioning; (Puillandre et al. 2021) to our COI dataset using the webserver available at https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html. This distance-based method is similar to the popular ABGD (Automatic Barcode Gap Discovery) (Puillandre et al. 2012) approach but has the advantage of providing a score that specifies the most likely species delimitation. We calculated genetic distances using simple p-distances and selected the species delimitation hypothesis associated to the best asap-score.

Prior to reconstructing the COI gene tree, the best evolutionary model (GTR+I) was selected based on the second-order Akaike information criterion (AICc) (Hurvich and Tsai 1989) implemented in JModelTest 2.1.10 (Darriba et al. 2012) with five substitution schemes, six gamma categories and default values for all other parameters. To account for different substitution rates among COI codon positions, we analysed our data set in two partitions, one with first and second codon positions, and the other with third positions (1 + 2, 3). Bayesian inference analysis was performed in MrBayes 3.2.7a (Ronquist et al. 2012). Two independent analyses of four MCMC chains run for three million generations with trees sampled every 1'000 generations were implemented, and 300'000 generations were discarded as a burnin after visually verifying run stationarity and convergence in Tracer 1.7.2 (Rambaut 2007). Visualization and editing of the 50% majority rule consensus tree were conducted in iTOL 6.7.5 (Letunic and Bork 2021).

Results

Water conductivity was high in Ounilla 2 salty (19330 and 19660 µS/cm), while it was lower in Ounilla 1 fresh (3890 and 2590 µS/cm). After the confluence of the two streams that forms the stream Oued El Maleh (Fig. 2A), the conductivity remained high (10570 and 12100 µS/cm; Table 1).

Sampling at the three study sites allowed us to identify seven Ephemeroptera species, including 24 nymphs of *C. vanharteni* (Table 2). The material is deposited at the Museum of Natural History of Marrakech (four *C. vanharteni* nymphs on slide).

Diagnosis

At the larval stage, *Cloeon vanharteni* can be distinguished from other species of *Cloeon* by the absence of hindwings pads; lateral spines present on tergites VIII and IX (sometimes also VII; Fig. 3); maxillary palp 2-segmented (Fig. 4); elongated claws with two rows of abundant short teeth (Fig. 5); gills with double lamellae, upper lamella roughly half of the size of the lower lamella.

At imaginal stage, by the absence of colouration of the costal and subcostal areas of female forewing; forceps of male imago with segment I and II clearly separated, male subgenital plate apically flattened (Gattolliat and Sartori 2008).

Table 2. Number of individuals per species collected in the three study sites.

Site	Date	Collected species						
		Cloeon vanharteni	***Cloeon peregrinator***	***Cloeon simile***	***Procloeon stagnicola***	***Caenis luctuosa***	***Caenis pusilla***	***Baetis pavidus***
Ounilla 2 salty	12/03/2022	24	16	32	28	46	0	0
	26/06/2022	0	0	3	3	8	0	2
Ounilla 1 fresh	12/03/2022	0	0	1	0	130	26	256
	26/06/2022	0	0	0	0	62	14	140
Oued El Maleh	12/03/2022	0	0	0	0	12	0	22
	26/06/2022	0	0	2	0	80	0	185

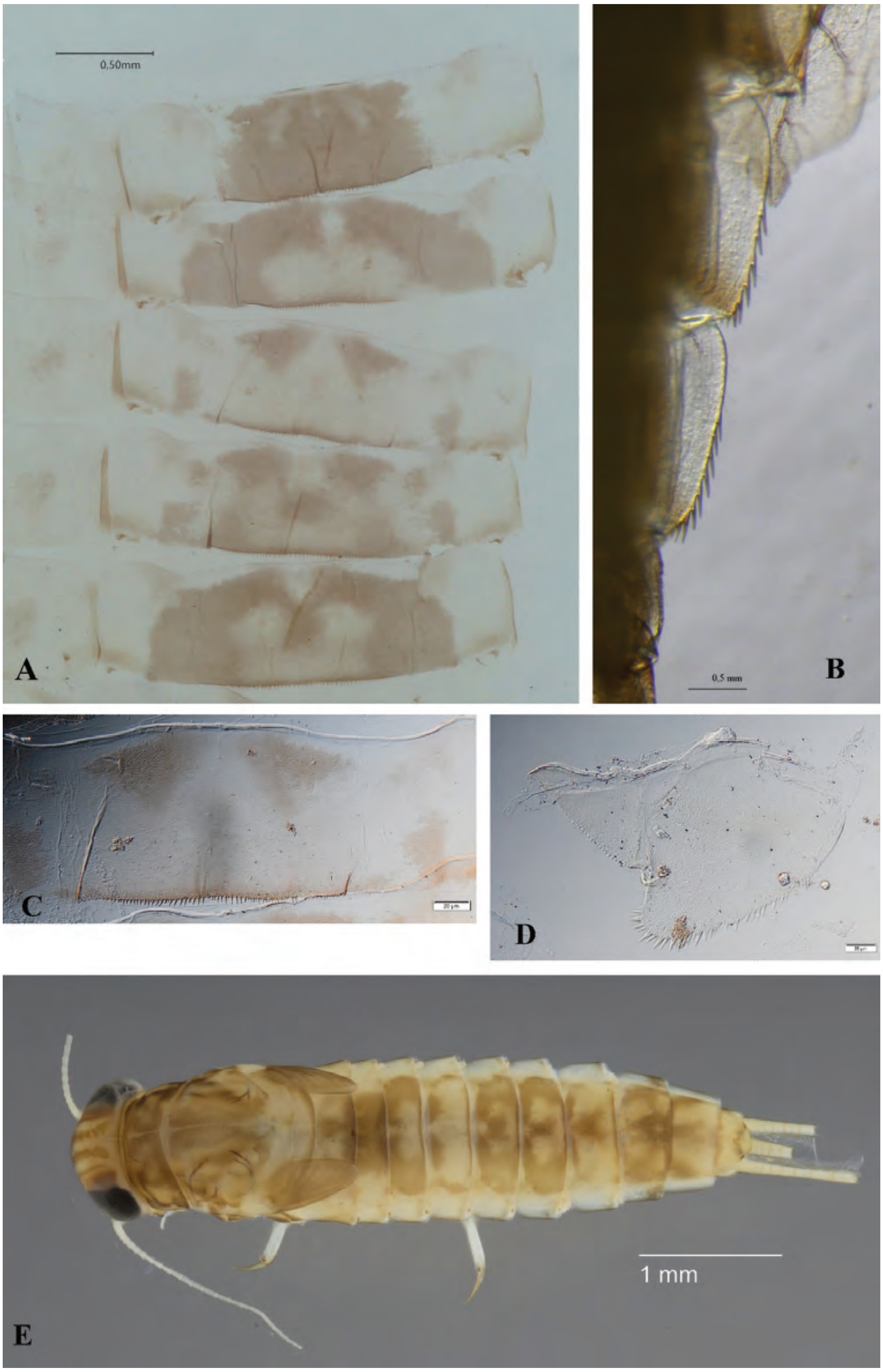


Figure 3. *Cloeon vanharteni* Gattolliat & Sartori, 2008, larva habitus and morphology. **A.** Abdominal tergites; **B.** Abdominal lateral spines; **C.** Tergite IV; **D.** Paraproct; **E.** Dorsal view of the larva.

Molecular analysis

The COI ingroup dataset was >96% complete and included 17% of parsimony informative sites. The five *Cloeon vanharteni* sequences, including the sequence from Morocco, formed a strongly supported monophyletic COI lineage, identified as a distinct species in the ASAP delimitation analysis (Fig. 6). Similarly, the three *Cloeon peregrinator* sequences were recovered as a distinct, strongly supported monophyletic lineage. The mean p-distance within the *C. vanharteni* COI lineage was 1.6% (range 0–2.5%), while it was 0.5% (range 0–0.8%) within the *C. peregrinator* lineage. The mean p-distance between both lineages was 17.8% (range 17.3%–18.3%).

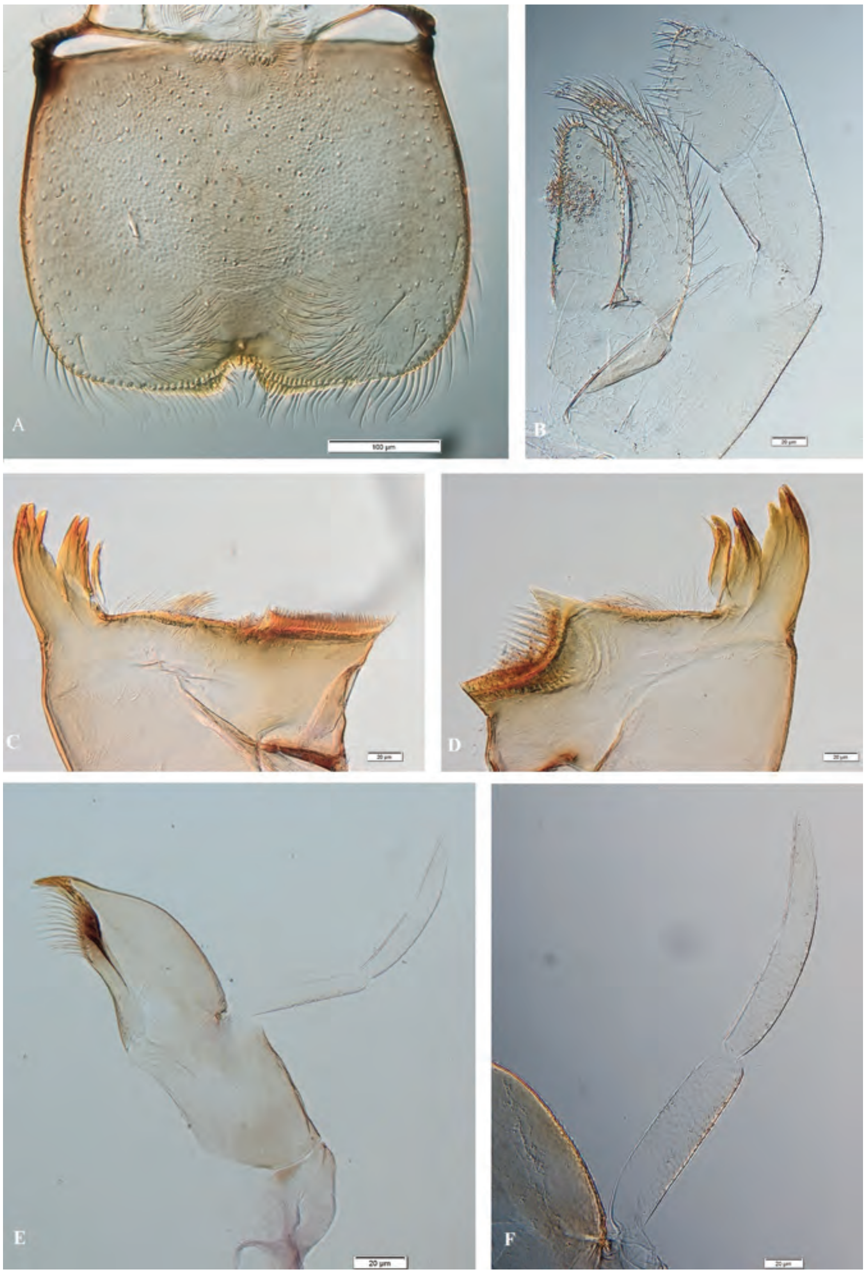


Figure 4. *Cloeon vanharteni* Gattolliat & Sartori, 2008, larva mouth parts. **A.** Labrum; **B.** Labrial palp; **C.** Left mandible; **D.** Right mandible; **E.** Maxilla; **F.** maxillar palp.

Table 3. Newly sequenced nymph specimens for this study, with collection information and accession numbers (OR codes: from GenBank; MZBM codes: from BOLD).

Specimen catalogue no	Species	Country	Locality	GPS coordinates	Date	Collector	Accession ID
CLS_OC220312_03	*Cloeon vanharteni*	Morocco	Ounilla salty steam	31,09406, -7,148652	12.iii.2022	M. Benlasri	MZBM701-23
B229	*Cloeon vanharteni*	Israel	Arugot stream	31.46165, 35.35542	25.vi.2014	Z. Yanai	OR345160
GBIFCH01137417	*Cloeon peregrinator*	Morocco	Oukaïmeden	31.197900, -7.858033	29.v.2014	J. Bojková & T. Soldán	OR345163
GBIFCH01137407	*Cloeon peregrinator*	Morocco	Ait Mansour	29.547722, -8.873694	31.v.2014	J. Bojková & T. Soldán	OR345162
CLS_SO220311_03	*Cloeon peregrinator*	Morocco	Ounilla salty steam	31,09406, -7,148652	11.iii.2022	M. Benlasri	MZBM702-23
GBIFCH01122671	*Procloeon stagnicola*	Morocco	Gorges Oued El Abid	32.066111, -6.677806	18.v.2014	J. Bojková & T. Soldán	OR345161

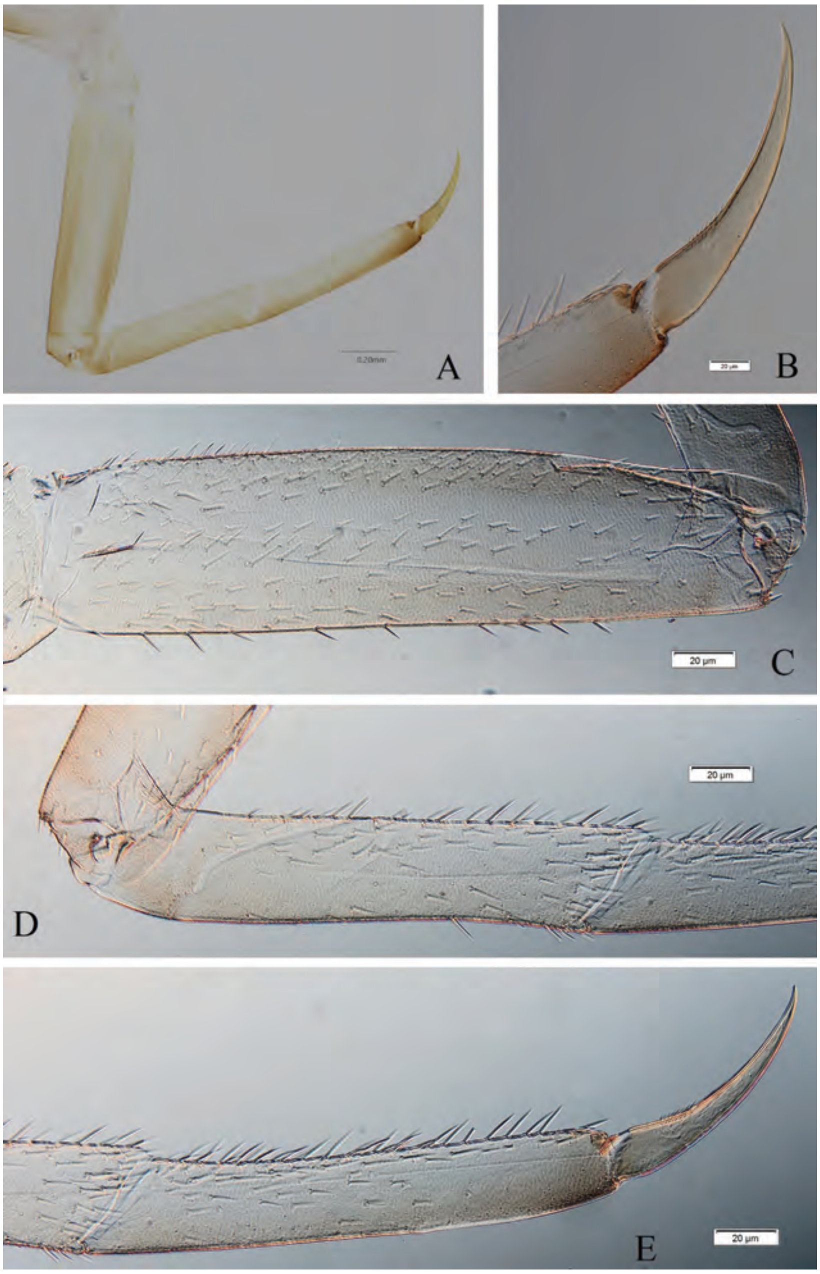


Figure 5. *Cloeon vanharteni* Gattolliat & Sartori, 2008, larva foreleg. **A.** Foreleg; **B.** Claw; **C.** Forefemur; **D.** Foretibia; **E.** Foretarsus and claw.

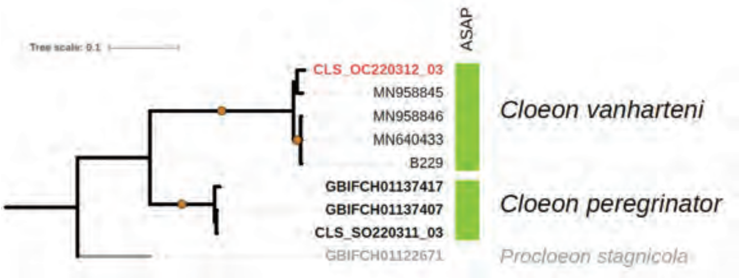


Figure 6. Bayesian majority-rule consensus COI tree including *Cloeon vanharteni* and *C. peregrinator*. Tips labelled with MN codes indicate sequences retrieved from GenBank, other codes represent newly obtained sequences from our samples. Bolded labels indicate sequences derived from Moroccan specimens, with the *C. vanharteni* Moroccan specimen highlighted in red. The B229 code represents a sequence originating from a specimen collected in Israel. Colored vertical boxes indicate species delimitation according to the ASAP method, with the corresponding species name next to each box. Circles on branches indicate Bayesian posterior probabilities > 0.95. The outgroup branch (*Procloeon stagnicola*) is presented in grey, along with its corresponding tip label and species name.

Discussion

Cloeon vanharteni has elongated claws with two rows of abundant small teeth and spines on the lateral margin of last abdominal segments. It clearly belongs to the Cloeoninae; this subfamily encompasses in the Maghreb the five genera *Centroptilum* Eaton, 1869, *Cheleocloeon* Wuillot & Gillies, 1993, *Cloeon* Leach, 1815, *Procloeon* Bengtsson, 1915 and *Similicloeon* Kluge & Novikova, 1992 (Gattolliat et al. 2023). *Cloeon vanharteni* possesses bilamellated gills and lateral spines on last tergites, the two characters clearly indicating that it does not belong to *Centroptilum*. The labial palp is clavate and does not present any thumb-like projection, separating it from *Cheleocloeon*. The upper lamella is around half of the lower lamella and cerci do not have conspicuous lateral spines, therefore the species does not belong to either *Similicloeon* or *Procloeon* (Gattolliat et al. 2023).

Cloeon vanharteni can be easily separated from all the other species of *Cloeon* previously reported from the Maghreb by the 2-segmented maxillary palp (3-segmented in all the other species). The species of the group *dipterum* (*Cloeon dipterum* and *Cloeon peregrinator*) possess elongated claws with two rows of teeth increasing in length towards the apex, the two rows reaching at least the half of the length of the claw; in *C. vanharteni*, all teeth are short, and the two rows reach at most the first third of the length of the claw. *Cloeon saharense* differs from all the other known species of *Cloeon* by the absence of spines on the lateral margins of last abdominal tergites.

The genus *Cloeon* is one of the most diverse genera of mayflies (Gattolliat et al. 2023). It encompasses 75 species (Salles et al. 2014), including 23 species reported from Africa (Gattolliat 2002). This genus presents a great potential of dispersion among the mayflies, even on some remote islands such as the Azores in the North Atlantic Ocean. This genus colonizes all kinds of still and standing habitats: ponds, lakes, stagnant waters, lentic habitats in streams, as well as in artificial habitats (Salles et al. 2014).

Cloeon vanharteni was described in 2008, when it was identified in a dry region of the UAE. Subsequent citations of this species in Israel, the Palestinian territories, and Jordan (Yanai et al. 2020) mainly concerns arid and semi-arid areas, such as the Jordan Valley, the Dead Sea region, and the central Negev desert (Alhejoj et al. 2020; Yanai et al. 2020). It is the most abundant mayfly to colonize newly formed dolines near the Dead Sea.

In Morocco, this species was collected in a single semi-arid area characterized by cold winters and hot summers, in a salty stream with a low flow, and a moderate temperature; its bottom is formed by pebbles, gravel, and sand. Despite conducting sampling efforts, carried out in these sites between 2020 and 2023, across multiple streams with lower conductivity (Iriri, Ait Douchene, and Ounilla 1) within the same basin (Fig. 1), we did not find the species in any other sites not even in the neighbouring stream that bears the same name but where the conductivity is low. This species seems to be resistant to high conductivity and summer temperatures.

The discovery of *Cloeon vanharteni* in the Maghreb is rather surprising but it makes sense if we consider the sub-desertic distribution and the poor knowledge of the still and standing freshwater habitats in this area: in the whole Maghreb, standing waters are poorly sampled in comparison to running waters. Additionally, *Cloeon* represents the genus of mayflies that possesses the greatest capacity for dispersal, primarily due to the female adult mayflies having a lifespan of over two weeks (Salles et al. 2014).

Acknowledgements

We want to thank the ecological team of SaliDraaJuj project for their contribution in the measurement of physico-chemical parameters in the field. The project is supported by the Natural History Museum of Marrakech, Cadi Ayyad University and the German Federal Ministry of Education and Research (BMBF), which funded this project. The SaliDraa جوج project fits within the framework of the Research for Sustainability (FONA).We would also like to thank Professor Florian Hesse and his working group for the barcoding work carried out in his laboratory. We would like to thank Zohar Yanai for sharing an unpublished COI sequence from Israel, and Jindřiška Bojková and Tomáš Soldán for providing specimens collected in Morocco in 2014. Finally, we are thankful to Dr. Roman Godunko and an anonymous reviewer for their valuable comments and corrections on our manuscript.

Responsibility for the content of this publication rests with the authors.

References

Alhejoj I, Sartori M, Gattolliat J-L (2020) Contribution to the mayflies (Insecta, Ephemeroptera) of Jordan. Check List 16: 237–242. https://doi.org/10.15560/16.2.237

Alhejoj I, Hiasat TH, Salameh E, Hamad AA, Al Kuisi M (2023) Use of the aquatic mayfly (Insecta: Ephemeroptera) as environmental bio-indicator in Jordan. International Journal of Design & Nature and Ecodynamics 18: 133–139. https://doi.org/10.18280/ijdne.180115

Benlasri M, Kaczmarek N, El Alami M, Ghamizi M, Berger E (2023) Inventory and pattern of distribution of mayflies (Insecta, Ephemeroptera) in the Draa river basin, southern Morocco. Alpine Entomology 7: 13–20. https://doi.org/10.3897/alpento.7.96436

Bouaicha R, Benabdelfadel A (2010) Variabilité et gestion des eaux de surface au Maroc. Sécheresse 21: 325–326. https://doi.org/10.1684/sec.2010.0272

Dakki M (1978) Notes faunistiques marocaines. 3. Sur la présence des genres *Oligoneuriella* et *Oligoneuriopsis* au Maroc (Ephemeroptera, Oligoneuriidae). Bulletin de l’Institut Scientifique, Rabat 3: 188.

Dakki M, Giudicelli J (1979) Description d'*0ligoneuriella skoura* n.sp. et d'*0ligoneuriopsis skhounate* n.sp., avec notes sur leur écologie (Ephem., 0ligoneuriidae). Bulletin de l'institut scientifique, Rabat 4: 13–28.

Dakki M, El Agbani MA (1983) Ephéméroptères d'Afrique du Nord. 3. Eléments pour la connaissance de la faune marocaine. Bulletin de l'Institut Scientifique, Rabat 7: 115–126.

Dakki M, Thomas AGB (1986) *Rhithrogena ayadi* n. sp., Ephéméroptère nouveau du Moyen Atlas marocain (Heptageniidae). Annales de Limnologie - International Journal of Limnology 22: 27–29. https://doi.org/10.1051/limn/1986002

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772–772. https://doi.org/10.1038/nmeth.2109

El Alami M, Dakki M, Errami M, Alba-Tercedor J (2000) Nouvelles données sur les Baetidae du Maroc (Insecta: Ephemeroptera). Zoologica Baetica 11: 105–113.

El Alami M, Benlasri M, Sartori M, Vuataz L, Ghamizi M (2022a) A new species of the genus *Prosopistoma* Latreille, 1833 (Ephemeroptera, Prosopistomatidae) from Morocco. ZooKeys1117: 203–218. https://doi.org/10.3897/zookeys.1117.83539

El Alami M, El Yaagoubi S, Gattolliat J-L, Sartori M, Dakki M (2022b) Diversity and Distribution of Mayflies from Morocco (Ephemeroptera, Insecta). Diversity 14: 498. https://doi.org/10.3390/d14060498

El Bazi RE, El Alami M, Khadri O, Errochdi S, Slimani M, Bennas N (2017) Contribution à l'étude de la biodiversité aquatique des aires protegées du Maroc. Les macroinvertébrés aquatiques du projet du Parc Naturel de Bouhachem (nord-ouest du Maroc) II: Ephemeroptera, Plecoptera, Trichoptera. Boletín de la SEA 61: 55–66.

Gattolliat J-L (2002) Etude systématique, cladistique et biogéographique des Baetidae (Ephemeroptera) de Madagascar. Thèse de doctorat. Université de Lausanne, faculté des sciences, Institut d'Ecologie Laboratoire de Zoologie et Ecologie Animale.

Gattolliat J-L, Sartori M (2008) Order Ephemeroptera. Arthropod Fauna of the UAE 1: 47–83.

Gattolliat J-L, Samraoui B, Benhadji N, Kechemir L, Zrelli S, El Yaagoubi S, El Alami El Moutaouakil M, Sartori M (2023) Baetidae (Baetidae, Ephemeroptera) in the Maghreb: state of the art, key, and perspectives. ZooKeys 1139: 137–163. https://doi.org/10.3897/zookeys.1139.94586

Houssni M, Mahroussi M, Sbih H, Kadiri M, Ater M (2020) Agriculture traditionnelle et agrodiversité dans les oasis du Sud du Maroc: cas des oasis de la région Drâa-Tafilalet. In: Research and innovation as tools for sustainable agriculture, food and nutrition security. MED-FORUM 2018. Bari, Italy.

Hurvich CM, Tsai C-L (1989) Regression and time series model selection in small samples. Biometrika 76: 297–307. https://doi.org/10.1093/biomet/76.2.297

Kaltenbach T, Vuataz L, Samraoui B, El Yaagoubi S, El Alami M, Gattolliat J-L (2022) Two new species of *Centroptilum* Eaton, 1869 from North Africa (Ephemeroptera, Baetidae). ZooKeys 1131: 71–97. https://doi.org/10.3897/zookeys.1131.91017

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20: 1160–1166. https://doi.org/10.1093/bib/bbx108

Khadri O, El Alami M, El Bazi R, Slimani M (2017) Ephemeroptera's diversity and ecology in streams of the ultramafic massif of Beni Bousera and in the adjacent non-ultramafic sites (NW, Morocco). Journal of Materials and Environmental Sciences 8: 3508–3523.

Kimmins DE (1938) A new moroccan ephemeropteron. Annals and Magazine of Natural History 1: 302–305. https://doi.org/10.1080/00222933808526771

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35: 1547. https://doi.org/10.1093/molbev/msy096

Lestage JA (1925) Ephéméroptères, Plécoptères et Trichoptères recueillis en Algérie par M. H. Gauthier et liste des espèces connues actuellement de l`Afrique du Nord. Bulletin de la Société d`Histoire Naturelle de l`Afrique du Nord 16: 8–18.

Letunic I, Bork P (2021) Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. Nucleic Acids Research 49: W293–W296. https://doi.org/10.1093/nar/gkab301

Mabrouki Y, Taybi AF, Alami ME, Berrahou A (2017) New and interesting data on distribution and ecology of Mayflies from Eastern Morocco (Ephemeroptera). Journal of Materials and Environmental Sciences 8: 2839–2859. https://www.jmaterenvironsci.com/Document/vol8/vol8_N8/283-JMES-2950-Mabrouki.pdf

Navás L (1929) Insectes névroptères et voisins de Barbarie (Septième série). Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 20: 57–60.

Ouahsine H, Lavandier P (1988) Dynamique des populations larvaires de *Baetis navasi* M.-L. (Ephemeroptera) dans un torrent du Haut-Atlas de Marrakech, Maroc. Annales de Limnologie - International Journal of Limnology 24: 167–171. https://doi.org/10.1051/limn/1988014

Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526–528. https://doi.org/10.1093/bioinformatics/bty633

Puillandre N, Brouillet S, Achaz G (2021) ASAP: assemble species by automatic partitioning. Molecular Ecology Resources 21: 609–620. https://doi.org/10.1111/1755-0998.13281

Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Molecular Ecology 21: 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Qninba A, El Agbani MA, Dakki M, Benhoussa A (1988) Evolution saisonnière de quelques peuplements d'invertébrés benthiques de l'Oued Bou Regreg (Maroc). Bulletin de l'Institut Scientifique 12: 149–156.

R Core Team O (2023) The R Project for Statistical Computing. https://www.r-project.org/ [June 8, 2023]

Rambaut A (2007) Tracer v. 1.4. http://tree.bio.ed.ac.uk/software/tracer/

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Salles FF, Gattolliat J-L, Angeli KB, De-Souza MR, Gonçalves IC, Nessimian JL, Sartori M (2014) Discovery of an alien species of mayfly in South America (Ephemeroptera). ZooKeys 399: 1–16. https://doi.org/10.3897/zookeys.399.6680

Stecher G, Tamura K, Kumar S (2020) Molecular Evolutionary Genetics Analysis (MEGA) for macOS. Molecular Biology and Evolution 37: 1237–1239. https://doi.org/10.1093/molbev/msz312

Thomas AGB, Bouzidi A (1986) Trois Ephéméroptères nouveaux du Haut Atlas marocain (Heptageniidae, Baetidae, Leptophlebiidae). Bulletin de la Société d'histoire naturelle de Toulouse 122: 7–10.

Vitte B (1991) *Rhithrogena mariae* n. sp., Ephéméroptere nouveau du Rif marocain (Ephemeroptera, Heptageniidae). Nouvelle revue d'entomologie 8: 89–96. https://eurekamag.com/research/007/758/007758666.php

Vitte B, Thomas AGB (1988) Compléments et corrections à la faune des Ephéméroptères d'Afrique du Nord. 2. Le genre *Choroterpes* Eaton, sous-genre *Euthraulus* Barnard (Ephemeroptera). Annales de Limnologie - International Journal of Limnology 24: 161–165. https://doi.org/10.1051/limn/1988013

Vuataz L, Sartori M, Wagner A, Monaghan MT (2011) Toward a DNA Taxonomy of Alpine *Rhithrogena* (Ephemeroptera: Heptageniidae) using a mixed yule-coalescent analysis of mitochondrial and nuclear DNA. PLoS ONE 6: e19728. https://doi.org/10.1371/journal.pone.0019728

Waterhouse AM, Procter JB, Martin DMA, Clamp M, Barton GJ (2009) Jalview Version 2–a multiple sequence alignment editor and analysis workbench. Bioinformatics 25: 1189–1191. https://doi.org/10.1093/bioinformatics/btp033

Wickham H (2011) The Split-Apply-Combine Strategy for Data Analysis. Journal of Statistical Software 40: 1–29. https://doi.org/10.18637/jss.v040.i01

Yanai Z, Gattolliat J-L, Dorchin N (2018) Taxonomy of *Baetis* Leach in Israel (Ephemeroptera, Baetidae). ZooKeys 794: 45–84. https://doi.org/10.3897/zookeys.794.28214

Yanai Z, Sartori M, Gattolliat J-L (2020) Contribution to the mayflies (Insecta, Ephemeroptera) of Israel and the Palestinian Authority. Check List 16: 229–237. https://doi.org/org/10.15560/16.2.229

Supplementary material 1

Methods DNA barcoding Duisburg-Essen

Authors: Mokhtar Benlasri

Data type: docx

Explanation note: The method used for the barcoding at the university of Duisburg-Essen to confirm the identificatio

Link: https://doi.org/10.3897/alpento.7.109562.suppl1

Alpine Entomology 7 2023, 153–166 | DOI 10.3897/alpento.7.111214

Alpine Entomology

Micro-endemism pattern and *Wolbachia* infection of *Quedius obliqueseriatus* (Coleoptera, Staphylinidae), a montane rove beetle endemic of the North-Western Caucasus

Angesom Gebremeskel[1], Maria Salnitska[1], Valeria Krivosheeva[1], Alexey Solodovnikov[2]

1 *X-BIO Institute, University of Tyumen, 6 Volodarskogo Str, Tyumen, 625003, Russia*
2 *Natural History Museum of Denmark at the University of Copenhagen, Zoological Museum, Universitetsparken 15, Copenhagen, 2100, Denmark*

https://zoobank.org/AF0F1779-F8D9-4AAE-9548-C14F79148231

Corresponding author: Alexey Solodovnikov (asolodovnikov@snm.ku.dk)

Academic editor: Dagmara Żyła ♦ **Received** 15 August 2023 ♦ **Accepted** 26 September 2023 ♦ **Published** 5 October 2023

Abstract

We conducted an integrative taxonomic study of a forest floor dwelling montane rove beetle *Quedius obliqueseriatus* Eppelsheim, 1889. It is one of many endemic species of the North-Western Caucasus, a region considered a global biodiversity hotspot. Examination of the morphological characters in 93 specimens of *Q. obliqueseriatus* and phylogenetic assessment of the COI barcode for 28 of them, revealed that this species in fact consists of two distinct (p-distance of 4.0%) allopatric lineages, western and eastern. They subtly differ in the structure of the aedeagus, which was not noticed in the previous revision of this species. Nuclear DNA markers (H3, ITS1, ITS2, Wg and 28S) sampled in both lineages, did not show any divergence. Variation of the non-genitalic morphological characters, such as body size or coloration, is continuous across both lineages. Discovery of microendemic lineages within an endemic rove beetle species highlights how little is understood about the patterns and drivers of endemism in arthropods of the North-Western Caucasus. We refrained from the description of a new species due to shortage of data from the area where newly discovered western and eastern lineages meet. As *Q. obliqueseriatus* was found to be largely infected with *Wolbachia*, we gave a review of this infection among insects and other arthropods and its impact on speciation. Finally, we described our method of removal of the *Wolbachia* COI amplicon by endonuclease restriction enzyme in order to get the desired beetle amplicon from infected specimens.

Key Words

integrative taxonomy, molecular markers, morphology, endemism, COI

Introduction

The North-Western Caucasus is an area of the globe with a very rich temperate flora and fauna characterized by the high rate of endemism. In the west it is limited by the coast of the Azov and Black seas, in the north by the Manych Depression and a line between the mouth of the Don River and Lake Manych, in the south by the state border with Abkhazia and in the east by the valley of the river Urup and the watershed of the Urup and Bolshaya Laba rivers (Fig. 1A). Overall, it is very diverse terrain that covers about 87,000 km^2 (Zamotajlov et al. 2010). Its landscapes and elevations range from the lowland wetlands of the Kuban River to the mountain peaks like Mount Tsakhvoa that reaches 3346 meters above sea level. The North-Western Caucasus stretches across four administrative regions of Russia: the Krasnodar and Stavropol Territories, and the Republics of Adygea and Karachay–Cherkessia. This area is placed among the global biodiversity hotspots (Krever et al. 2001; Mittermeier et al. 2005; Egorov et al. 2020) and it is very attractive for naturalists and scientists experiencing and exploring biodiversity. Nevertheless, knowledge about the North-West Caucasian biodiversity remains incomplete, especially as far as insects and other arthropods are concerned.

Detailed entomological studies of the North-Western Caucasus are of broad scientific interest because they shed light on the speciation processes leading to significant diversification and originality of the regional entomofauna. According to Zamotajlov et al. (2010), out of 1939 beetle (Coleoptera) species recorded in the North-Western Caucasus, around 600 are endemic to this region. Many of them have very narrow distributions that occupy a mountain range or a system of close by ranges, with a sister species across a valley. In particular, the mainly predatory rove beetles (Staphylinidae) that inhabit soil, leaf litter or other ground-based microhabitats at various elevations of the North-West Caucasian mountains have such endemics, many of which are still unknown or poorly studied (Solodovnikov 1998, 2001).

One such example is a presumably monophyletic group of narrowly distributed, apterous rove beetle species that includes *Quedius humosus* Solodovnikov, 2005 confined to the low elevation forests around the Black Sea coast in the south-east, *Quedius lgockii* Roubal, 1911, confined to a few close alpine localities, and *Quedius obliqueseriatus* Eppelsheim, 1889 confined to a larger area of the mountain forests of low and middle elevations (Solodovnikov 2004, 2005; Salnitska and Solodovnikov 2019). All three species clearly differ from each other morphologically, especially by the structure of the aedeagus (Salnitska and Solodovnikov 2019). Among them, *Q. obliqueseriatus* has the widest distribution (Fig. 1A) where it occurs in forest leaf litter from 200–600 m in the foothills (Fig. 1B) to 1600–1800 m at the timber line. The habitus of *Q. obliqueseriatus* (Fig. 2) shows significant morphological variation. Beetles vary in body size, and in the coloration of their pronotum, elytra and to some extent abdomen (from pale, reddish, to dark, blackish). The aedeagus also shows a seemingly continuous variation in the pattern of sensory peg setae on the paramere (Fig. 3), and the shape of the apex of the median lobe (Fig. 4).

This study was prompted by the distribution range of *Q. obliqueseriatus*, which is significantly larger than in other similarly apterous species of this group, and the above mentioned morphological variation. It aims to test the integrity of *Q. obliqueseriatus* as a species using DNA and morphological data, as well as to explore potential geographic pattern within the morphological variation. Therefore, we sampled as much material as possible from the entire distribution area of this species and sequenced several commonly used mitochondrial and nuclear mark-

Figure 1. Distribution and sampling of *Quedius obliqueseriatus* in the North-Western Caucasus. **A.** North-Western Caucasus terrain and sampled localities. **B.** Example of sampled habitats of *Q. obliqueseriatus*. Numbers represent the names of localities as follows: 1. Aderbienka 2. Pshada 3. Archipo-Osipovka 4. Bzhyd 5. Defanovka 6. Moldavanovka 7. Olginka 8. Nebug 9. Kirpichnoe 10. Krivenkovskoe 11. Induk 12. Semashko 13. Shepsi 14. Druzhba 15. Terziyan 16. Apsheronsk 17. Tatyanovka 18. Temnolesskaya 19. Vardane 20. Solokh Aul 21. Babuk Aul 22. Gorniy Vozdukh 23. Medoveevka 24. Vardane Verino 25. Chvizhepse 26. Krasnaya Polyana 27. Esto-Sadok 28. Aibga 29. Atschischo. Dotted purple and orange lines or question marks indicate hypothesized distribution area of the western and eastern clades, respectively. Photos by M. Salnitska.

ers. In the course of the molecular work, we discovered that a significant proportion of specimens were infected with the microbial endosymbiont *Wolbachia,* whose COI sequence was amplified instead of the desired beetle COI fragment. Discovery of the *Wolbachia* infection became an interesting side-track, which necessitated an addition of a concise discussion about *Wolbachia* and design of an additional laboratory experiment to amplify beetle sequences from the infected specimens. Before proceeding to the presentation of the methods, results and conclusions of our study, it is necessary to introduce 1) our choice of molecular markers for species delimitation and 2) the phenomenon of *Wolbachia* infection in insects and its impact on speciation and species delimitation studies.

Choice of molecular markers for our study

Species delimitation using molecular markers is widely used in Coleoptera and Staphylinidae in particular, with an agreement that a combination of mitochondrial and nuclear gene fragments provide the most reliable results, especially if they show congruence with morphology (Song and Ahn 2014; Lee et al. 2020; Muñoz-Tobar and Caterino 2020; Tokareva et al. 2021; Yoo et al. 2022; Hansen and Jenkins Shaw 2023). A few studies on Staphylinidae used several molecular markers for species delimitation purposes. Song and Ahn (2014) assessed the accuracy of species delimitation and phylogenetic relationships of the *Aleochara fucicola* species complex using two mitochondrial (COI and COII) and three nuclear genes (CAD, EF1-α and Wg). Von Beeren et al. (2016a, 2016b) applied the mitochondrial COI and two nuclear genes (Wg and CAD) to survey species boundaries for the army ant symbionts. Muñoz-Tobar and Caterino (2020) used the mitochondrial COI and the nuclear Wg genes to examine the concordance of morphological characters and geography with hypothesized species boundaries in the genus *Panabachia*. Yoo et al. (2021) and Lee et al. (2020) sequenced the mitochondrial COI and the nuclear 28S genes to study species delimitation of *Phucobius* and some Korean *Oxyporus*, respectively. At the same time, a number of species delimitation studies in Staphylinidae were based on the COI fragments alone, or in combination with morphology. Using COI alone, Chatzimanolis and Caterino (2007) examined the phylogeographic structure of *Sepedophilus castaneus* (Tachyporinae), Caterino et al. (2015) explored relationships and gene flow among island and mainland populations of four species, and Serri et al. (2016) tested the intraspecific genetic variation in Steninae. Using the barcoding fragment of COI and morphology, Brunke et al. (2020a) explored species limits in the genus *Quedionuchus*, Lee et al. (2020) in the genus *Coprophilus*, Tokareva et al. (2021) in the genus *Oxyporus* and Hansen and Jenkins Shaw (2023) in the genus *Lobrathium*. Brunke et al. (2020b), Salnitska and Solodovnikov (2021) and Hansen et al. (2022) applied COI barcoding and morphological characters for delimiting species in the genus *Quedius*. Other molecular markers repeatedly used in species level studies in Coleoptera are the nuclear H3, ITS1 and ITS2 (Downie and Gullan 2004; Fossen et al. 2016; Svante et al. 2017). Based on the reviewed literature, we aimed to sequence mitochondrial COI and nuclear H3, ITS1, ITS2, Wg and 28S to explore integrity of *Q. obliqueseriatus* as a species.

Wolbachia and its impact on speciation and species delimitation studies in insects

Wolbachia are maternally inherited obligate intracellular alpha-proteobacteria and a member of the order Rickettsiales (Werren et al. 2008). *Wolbachia pipientis* and related species are known to infect arthropods and nematodes and cause diverse complex symptoms such as vitamin deficiency, cytoplasmic incompatibility and other reproduction abnormalities, as well as parthenogenesis in their hosts (Werren et al. 2008; Hosokawa et al. 2010; Zug and Hammerstein 2015; Nugapola et al. 2017; Schuler et al. 2018; Jiménez et al. 2019).

Since the first detection and description of *Wolbachia* in *Culex pipiens* (Hertig and Wolbach 1924; Hertig 1936), many other arthropod species were reported to harbor similar endosymbionts and to show equivalent mating incompatibilities. *Wolbachia* is now known as the most abundant and widespread intracellular bacterium on Earth (Roy et al. 2015; Boonsit and Wiwatanaratanabutr 2021). In a survey of 157 species of Neotropical arthropods from Panama, *Wolbachia* were detected in 26 of 154 insect species from all major orders (16.9%) (Werren et al. 1995). In a detailed screening of *Wolbachia* infection for 15 colonies of the very common soil-feeding termites *Cubitermes* spp. *affinis subarquatus* (Termitidae, Termitinae) in Central Africa, Roy et al. (2015) showed that 50% of the individuals were *Wolbachia* positive. *Wolbachia* infections were also common among four mosquito species in Sri Lanka (Nugapola et al. 2017), in moths from three different geographic regions of Thailand (Boonsit and Wiwatanaratanabutr 2021), or in an insular radiation of damselflies (Lorenzo-Carballa et al. 2019), to mention just a few diverse examples for insects.

Non-insect arthropods, such as crustaceans (Rousset et al. 1992; Bouchon et al. 1998), arachnids (Breeuwer and Jacobs 1996) and mites (Sourassou et al. 2014) were also found to harbor *Wolbachia*. While *Wolbachia* is a frequent reproductive parasite in arthropods, in filarial nematodes it is an obligate mutualist (Lo et al. 2007; Hilgenboecker et al. 2008; Wasala et al. 2019; Manoj et al 2021).

The transmission of *Wolbachia* from one infected organism to another is maternal, via the cytoplasm of the egg. It was observed that *Wolbachia* are evenly distributed within female germ lines, but concentrate in the future oocyte during oogenesis (Werren 1997; Stouthamer et al. 1999). Once the oocyte is built, *Wolbachia* again disperse throughout the egg. There is evidence that *Wolbachia* utilize their host's microtubule cytoskeleton to localize in particular parts of the cell (Ferree et al. 2005). There is further evidence that *Wolbachia* are capable of moving from outside

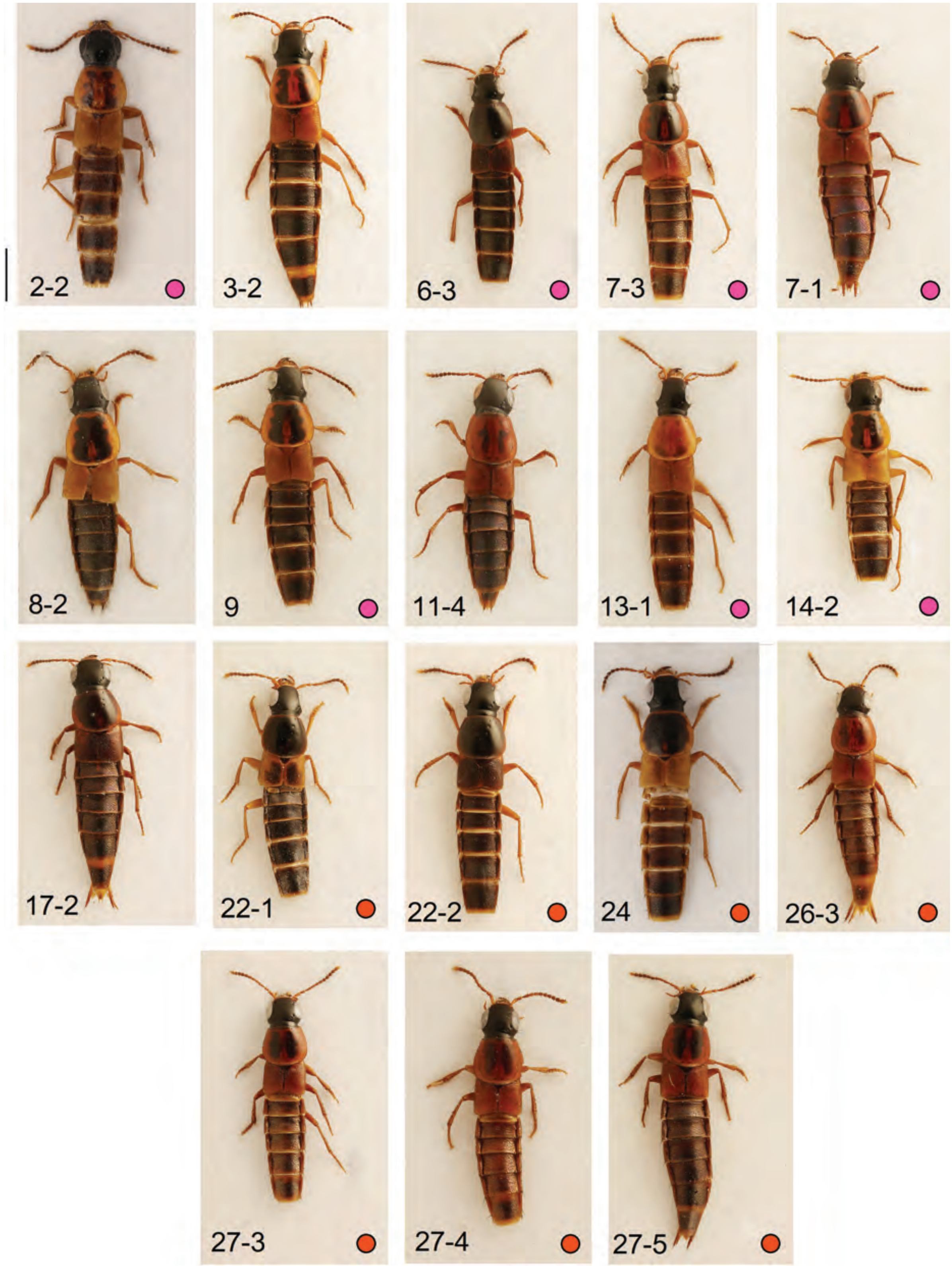


Figure 2. Habitus diversity of *Quedius obliqueseriatus*. Numbers correspond to the specimen code in the Suppl. material 1: table S2 that consists of the locality code (from 1 to 29, also used in Fig. 1) and sequential number of a specimen from a given locality. Purple dots indicate specimens from the western clade, orange dots indicate specimens from the eastern clade, as in Fig. 5. Scale bar: 1 mm.

the reproductive tissues into the female germ line. Frydman et al. (2006) have shown that *Wolbachia* can cross different tissues to reach the germ line when injected into *Drosophila melanogaster*. *Wolbachia* are not always exclusive to the reproductive tissues of their hosts. In some insect species they were also found in somatic tissues like muscles (Dobson et al. 1999) or nerves (Rigaud et al. 1991). Infection of the nervous tissue with this bacterium suggests a possible influence on the host's behavior. Therefore, interactions of *Wolbachia* with the host species can range from parasitic to symbiotic. The success of *Wolbachia* is attributed to its efficient maternal transmission and to the impact on host reproduction that favors infected females, called the sperm-egg cytoplasmic incompatibility (Serbus et al. 2008).

Manipulation of host reproduction by *Wolbachia* plays an important role in a variety of evolutionary processes of the host species (Werren 1998; Bordenstein 2003). The presence of diverse symbionts is thought to increase speciation rates through the spread of symbiont strains that encode cytoplasmic incompatibility in their hosts, and which may produce barriers to gene flow (Bordenstein et al. 2001; Telschow et al. 2005). In fact, the first suggestion that cytoplasmic elements have the potential to influence host speciation, given postzygotic isolation, was published long ago (Laven 1959). *Wolbachia* infections can, for example, be responsible for reproductive isolation between sister species or for lethality of hybrid males. In particular, *Wolbachia* can induce a mating incompatibility in their hosts that terminates or at least reduces offspring production between infected males and uninfected females. In particular, *Wolbachia* induced cytoplasmic incompatibility where male and female gametes were unable to form viable offspring due to differences in parental *Wolbachia* infection status. When *Wolbachia* infected males mated with uninfected females (unidirectional infection), few or no offspring were produced, while all other crosses were fertile (Hoffmann and Turelli 1997). As a result, once infection levels in a population surpass a threshold, *Wolbachia* is predicted to sweep through the host population (Kriesner et al. 2013; Schuler et al. 2016). The reproductive advantage of *Wolbachia* infected individuals can result in rapid spread of the endosymbiont (Schuler et al. 2013). Moreover, the co-maternally inherited mitochondrial DNA can hitchhike with the spreading *Wolbachia*, replacing mitochondrial haplotypes associated with uninfected individuals (Schuler et al. 2016). Thus, *Wolbachia* infected populations typically exhibit lower mitochondrial diversity than uninfected populations (Jiggins 2003; Hurst and Jiggins 2005). Reproductive isolation can be also favored for example, when both partners are infected with different strains of *Wolbachia* causing bidirectional cytoplasmic incompatibility, with both mating directions being infertile (Bordenstein et al. 2001; Kodandaramaiah et al. 2013). All these have generated interest in the possible role of *Wolbachia* in promoting speciation or maintaining species boundaries (Werren 1998; Bordenstein 2003; Brucker and Bordenstein 2012; Schuler et al. 2016).

A number of studies explored species boundaries for insects infected with *Wolbachia*. Gebiola et al. (2012) conducted an integrative taxonomic study for delimiting wasp species within the *Pnigalio soemius* complex. They confirmed a trend towards host specificity within the presumed polyphagous *P. soemius* and suggested that *Wolbachia* infection could have played a major role in the reproductive isolation and genetic diversification of at least two species. Ritter et al. (2013) tested for cryptic speciation for two butterfly species, *Phengaris teleius* and *Phengaris nausithous*, based on a comprehensive sample across their Palaearctic ranges using COI gene sequences, nuclear microsatellites and tests for *Wolbachia*. In both species, a deep mitochondrial split occurring 0.65–1.97 million years ago was observed that did not correspond with microsatellite data but was concordant with *Wolbachia* infection. Ritter et al. (2013) rejected the hypothesis of cryptic speciation within *P. teleius* and *P. nausithous* in favor of the explanation that the major splits in the mtDNA phylogeny in both species were caused by *Wolbachia* infections. Furthermore, they concluded that geographic isolation during Pleistocene glaciations contributed to differentiation of mitochondrial and nuclear genomes. Kodandaramaiah et al. (2013) showed that the satyrine butterfly *Coenonympha tullia*, a species uniform in nuclear genes and morphology, having a deep split between two mitochondrial clades, each infected by two different *Wolbachia* strains, respectively. Plewa et al. (2018) used different sets of data (morphology, genetics and ecology) to verify the taxonomic status of *Monochamus sartor sartor* and *M. s. urussovii* (Coleoptera: Cerambycidae) across their entire range. Their morphological and molecular data showed that both subspecies have distinct but very weakly diverged mitochondrial haplogroups. Moreover, each subspecies is infected by different strains of the intracellular bacterium *Wolbachia*, which could be one of the factors causing their genetic isolation, regardless of geographic isolation.

Material and methods

Specimen acquisition

Material for this study was examined from the collections of the Zoological Institute of the Russian Academy of Science in St. Petersburg (**ZIN**) and the University of Tyumen (**UTMN**). A special field trip to sample *Q. obliqueseriatus* in the mountain foothills along the Black Sea coast in Russia was organized in 2022 (Fig. 1B). All geographic localities for the material in this study are shown in Fig. 1A, which was produced using QGIS 2.18.22 based on coordinates given on the labels or found by us when toponyms on the labels were recorded only verbally. All examined material is listed in the Suppl. material 1: table S2.

Morphological character examination and documentation

For the study of morphological characters, beetles were examined under the dissecting microscope (Zeiss Stemi 305) and photographed with a Canon EOS 5D Mark III DSLR (Canon Inc.) digital camera with a macro lens Canon MP-E 65mm F2.8 1–5x (Canon Inc.) mounted on a Cognisys Stackshot 3X macro rail connected with a controller and a macro flash Macro Twin Lite MT-24EX Flash (Canon Inc.). Aedeagi were dissected under the dissecting microscope, and the paramere was detached from median lobe. The median lobe and underside of the paramere with peg setae were photographed from soft preparations of these structures in glycerin using the

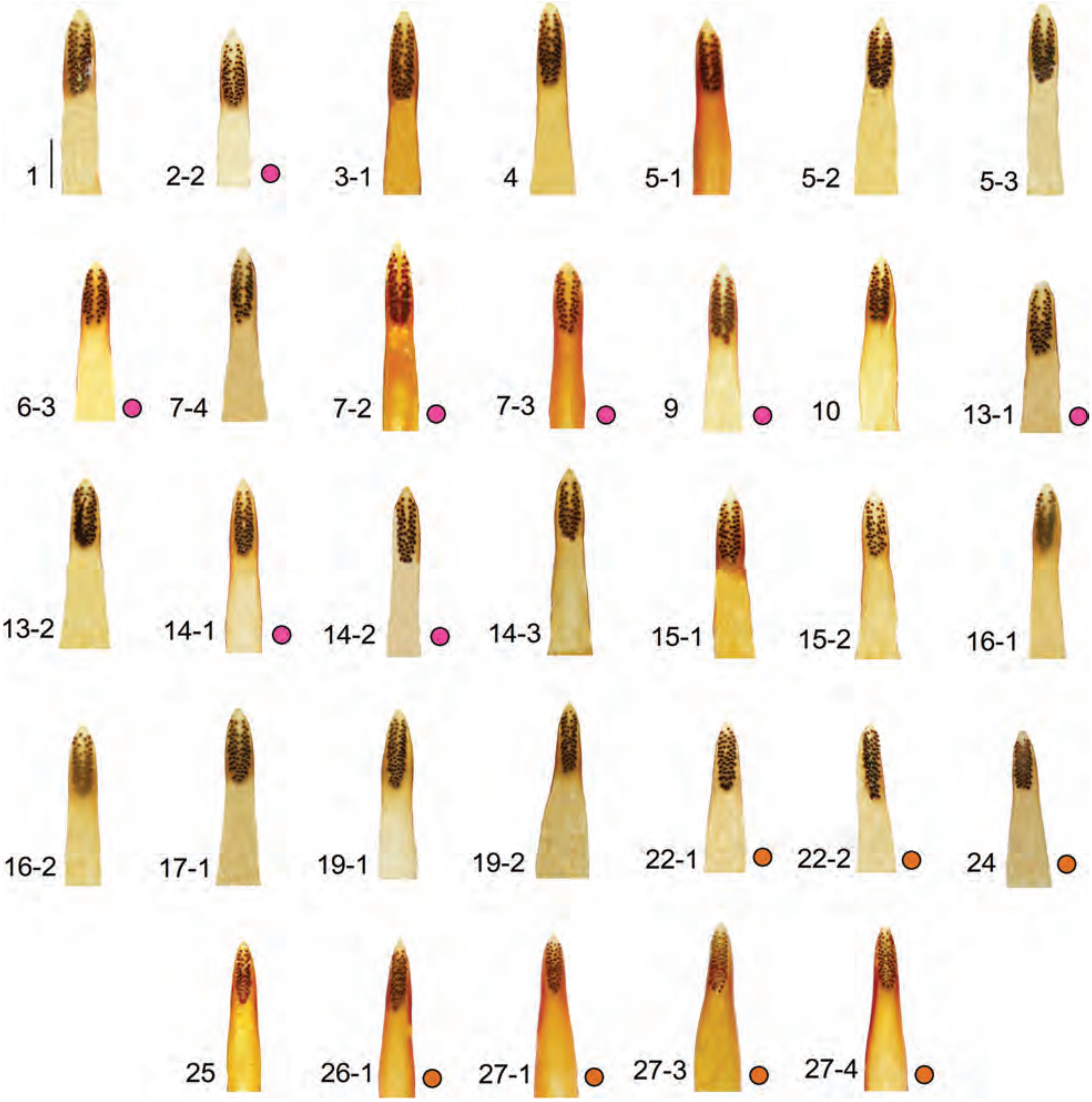


Figure 3. Variability of the sensory peg setae arrangement on the underside of the parameral apex in *Quedius obliqueseriatus*. Numbers correspond to the specimen code in the Suppl. material 1: table S2 that consists of the locality code (from 1 to 29, also used in Fig. 1) and sequential number of a specimen from a given locality. Purple dots indicate specimens from the western clade, orange dots indicate specimens from the eastern clade, as in Fig. 5. Scale bar: 0.25 mm.

same photo system described above. All dissected aedeagi were preserved in the same vials separated with cotton tissue under their respective specimens.

Molecular work

Molecular work was performed mainly in the Laboratory of Insect Systematics and Phylogenetics of the Institute of Environmental and Agricultural Biology (X-BIO), University of Tyumen (Tyumen, Russia). Some of the molecular work was performed in the Antimicrobial Resistance Laboratory of the same institute.

DNA extraction

The DNA extraction is carried out using Qiagen's DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). In the first step, 180 µl of buffer ATL was added to the vacuum dried specimens in the Eppendorf tube and immediately 20 µl of proteinase K solution was added, after a short vortex it was incubated at 55 °C for 24 hours. In the second step, 200 µl of buffer AL was added and immediately a short vortex was required followed by incubation for 10 minutes at 70 °C. After the addition of 200 µl of 96% ethanol, the total volume was transferred to a labelled mini spin column and centrifuged at 8000 rpm for 1 minute.

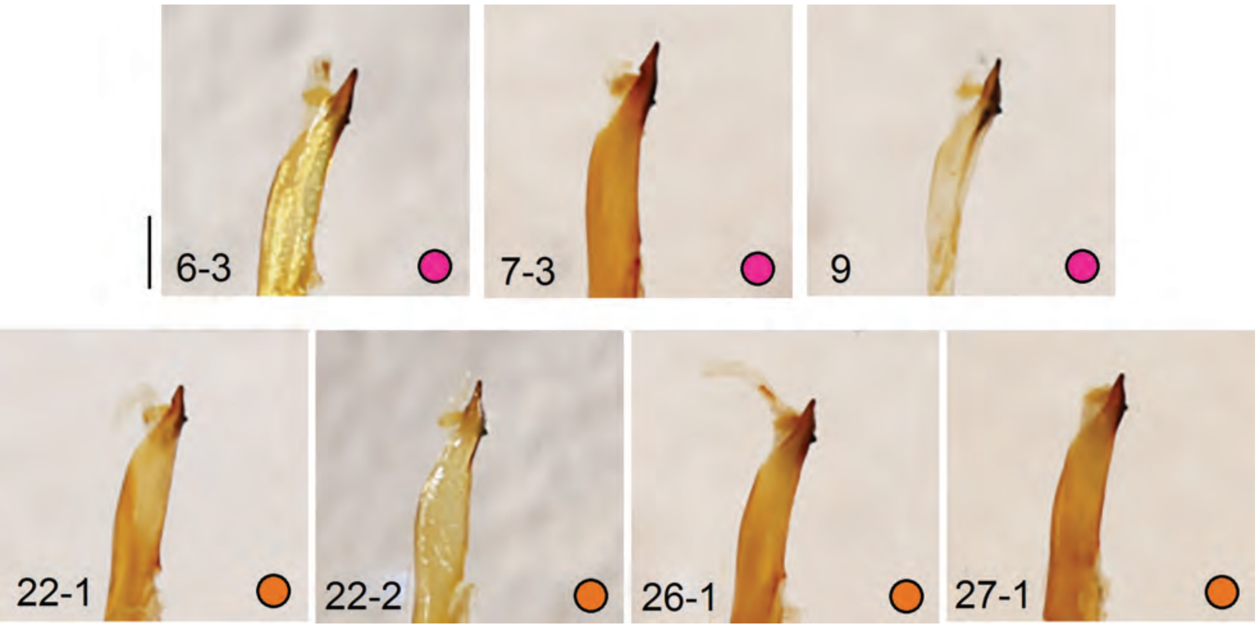


Figure 4. Variability of the apical portion of the aedeagus median lobe in *Quedius obliqueseriatus*, in lateral view. Numbers correspond to the specimen code in the Suppl. material 1: table S2 that consists of the locality code (from 1 to 29, also used in Fig. 1) and sequential number of a specimen from a given locality. Purple dots indicate specimens from the western clade, orange dots indicate specimens from the eastern clade, as in Fig. 5. Scale bar: 0.25 mm.

Next, the mini spin column was moved to new collection tube and the flow through was discarded. 500 µl of buffer AW1 was added followed by centrifugation at 8000 rpm for 1 minute and discarding the flow through. Another 500 µl of buffer AW2 was added, followed by centrifugation at 14000 rpm for 3 minutes and discarding the flow through. Finally, 60 µl of elution buffer AE was added, followed by centrifugation at 8000 rpm for 1 minute. The flow through containing the DNA extract was transferred to a new Eppendorf tube and stored at -20 °C.

PCR

The targeted regions were amplified using the primers listed in Suppl. material 1: table S1. The primers (HCO 3198 and LCO 1490) were used to amplify a 658 bp fragment of the cytochrome oxidase (COI) mitochondrial gene. Typical polymerase chain reaction (PCR) was conducted with a PCR master mix containing a total volume of 20 µl in each PCR tube. This premix contains 4 µl of Red Buffer (Evrogen), 2 µl of primers (1 µl each), 0.4 µl of dNTPs, 0.5 µl of Taq Polymerase, 2 µl of DNA extract and 11.1 µl of sterile distilled water. PCR was performed under the following cycling conditions: initial denaturation for 3 minutes at 94 °C; 35 cycles of: 30 seconds at 94 °C, annealing temperature of 51 °C for 30 seconds and 72 °C for 30 seconds; followed by a final extension temperature of 72 °C for 5 minutes (Hebert et al. 2003; Schomann and Solodovnikov 2017).

Amplification of a 464 bp fragment of Wg was performed using a nested reaction. The first reaction used the external primers (Wg550F–WgAbRZ) and consisted of an initial denaturation for 3 min at 94 °C, 35 cycles of: 30 s of denaturation at 94 °C, 30 s of annealing at 53 °C and 1.5 min of extension at 72 °C, followed by a 5 min final extension at 72 °C. The product of this is then used as a template for a reaction using the internal primers (Wg578F–WgAbR) and consisting of the same temperature profile for the external primers (Wild and Maddison 2008; Schomann and Solodovnikov 2017).

The amplification profile of a 802 bp fragment of 28S consisted of an initial denaturation for 2 min at 94 °C, 35 cycles of: 45 s at 94 °C, 30 s at 53–58 °C and 1 min at 72 °C, followed by a 2 min final extension at 72 °C (Yoo et al. 2021).

The amplification profile of a 308 bp fragment of H3 consisted of an initial denaturation for 5 min at 95 °C, 35 cycles of: 30 s at 95 °C, 30 s at 55 °C and 1 min at 72 °C, followed by a 8 min final extension at 72 °C (Fossen et al. 2016).

The amplification profiles of 477 bp and 602 bp fragments of both ITS1 and ITS2, respectively, were the same: an initial denaturation for 2 min at 94 °C, 35 cycles of: 1 min at 94 °C, 1 min at 50 °C and 2 min at 72 °C, followed by a 7 min final extension at 72 °C (Downie and Gullan 2004; Ashfaq et al. 2010).

In all cases the final PCR products were separated in 1% agarose gel by electrophoresis and the gel was docked under UV-illuminator apparatus to visualize the DNA bands.

DNA cleaning, sequencing and alignment

Post PCR products were cleaned using the Cleanup S Cap kit, according to manufacturer's instructions (https://evrogen.ru/kit-user-manuals/BC041.pdf). Sequencing was performed commercially by Evrogen (https://evrogen.ru). All sequences were generated in both directions (with forward and reverse primers) and confirmed with sense and antisense strands. Sequences were cleaned and aligned manually using MEGA version 6.0 (Tamura et al. 2013) and BIOEDIT 7.0 (Hall 1999). All genes are in protein-coding regions, so manual alignment of sequences was straightforward.

Detection of *Wolbachia* infection

Sequences from all 23 samples were blasted using GenBank nucleotide BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). For 23 specimens, COI fragments were identified as belonging to *Wolbachia* rather than *Q. obliqueseriatus*. Of these, we further tested 13 of them for *Wolbachia* infection by amplifying the gene *Wolbachia* surface protein (wsp), commonly used as markers to detect the presence of the bacteria (Conte et al. 2019; Shaikevicha et al. 2019; Kirik et al. 2020). We used *Wolbachia*-specific primer pairs, wsp81F and wsp691R (Shaikevicha et al. 2019), amplifying a ~ 550 bp fragment of the wsp gene. The amplification profile for wsp consisted of an initial denaturation for 5 min at 94 °C, 35 cycles of: 30 s at 94 °C, 30 s at 55 °C and 1 min at 72 °C, followed by a 10 min final extension at 72 °C (Shaikevicha et al. 2019).

Removal of *Wolbachia* COI amplicon

We compared *Wolbachia* and *Q. obliqueseriatus* COI sequences using NEBcutter V2.0 (http://nc2.neb.com/NEBcutter2/) and found a SspI restriction site that belongs to *Wolbachia* and is absent in *Q. obliqueseriatus* sequences. An endonuclease restriction enzyme (SibEnzyme, http://sibenzyme.com/pcr-fragments-restriction/) was used to differentiate the *Q. obliqueseriatus* DNA from *Wolbachia* COI amplicon by cutting the *Wolbachia* mitochondrial COI DNA segment at the AAT↑ATT / TTA↓TAA site. Endonuclease restriction enzyme was applied into the cleaned PCR DNA product of *Q. obliqueseriatus* with *Wolbachia* infection. The standard protocol was as follows: total reaction volume of 20 µl, which contained restriction buffer (X10) – 2 µl, restriction endonuclease – 1 µl, PCR DNA fragment – 10 µl and purified water – 7 µl. The reaction mixture was incubated at optimum temperature of 37 °C for 2 hours. 20 µl of the reaction mixture was applied to 1% agarose gel for control electrophoresis and to separate the DNA bands. One clear band approximately 600 bp and two clear bands approximately 300 bp were obtained. We cut out the 600 bp length band from the gel and cleaned it. DNA cleaning was conducted on the excised gel using the Evrogen cleaning kit (https://evrogen.ru/kit-user-manuals/BC041.pdf). Sequencing was performed commercially by Evrogen (https://evrogen.ru).

Molecular phylogenetic analysis for species delimitation

First, we performed alignment of sequences individually for all sequenced markers in MEGA version 6.0 (Tamura et al. 2013); including an outgroup *Quedius maurorufus* COI sequence. No variation was found for any of them except COI. For COI, the substitution model GTR + G was selected based on the Akaike information criterion (AIC), using JMODELTEST (Guindon and Gascuel 2003) run on CIPRES (https://www.phylo.org/index.php/; Miller et al. 2010). The Bayesian analysis was performed using MrBayes 3.2.7a (Ronquist et al. 2012). The analysis was run twice using 4 simultaneous chains for 10 000 000 generations with tree sampling every 1000 generations and discarding 25% of each run as burn-in. Convergence was judged by stabilization of the standard deviation of the split frequencies around 0.01. The overlay plot was checked for even distribution in both runs. The values of estimated sample size (ESS) and potential scale reduction factor (PSRF) were checked to reach a value of more than 100 for almost per all parameters, and 1.0, respectively.

The estimates of evolutionary divergence (p-distance) between sequences were computed in MEGA version 6 (Tamura et al. 2013) and differences in the composition bias among sequences (Tamura and Kumar 2002) were accounted for. The haplotype network was produced in PopART, using integer NJ network parameter (Leigh and Bryant 2015).

Results

As shown in detail in the Suppl. material 1: table S2, our sample consisted of 93 specimens (55 males and 38 females) of the traditionally (e.g., Solodovnikov 2004; Salnitska and Solodovnikov 2019) morphologically defined *Q. obliqueseriatus*, with samples collected from 29 localities across nearly its entire distribution (Fig. 1A). Of these, we were able to extract DNA from 70 specimens, which represented nearly all localities. From these extracts, we successfully amplified beetle COI from 22 specimens, Wg from 31 specimens, 28S from 11 specimens, H3 from 9 specimens, ITS1 from 5 specimens and ITS2 from 5 specimens. For 23 specimens, we were not able to amplify beetle COI because primers always picked up a COI fragment that blasted as *Wolbachia*. Of the 23 *Wolbachia* infected *Q. obliqueseriatus* specimens, 6 specimens were successfully freed from the *Wolbachia* amplicon using the endonuclease restriction enzyme as described above in the Material and Methods section. As a result, we obtained 28 COI sequences for *Q. obliqueseriatus* for our study.

Sequence alignments conducted for each gene individually revealed that only COI showed variation within *Q. obliqueseriatus* (fasta files of the aligned sequences for each marker are included in the Suppl. material 1 and named respectively as H3, ITS1, ITS2, Wg, and 28S).

Therefore, we conducted phylogenetic analysis with the COI gene fragment only.

Phylogenetic analysis of the COI data revealed with strong statistical support that *Q. obliqueseriatus* consists of two clades, here designated as “western” and “eastern” (Fig. 5A). Both clades are genetically divergent from each other (Fig. 5B) with p-distance of 4.0% (Suppl. material 1: table S3). Populations of the western clade are mainly distributed from around Pshada and Moldavanovka villages in the west to about Mt. Semashkho, and Shepsi and Druzhba villages in the east. Populations of the eastern clade are distributed from around Vardane and Solokh-Aul villages in the west to Vardane Verino and Krasnaya Polyana villages in the east (Fig. 5C). It should be noted that nuclear markers that we sampled from specimens across both “western”and “eastern” clades, did not show any variation.

Examination of the external morphology of the sequenced *Q. obliqueseriatus* specimens revealed no characters associated with either eastern or western clades. Smaller and larger specimens, darker and paler, with or without spots on pronotum and elytra, with variously shaped spots, occur among specimens in both clades (Fig. 2). Examination of the paramere revealed that most of the specimens from the western clade have sensory peg setae arranged in two irregular longitudinal groups with a distinct setae free area in between, at least apically (see examples marked with purple dot in Fig. 3). At the same time, all specimens from the eastern clade (see examples marked with orange dot in Fig. 3) have these rows indistinct, the distribution of sensory peg setae strongly diffuse, at most with an unclear setae free area between them.

The sensory peg setae arrangement revealed that additional specimens without COI data could be assigned to either of eastern and western molecular clades. For example (Fig. 3) specimen 1, all specimens in the same row from 3-1 to 5-3, the specimens 7-4, 10, 13-2, and all from 15-1 to 16-2 share a pattern characteristic of the western clade. At the same time, specimens 19-2, 22-1 and 25 (Fig. 3) share a pattern characteristic of the eastern clade. However, there are specimens (e.g., 17-1 or 19-1) that are difficult to assign to either of the clades based on morphology.

Examination of the median lobe in lateral view revealed that sequenced specimens from the western clade usually have the subapical tooth located at a slightly longer distance from the apex of median lobe (Fig. 4, upper row of examples marked with purple dot), while in the sequenced specimens from the eastern clade this tooth is usually located slightly closer to the apex of median lobe (Fig. 4, lower row of examples marked by orange dot). However, this morphological character is more subtle than the difference in sensory peg setae fields and does not show a distinct gap between both molecular clades. For example,

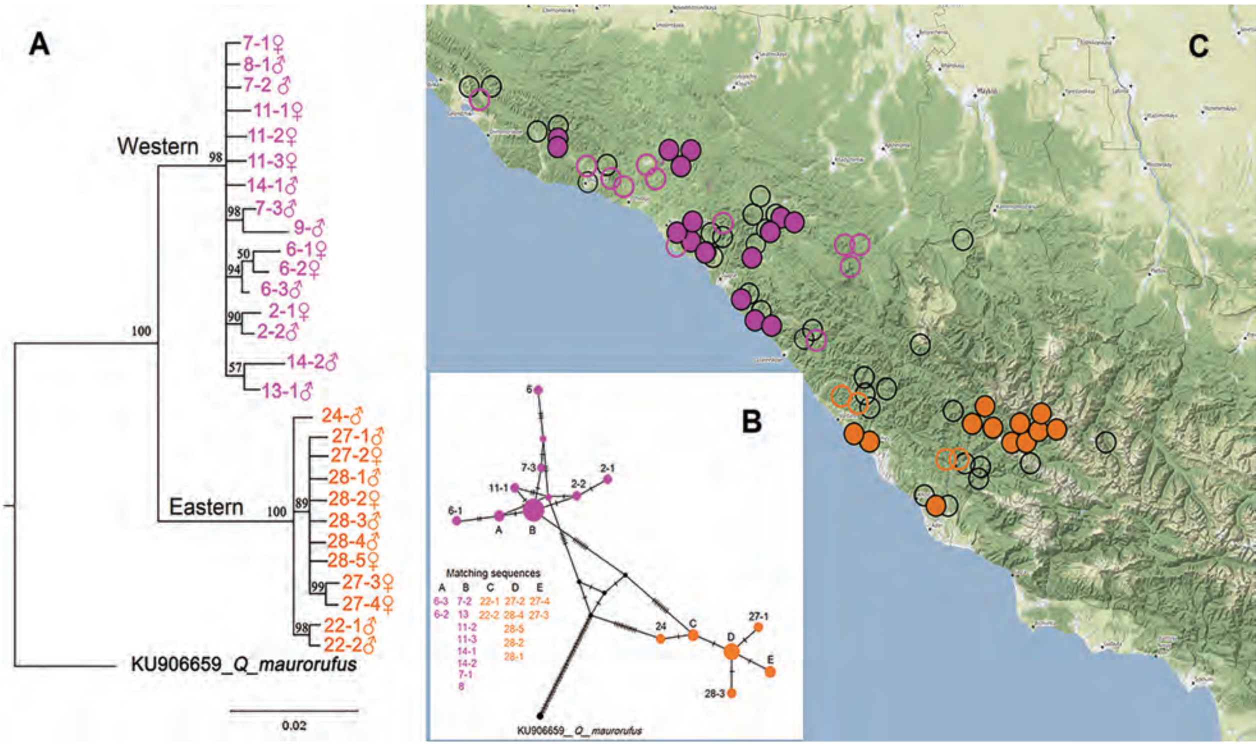


Figure 5. Micro-endemic forms of *Quedius obliqueseriatus* in the North-Western Caucasus, their phylogeny, genetic diversity, and geographic distribution. **A.** COI barcode-based Bayesian phylogenetic tree. **B.** Haplotype network. **C.** Geographic distribution. Purple color indicates specimens from western clade, orange color indicates specimens from eastern clade. Filled circles in **C** (the map) indicate sequenced specimens; open colored circles in **C** (the map) indicate non-sequenced males assigned to either western or eastern clade by the shape of the paramere only; open non-colored (black) circles in **C** (the map) indicate non-sequenced material without available males, thus unassigned to any clade. Numbers at terminals (branches) of the tree in A correspond to the specimen code in the Suppl. material 1: table S2 that consists of the locality code (from 1 to 29, also used in Fig. 1) and sequential number of a specimen when there is more than one from a given locality. Numbers at nodes in the tree in **A** indicate posterior probability in percentage.

the specimens 9 and 22-2 in Fig. 4 have the same distance between the subapical tooth and the apex of median lobe, even though they belong to different molecular clades.

Specimens infected by *Wolbachia* are widespread across the entire range of *Q. obliqueseriatus*. They belong to both western and eastern molecular clades (Suppl. material 1: fig. S1) and include males and females (Suppl. material 1: table S2). There is not any appreciable morphological trait associated with the *Wolbachia*-infected specimens. Generally, 24% of the specimens are infected with *Wolbachia*; of the infected specimens, 13 are males and 10 females.

Discussion

Our molecular and morphological examination revealed that *Quedius obliqueseriatus* consists of two lineages, here called western and eastern, that are clearly separable by COI barcoding and subtly separable by the characters of the aedeagus, mainly by the arrangement of sensory peg setae of the paramere. Because of the limited DNA-grade material or males for morphological examination, we still do not know exactly how both lineages are distributed. Based on the available data, these clades are allopatric and replace each other from west to east. However, it is not possible to confident in that due to the lack of the DNA-grade material from the area located between sequenced specimens from both clades (i.e., from such localities as Tatyanovka, Temnolesskaya, Vardane, Solokh-Aul and Babuk-Aul) (Figs 1A, 5C). There may be a zone of transition from one form to another, or a zone where they co-occur. Denser specimen sampling and more DNA-grade material is desired, especially from the geographic area where both forms meet.

The molecular divergence between both western and eastern lineages of *Q. obliqueseriatus* in COI with p-distance of 4.0% is strong enough to consider them as separate species by analogy with some other cases in beetles and other insects (e.g., Salnitska and Solodovnikov 2021; Yoo et al. 2022). However, there is no easy or uniform numerical threshold of molecular distance to determine species boundaries, and these instead vary case by case (Lukhtanov 2019). Examples in Staphylinidae vary too and depend on various considerations. Salnitska and Solodovnikov (2021) considered 4.4–7.7% distance among COI barcodes as inter-specific among species of the *Q. umbrinus* complex given the subtle morphological difference among them and distributional considerations. Yoo et al. (2022), also exploring morphology and nuclear marker along with the COI barcode data, considered interspecific divergence in COI barcode among the *Cafius* species ranging from 4.90% to 14.59%. In Tokareva et al. (2021) COI barcode-based distance among species of *Oxyporus* was lower than in either of the mentioned *Q. umbrinus* or *Cafius* complexes, but clearly supported by a hiatus in the endophallus structure.

Due to lack of divergence in the sampled nuclear molecular markers of *Q. obliqueseriatus*, the rather subtle nature of morphological difference between both COI-based lineages, and lack of any molecular data from the zone of potential contact of both forms, we consider the description of this potential new species premature, pending more material to be examined. Moreover, since the precise geographic origin of the type material for *Q. obliqueseriatus* collected by Hans Leder in the second half of the XIX-th century in "Circassia" (a broad area of Western Caucasus) is not clear (Eppelsheim 1889), we can only assume that the lectotype designated and illustrated in Solodovnikov (2004) belongs to the western clade because it has sensory peg setae clearly divided into two irregular rows. Therefore, the eastern clade represents a potential new species.

Discovery of two forms of an apterous and relatively narrowly distributed montane species that are clearly molecularly distant and somewhat subtly morphologically different, stresses a high degree of micro-endemism of the North-Western Caucasus that is not easy to detect by morphological investigations alone. Exploring and mapping distributions of such species in detail across various taxonomic and ecological groups of beetles and other arthropods may recover common patterns that in turn may reveal the origins of such endemism.

In case of the presumably monophyletic *Q. obliqueseriatus*-group, *Q. humosus* is restricted to the forest litter at low elevations of the south-eastern part of the North-Western Caucasus. Another species, *Q. lgockii*, is confined to high elevations above the timber line of the core montane area of the North-Western Caucasus. Finally, the here discovered western and eastern clades of *Q. obliqueseriatus* are both restricted to the forest belt stretching through a wide range of elevations and replacing each other from west to east, respectively. Interestingly, their ranges roughly coincide with two geo-botanical provinces in the western Transcaucasia recognized by Shiffers (1953). The western province is drier and of a Mediterranean aspect, the eastern is more humid and subtropical. These areas are thus used by various entomologists to define local regions in the faunistic works on the North-Western Caucasus (Ohrimenko 1992; Zamotailov 1992; Solodovnikov 1998). A thorough test for the monophyly of *Q. obliqueseriatus*-group along with the detailed molecular investigation of all endemic species of this complex may shed light on the ecological dimension of their diversification.

Finally, a *Wolbachia*-infection could have acted as a trigger for speciation in *Q. obliqueseriatus*, a process discussed for other *Wolbachia*-infected insects (Shoemaker et al. 1999; Sun et al. 2011; Leronzo-Carballa et al. 2019). It may be an interesting research program to further investigate strains of *Wolbachia* within both clades of *Q. obliqueseriatus*, to screen other narrowly distributed endemics for *Wolbachia* infections and compare their infection rates to widespread species. Our study does not have enough data to speculate on the potential role of *Wolbachia* in the micro-endemism pattern displayed by *Q. obliqueseriatus*. However, the discovered high rate of infection is noteworthy. On the practical side, we here demonstrated how to remove the *Wolbachia* amplicon that hinders the barcoding of the desired gene fragment in an infected insect via the application of endonuclease restriction enzyme and subsequent excision following gel electrophoresis.

Acknowledgements

We thank all members of the Laboratory of Insect Systematics and Phylogenetics of the Institute of Environmental and Agricultural Biology (X-BIO), University of Tyumen (Tyumen, Russia), where most of this work was based. We express our gratitude to the employees of the Antimicrobial Resistance Laboratory of the same institution, where we performed some molecular experiments, for their kind assistance. We are also grateful to all colleagues (mostly mentioned as collectors in Suppl. material 1: table S2) who participated or helped in the organization of our expeditions. Igor Orlov is thanked for helping to obtain photos for some of the Figures. Finally, we express our gratitude to Adam Brunke and Karina Lucas Silva-Brandão for providing their useful comments as reviewers.

References

Ashfaq M, Noor AR, Mansoor S (2010) DNA-based characterization of an invasive mealybug (Hemiptera: Pseudococcidae) species damaging cotton in Pakistan. Applied Entomology and Zoology 45 (3): 395–404. https://doi.org/10.1303/aez.2010.395

Boonsit P, Wiwatanaratanabutr I (2021) Infection density, diversity, and distribution of *Wolbachia* bacteria in moths (Order Lepidoptera): First systematic report from Thailand. Journal of Asia-Pacific Entomology 24: 764–771. https://doi.org/10.1016/j.aspen.2021.06.012

Bordenstein SR (2003) Symbiosis and the origin of species. In: Bourtzis K, Thomas AM (Eds) Insect Symbiosis, 283–304. https://doi.org/10.1201/9780203009918.ch17

Bordenstein SR, O'Hara F, Werren JH (2001) *Wolbachia*-induced incompatibility precedes other hybrid incompatibilities in Nasonia. Nature 409: 707–710. https://doi.org/10.1038/35055543

Bouchon D, Rigaud T, Juchault P (1998) Evidence for widespread *Wolbachia* infection in isopod Crustaceans: molecular identification and host feminization. Proceedings of the Royal Society of London, Series B: Biological Sciences 265: 1081–1090. https://doi.org/10.1098/rspb.1998.0402

Breeuwer JAJ, Jacobs G (1996) *Wolbachia*: Intracellular manipulators of mite reproduction. Experimental and Applied Acarology 20: 421–434. https://doi.org/10.1007/BF00053306

Brucker RM, Bordenstein SR (2012) Speciation by symbiosis. Trends in Ecology and Evolution 27: 443–451. https://doi.org/10.1016/j.tree.2012.03.011

Brunke AJ, Salnitska M, Hansen AK, Zmudzinska A, Smetana A, Buffam J, Solodovnikov A (2020a) Are subcortical rove beetles truly Holarctic? An integrative taxonomic revision of north temperate *Quedionuchus* (Coleoptera: Staphylinidae: Staphylininae). Organisms Diversity & Evolution 20: 77–116. https://doi.org/10.1007/s13127-019-00422-2

Brunke AJ, Zmudzinska A, Buffam J (2020b) An Integrative Taxonomic Review of the *Quedius* erythrogaster Mannerheim Species Group in North America (Coleoptera: Staphylinidae: *Quediini*). The Coleopterists Bulletin 74(4): 897–921. https://doi.org/10.1649/0010-065X-74.4.897

Caterino MS, Chatzimanolis S, Richmond MP (2015) On the origins of the insect fauna of California's Channel Islands: a comparative phylogeographic study of island beetles. Monographs of the Western North American Naturalist 7(1): 276–296. https://doi.org/10.3398/042.007.0121

Chatzimanolis S, Caterino MS (2007) Toward a better understanding of the "transverse range break": lineage diversification in southern California. Evolution 61(9): 2127–2141. https://doi.org/10.1111/j.1558-5646.2007.00186.x

Conte CA, Segura DF, Milla FH, Augustinos A, Cladera JL, Bourtzis K, Lanzavecchia SB (2019) *Wolbachia* infection in Argentinean populations of *Anastrepha fraterculus* sp1: preliminary evidence of sex ratio distortion by one of two strains. BMC Microbiology 19(1): 289. https://doi.org/10.1186/s12866-019-1652-y

Dobson SL, Bourtzis K, Braig HR, Jones BF, Zhou WG, Rousset F, O'Neill SL (1999) *Wolbachia* infections are distributed throughout insect somatic and germ line tissues. Insect Biochemistry and Molecular Biology 29: 153–160. https://doi.org/10.1016/S0965-1748(98)00119-2

Downie DA, Gullan PJ (2004) Phylogenetic analysis of mealybugs (Hemiptera: Coccoidea: Pseudococcidae) based on DNA sequences from three nuclear genes, and a review of the higher classification. Systematic Entomology 29: 238–259. https://doi.org/10.1111/j.0307-6970.2004.00241.x

Egorov AV, Zernov AS, Onipchenko VG (2020) North-Western Caucasus. In: Noroozi J (Ed.) Plant Biogeography and Vegetation of High Mountains of Central and South-West Asia. Plant and Vegetation, vol 17. Springer, Cham, 315–360. https://doi.org/10.1007/978-3-030-45212-4_9

Eppelsheim E (1889) Neue Staphylinen aus den Kaukasusländern, besonders aus Circassien.Wiener. Entomologische Zeitung 8: 11–22. https://doi.org/10.5962/bhl.part.20020

Ferree PM, Frydman HM, Li JM, Cao J, Wieschaus E, Sullivan W (2005) *Wolbachia* utilizes host microtubules and dynein for anterior localization in the Drosophila oocyte. Plos Pathogens 1: 111–124. https://doi.org/10.1371/journal.ppat.0010014

Fossen EI, Ekrem T, Nilsson AN, Bergsten J (2016) Species delimitation in northern European water scavenger beetles of the genus *Hydrobius* (Coleoptera, Hydrophilidae). ZooKeys 564: 71–120. https://doi.org/10.3897/zookeys.564.6558

Frydman HM, Li JM, Robson DN, Wieschaus E (2006) Somatic stem cell niche tropism in *Wolbachia*. Nature 441: 509–512. https://doi.org/10.1038/nature04756

Gebiola M, Gómez-Zurita J, Monti MM, Navone P, Bernardo U (2012) Integration of molecular, ecological, morphological and endosymbiont data for species delimitation within the *Pnigalio soemius* complex (Hymenoptera: Eulophidae). Molecular Ecology 21(5): 1190–1208. https://doi.org/10.1111/j.1365-294X.2011.05428.x

Guindon S, Gascuel O (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52: 696–704. https://doi.org/10.1080/10635150390235520

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Hansen AK, Brunke A, Simonsen T, Solodovnikov A (2022) Revision of *Quedius* sensu stricto (Coleoptera: Staphylinidae). Acta Entomologica 62(1): 225–299. https://doi.org/10.37520/aemnp.2022.017

Hansen AK, Jenkins Shaw J (2023) High altitude morphotype of the widespread *Lobrathium multipunctum* (Gravenhorst, 1802) (Coleoptera, Staphylinidae, Paederinae) revealed by DNAbarcoding. Contributions to Entomology 73(1): 1–11. https://doi.org/10.3897/contrib.entomol.73.e102511

Hebert PD, Cywinska A, Ball SL (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society B, Biological Sciences 270: 313–321. https://doi.org/10.1098/rspb.2002.2218

Hertig M (1936) The rickettsia, *Wolbachia pipientis* (gen. et sp.n.) and associated inclusions of the mosquito, *Culex pipiens*. Parasitology 28: 453–486. https://doi.org/10.1017/S0031182000022666

Hertig M, Wolbach SB (1924) Studies on Rickettsia-like micro-organisms in insects. Journal of Medical Research 44: 329–374.

Hilgenboecker K, Hammerstein P, Schlattmann P, Telschow A, Werren JH (2008) How many species are infected with *Wolbachia*? - a statistical analysis of current data. FEMS Microbiology Letters 281: 215–220. https://doi.org/10.1111/j.1574-6968.2008.01110.x

Hoffmann AA, Turelli M (1997) Cytoplasmatic incompatibility in insects. In: O'Neill SL, Hoffmann AA, Werren JH (Eds) Influential passengers: Inherited microorganisms and Arthropod Reproduction, 42–80.

Hosokawa T, Koga R, Kikuchi Y, Meng XY, Fukatsu T (2010) *Wolbachia* as a bacteriocyte associated nutritional mutualist. PNAS 107: 769–774. https://doi.org/10.1073/pnas.0911476107

Hurst GDD, Jiggins FM (2005) Problems with mitochondrial DNA as a marker in population, phylogeographic and phylogenetic studies: the effects of inherited symbionts. Proceedings of the Royal Society B, Biological Sciences 272: 1525–1534. https://doi.org/10.1098/rspb.2005.3056

Jiggins FM (2003) Male-killing *Wolbachia* and mitochondrial DNA: selective sweeps, hybrid introgression and parasite population dynamics. Genetics 164: 5–12. https://doi.org/10.1093/genetics/164.1.5

Jimenez NE, Gerdtzen ZP, Olivera-Nappa Á, Salgado JC, Conca C (2019) A systems biology approach for studying *Wolbachia* metabolism reveals points of interaction with its host in the context of arboviral infection. PLoS Neglected Tropical Diseases 13(8): e0007678. https://doi.org/10.1371/journal.pntd.0007678

Kirik H, Tummeleht L, Lilja T, Kurina O (2020) Novel Mitochondrial DNA Lineage Found among *Ochlerotatus communis* (De Geer, 1776) of the Nordic-Baltic Region. Insects 11: 397. https://doi.org/10.3390/insects11060397

Kodandaramaiah U, Simonsen TJ, Bromilow S, Wahlberg N, Sperling F (2013) Deceptive single-locus taxonomy and phylogeography: *Wolbachia*-associated divergence in mitochondrial DNA is not reflected in morphology and nuclear markers in a butterfly species. Ecology and Evolution 3(16): 5167–5176. https://doi.org/10.1002/ece3.886

Krever V, Zazanashvili N, Jungius H, Williams L, Petelin D [Eds] (2001) Biodiversity of the Caucasus ecoregion. An analysis of biodiversity and current threats and initial investment Portfolio. Signar 5, Moscow.

Kriesner P, Hoffmann AA, Lee SF, Turelli M, Weeks AR (2013) Rapid sequential spread of two *Wolbachia* variants in *Drosophila simulans*. PLoS Pathogens 9: e1003607. https://doi.org/10.1371/journal.ppat.1003607

Laven H (1959) Speciation by cytoplasmic isolation in the *Culex pipiens* complex. Cold Spring Harbor Symposia on Quantitative Biology 24: 166–173. https://doi.org/10.1101/SQB.1959.024.01.017

Lee J, Lee JS, Ahn KJ (2020) Reappraisal of Korean *Oxyporus* Fabricius (Coleoptera: Staphylinidae: Oxyporinae), including a new species based on morphological and molecular characters. Journal of Asia-Pacific Entomology 23(3): 680–688. https://doi.org/10.1016/j.aspen.2020.04.012

Leigh JW, Bryant D (2015) POPART: Full-feature software for haplotype network construction. Methods in Ecology and Evolution 6(9): 1110–1116. https://doi.org/10.1111/2041-210X.12410

Lo N, Paraskevopoulos C, Bourtzis K, O'Neill SL, Werren JH, Bordenstein SR, Bandi C (2007) Taxonomic status of the intracellular bacterium *Wolbachia pipientis*. International Journal of Systematic and Evolutionary Microbiology 57: 654–657. https://doi.org/10.1099/ijs.0.64515-0

Lorenzo-Carballa MO, Torres-Cambas Y, Heaton K, Hurst GDD, Charlat S, Sherratt TN, Van Gossum H, Cordero-Rivera A, Beatty CD (2019) Widespread *Wolbachia* infection in an insular radiation of damselflies (Odonata, Coenagrionidae). Scientific Reports 9: 11933. https://doi.org/10.1038/s41598-019-47954-3

Lukhtanov VA (2019) Species delimitation and analysis of cryptic species diversity in the XXI century. Entomological Review 99(4): 463–472. https://doi.org/10.1134/S0013873819040055

Manoj RRS, Latrofa MS, Epis S, Otranto D (2021) *Wolbachia*: endosymbiont of onchocercid nematodes and their vectors. Parasites Vectors 14: 245. https://doi.org/10.1186/s13071-021-04742-1

Martinsson S, Rhodén C, Erséus C (2017) Barcoding gap, but no support for cryptic speciation in the earthworm *Aporrectodea longa* (Clitellata: Lumbricidae). Mitochondrial DNA Part A 28(2): 147–155. https://doi.org/10.3109/19401736.2015.1115487

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. [Paper presentation]. Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA. November), 1–8. https://doi.org/10.1109/GCE.2010.5676129

Mittermeier RA, Gill PR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB (2005) Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. Conservation International, Washington DC.

Muñoz-Tobar SI, Caterino MS (2020) Mountains as islands: Species delimitation and evolutionary history of the ant-loving beetle genus *Panabachia* (Coleoptera, Staphylinidae) from the Northern Andes. Insects 11: 64. https://doi.org/10.3390/insects11010064

Nugapola NWN, De Silva WAP, Karunaratne SHP (2017) Distribution and phylogeny of *Wolbachia* strains in wild mosquito populations in Sri Lanka. Parasites & Vectors 10: 230. https://doi.org/10.1186/s13071-017-2174-9

Okhrimenko NV (1992) Leaf beetles (Coleoptera, Chrysomelidae) North-Western Caucasus. Candidate's Dissertation in Biology. Institute of Evolutionary Morphology and Ecology of Animanimals, Russian Academy of Sciences, Moscow.

Plewa R, Sikora K, Gutowski JM, Jaworski T, Tarwacki G, Tkaczyk M, Rossa R, Hilszczański J, Magoga G, Kajtoch Ł (2018) Morphology, genetics and *Wolbachia* endosymbionts support distinctiveness of *Monochamus sartor sartor* and *M. s. urussovii* (Coleoptera: Cerambycidae). Arthropod Systematics & Phylogeny 76 (1): 123–135. https://doi.org/10.3897/asp.76.e31945

Rigaud T, Soutygrosset C, Raimond R, Mocquard JP, Juchault P (1991) Feminizing endocytobiosis in the terrestrial Crustacean *Armadillidium vulgare* latr. (Isopoda) - recent acquisition. Endocytobiosis and Cell Research 7: 259–273.

Ritter S, Michalski SG, Settele J, Wiemers M, Fric ZF, Sielezniew M, Šašić M, Rozier Y, Durka W (2013) *Wolbachia* infections mimic cryptic speciation in two parasitic butterfly species, *Phengaris teleius* and *P. nausithous* (Lepidoptera: Lycaenidae). PLoS ONE 8(11): e78107. https://doi.org/10.1371/journal.pone.0078107

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rousset F, Bouchon D, Pintureau B, Juchault P, Solignac M (1992) *Wolbachia* endosymbionts responsible for various alterations of sexuality in arthropods. Proceedings of the Royal Society B, Biological Sciences 250: 91–98. https://doi.org/10.1098/rspb.1992.0135

Roy V, Girondot M, Harry M (2015) The distribution of *Wolbachia* in *Cubitermes* (Termitidae, Termitinae) castes and colonies: A modelling approach. PLoS ONE 10(2): e0116070. https://doi.org/10.1371/journal.pone.0116070

Salnitska M, Solodovnikov A (2019) Rove beetles of the genus *Quedius* (Coleoptera, Staphylinidae) of Russia: a key to species and annotated catalogue. ZooKeys 847: 1–100. https://doi.org/10.3897/zookeys.847.34049

Salnitska M, Solodovnikov A (2021) DNA barcode sheds light on species boundaries in the common morphologically variable rove beetle *Quedius umbrinus*-complex that puzzled taxonomists for more than a century (Coleoptera, Staphylinidae). Systematics and Biodiversity 19: 859–874. https://doi.org/10.1080/14772000.2021.1943559

Schomann AM, Solodovnikov A (2017) Phylogenetic placement of the austral rove beetle genus *Hyperomma* triggers changes in classification of Paederinae (Coleoptera: Staphylinidae). Zoologica Scripta 46: 336–347. https://doi.org/10.1111/zsc.12209

Schuler H, Bertheau C, Egan SP, Feder JL, Riegler M, Schlick-Steiner BC, Steiner FM, Johannesen J, Kern P, Tuba K, Lakatos F, Köppler K, Arthofer W, Stauffer C (2013) Evidence for a recent horizontal transmission and spatial spread of *Wolbachia* from endemic *Rhagoletis cerasi* (Diptera: Tephritidae) to invasive *Rhagoletis cingulata* in Europe. Molecular Ecology 22: 4101–4111. https://doi.org/10.1111/mec.12362

Schuler H, Egan SP, Hood GR, Busbee RW, Driscoe AL, Ott JR (2018) Diversity and distribution of *Wolbachia* in relation to geography, host plant affiliation and life cycle of a heterogonic gall wasp. BMC Evolutionary Biology 18: 37. https://doi.org/10.1186/s12862-018-1151-z

Schuler H, Köppler K, Daxböck-Horvath S, Rasool B, Krumböck S, Schwarz D, Hoffmeister TS, Schlick-Steiner BC, Steiner FM (2016) The hitchhiker's guide to Europe: the infection dynamics of an ongoing *Wolbachia* invasion and mitochondrial selective sweep in *Rhagoletis cerasi*. Molecular Ecology 25: 1595–1609. https://doi.org/10.1111/mec.13571

Serbus LR, Casper-Lindley C, Landmann F, Sullivan W (2008) The genetics and cell biology of *Wolbachia*-host interactions. Annual Review of Genetics 42: 683–707. https://doi.org/10.1146/annurev.genet.41.110306.130354

Serri S, Frisch J, von Rintelen T (2016) Genetic variability of two ecomorphological forms of *Stenus* Latreille, 1797 in Iran, with notes on the infrageneric classification of the genus (Coleoptera, Staphylinidae, Steninae). ZooKeys 626: 67–86. https://doi.org/10.3897/zookeys.626.8155

Shaikevich E, Bogacheva A, Rakova V, Ganushkina L, Ilinsky Y (2019) *Wolbachia* symbionts in mosquitoes: Intra- and inter super group recombinations, horizontal transmission and evolution. Molecular Phylogenetics and Evolution 134: 24–34. https://doi.org/10.1016/j.ympev.2019.01.020

Shiffers EV (1953) Vegetation of the North Caucasus and Its Nature Forage Resources. USSR Academy of Sciences, Moscow–Leningrad. [in Russian]

Shoemaker DD, Katju V, Jaenike J (1999) *Wolbachia* and the evolution of reproductive isolation between *Drosophilla recens* and *Drosophila subquinaria*. Evolution 53: 1157–1164. https://doi.org/10.1111/j.1558-5646.1999.tb04529.x

Solodovnikov AY (1998) Fauna of Staphylinids (Coleoptera, Staphylinidae) of the Northwestern Caucasus. Subfamilies Staphylininae, Xantholininae, Paederinae, Steninae, and Oxyporinae. Entomological Review 78: 323–342.

Solodovnikov AY (2001) Revision of the little-known apterous Paederinae (Coleoptera: Staphylinidae) from "Circassia" (North-Western Caucasus), with description of *Lathrobium* (*Lobrathium*) *bettae* sp. n. Russian Entomological Journal 10(1): 1–11.

Solodovnikov AY (2004) Taxonomy and faunistics of some West Palearctic *Quedius* STEPHENS subgenus *Raphirus* STEPHENS (Coleoptera: Staphylinidae: Staphylininae). Koleopterologische Rundschau 74: 221–243.

Solodovnikov AY (2005) New and little-known species of *Quedius* from West Palaearctic (Coleoptera: Staphylinidae: Staphylininae). Zootaxa 902: 1–13. https://doi.org/10.11646/zootaxa.902.1.1

Song JH, Ahn KJ (2014) Species delimitation in the *Aleochara fucicola* species complex (Coleoptera: Staphylinidae: Aleocharinae) and its phylogenetic relationships. Zoologica Scripta 43: 629–640. https://doi.org/10.1111/zsc.12077

Sourassou NF, Hanna R, Breeuwer JAJ, Negloh K, de Moraes GJ, Sabelis MW (2014) The endosymbionts *Wolbachia* and *Cardinium* and their effects in three populations of the predatory mite *Neoseiulus paspalivorus*. Experimental and Applied Acarology 64: 207–221. https://doi.org/10.1007/s10493-014-9820-0

Stouthamer R, Breeuwer JAJ, Hurst GDD (1999) *Wolbachia pipientis*: microbial manipulator of arthropod reproduction. Annual Review of Microbiology 53: 71–102. https://doi.org/10.1146/annurev.micro.53.1.71

Sun XJ, Xiao JH, Cook J, Feng G, Huang DW (2011) Comparisons of host mitochondrial, nuclear and endosymbiont bacterial genes reveal cryptic fig wasp species and the effects of *Wolbachia* on host mtDNA evolution and diversity. BMC Evolutionary Biology 11: 86. https://doi.org/10.1186/1471-2148-11-86

Tamura K, Kumar S (2002) Evolutionary distance estimation under heterogeneous substitution pattern among lineages. Molecular Biology and Evolution 19: 1727–1736. https://doi.org/10.1093/oxfordjournals.molbev.a003995

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30: 2725–2729. https://doi.org/10.1093/molbev/mst197

Telschow A, Hammerstein P, Werren JH (2005) The effect of *Wolbachia* versus genetic incompatibilities on reinforcement and speciation. Evolution 59(8): 1607–1619. https://doi.org/10.1111/j.0014-3820.2005.tb01812.x

Tokareva AS, Konstantinov FV, Brunke AJ, Solodovnikov A (2021) DNA-barcode and endophallus morphology delimit congruent species in a systematic revision of the oxyporine rove beetles of Russia (Coleoptera: Staphylinidae: Oxyporinae). Contributions to Zoology 90: 344–407. https://doi.org/10.1163/18759866-bja10020

Von Beeren C, Maruyama M, Kronauer DJC (2016a) Community sampling and integrative taxonomy reveal new species and host specificity in the army ant-associated beetle genus *Tetradonia* (Coleoptera, Staphylinidae, Aleocharinae). PLoS ONE 11(11): e0165056. https://doi.org/10.1371/journal.pone.0165056

Von Beeren C, Maruyama M, Kronauer DJC (2016b) Cryptic diversity, high host specificity and reproductive synchronization in army ant-associated *Vatesus* beetles. Molecular Ecology 25: 990–1005. https://doi.org/10.1111/mec.13500

Wasala SK, Brown AMV, Kang J, Howe DK, Peetz AB, Zasada IA, Denver DR (2019) Variable abundance and distribution of *Wolbachia* and *Cardinium* endosymbionts in plant-parasitic nematode field populations. Frontiers in Microbiology 10: 964. https://doi.org/10.3389/fmicb.2019.00964

Werren JH (1997) Biology of *Wolbachia*. Annual Review of Entomology 42: 587–609. https://doi.org/10.1146/annurev.ento.42.1.587

Werren JH (1998) *Wolbachia* and speciation. In: Berlocher SH, Howerd D (Eds) Endless forms. Species and speciation, 245–260.

Werren JH, Baldo L, Clark ME (2008) *Wolbachia*: master manipulators of invertebrate biology. Nature Reviews Microbiology 6: 741–751. https://doi.org/10.1038/nrmicro1969

Werren JH, Windsor D, Guo LR (1995) Distribution of *Wolbachia* among neothropical arthropods. Proceedings of the Royal Society B, Biological Sciences 262: 197–204. https://doi.org/10.1098/rspb.1995.0196

Wild AL, Maddison DR (2008) Evaluating nuclear protein–coding genes for phylogenetic utility in beetles. Molecular Phylogenetics and Evolution 48: 877–891. https://doi.org/10.1016/j.ympev.2008.05.023

Yoo IS, Frank JH, Jung JK, Ahn KJ (2022) Integrative taxonomy of coastal *Cafius bistriatus* (Erichson) species complex (Coleoptera, Staphylinidae). ZooKeys 1100: 57–70. https://doi.org/10.3897/zookeys.1100.79435

Yoo IS, Lee JS, Ôhara M, Ahn KJ (2021) Three synonyms of the coastal *Phucobius* Sharp species (Coleoptera: Staphylinidae) are proposed based on morphological and molecular characters. Journal of Asia-Pacific Entomology 24(1): 320–328. https://doi.org/10.1016/j.aspen.2020.12.015

Zamotailov AS (1992) Fauna of ground beetles (Coleoptera, Carabidae) North-West Caucasus. Methodic manual. Krasnodar: KGAU.

Zamotajlov AS, Orlov VN, Nabozhenko MV, Okhrimenko NV, Khatschikov EA, Shapovalov MI, Shokhin IV (2010) Analysis of the ways of formation of the entomofaunistic complexes in the Northwest Caucasus based on the material on coleopterous insects (Coleoptera). Entomological Review 90(3): 333–371. https://doi.org/10.1134/S0013873810030048

Zug R, Hammerstein P (2015) Bad guys turned nice? A critical assessment of *Wolbachia* mutualisms in arthropod hosts. Biological Reviews 90: 89–111. https://doi.org/10.1111/brv.12098

Supplementary material 1

Suuplementary files in zip archive

Authors: Angesom Gebremeskel, Maria Salnitska, Valeria Krivosheeva, Alexey Solodovnikov

Data type: zip

Explanation note: **table S1.** Primers used in this study. **table S2.** All examined *Quedius obliqueseriatus* specimens. **table S3.** Genetic divergence of COI (*Quedius obliqueseriatus*) using uncorrected p-distance. **figure S1.** Distribution of the sequenced Wolbachia-free (green) and infected (yellow) individuals among the sequenced specimens of *Quedius obliqueseriatus* in the North-Western Caucasus. Dotted purple and orange lines indicate rough distribution area of the western and eastern clades, respectively. **QO- DNA** sequences for all markers used (in fasta files).

Link: https://doi.org/10.3897/alpento.7.111214.suppl1

Alpine Entomology 7 2023, 167–184 | DOI 10.3897/alpento.7.111147

Alpine Entomology

Annotated checklist of the Hydrophiloidea of Switzerland (Coleoptera)

Vivien Cosandey[1], Yannick Chittaro[2], Andreas Sanchez[2]

1 *Muséum d'histoire naturelle, Malagnou 1, CH-1208 Genève, Switzerland*
2 *info fauna, Avenue Bellevaux 51, CH-2000 Neuchâtel, Switzerland*

https://zoobank.org/03D26E52-650F-45B2-B64B-782816BD911C

Corresponding author: Vivien Cosandey (vivien.cosandey@bluewin.ch)

Academic editor: C. Germann ♦ **Received** 14 August 2023 ♦ **Accepted** 20 September 2023 ♦ **Published** 6 October 2023

Abstract

Access to large, high-quality databases is one of the major needs in biodiversity studies. Faunistical data are essential but are often scarce and have to be compiled from various sources. On the basis of more than 30,000 occurrences obtained from specimens held in museum and private collections, as well as from literature data, we present the first updated checklist of the Swiss species of Hydrophiloidea (Georissidae, Helophoridae, Hydrochidae, Hydrophilidae, and Spercheidae) since 1900. In total, 105 species are retained as part of the Swiss fauna, while 16 species, which were recorded from Switzerland in the past, are excluded from this list, either due to insufficient documentation or because their records were based on misidentified material. *Cercyon alpinus*, *Cercyon castaneipennis*, *Cercyon tatricus*, *Helophorus montenegrinus*, *Megasternum immaculatum*, *Pachysternum capense*, and *Paracymus scutellaris* are recorded for the first time in Switzerland. This work is a further step towards the comprehension of the whole Swiss beetle fauna.

Key Words

distribution, faunistics, Insecta, new country records, species list, water scavenger beetles

Introduction

Worldwide, the super-family Hydrophiloidea currently includes the following families: Epimetopidae, Georissidae, Helophoridae, Hydrochidae, Hydrophilidae, Spercheidae, and Syntelidae (Bouchard et al. 2011), while Histeridae and Sphaeritidae were recently removed and placed in the super-family Histeroidea (Zhou et al. 2020). The super-family Hydrophiloidea comprises more than 3,300 species (Hansen 1999; Short and Fikáček 2011), most of which belong to Hydrophilidae (2,800 species). Modern molecular methods have shown that the small and moderately diverse families (Epimetopidae, Georissidae, Helophoridae, Hydrochidae, and Spercheidae), around 500 species in total, represent basal lineage of the Hydrophiloidea (Short and Fikáček 2013).

Hydrophiloidea are mostly associated with freshwater environments (Jäch and Balke 2008), but exceptions are found in each family, except for Hydrochidae, which are all strictly aquatic (Jäch 1998) and Georissidae, which are all typical shore beetles (Jäch and Balke 2008). Adults of Helophoridae are mostly aquatic with a few strictly terrestrial species (Jäch 1998), feeding on roots and decaying plant material (Hansen 1987). The larvae of Helophoridae are not aquatic but live in soil or vegetation (Angus 1992). Over the course of their evolutionary history, the Hydrophilidae have undergone numerous transitions from aquatic to semi-aquatic and to terrestrial environments (Bloom et al. 2014). Today, they exhibit a wide ecological range, with species specialized in a variety of particular aquatic environments such as waterfalls or subterranean streams (Short and Fikáček 2013) but also terrestrial environments with many coprophagous species, and even myrmecophilous and flower visiting species (Broun 1886; Hudson 1934; Spangler 1962). Many are generalists, feeding on decaying plant material and feces. Adults and larvae live in the same habitats, but the former are detritivorous or feed on algae, while the latter are mostly recorded as predaceous. The ecological diversity of Hydrophiloidea is also apparent in their wide range of size, from ca. 1 to over 50 mm.

All the Hydrophiloidea families are present in Switzerland, with the exception of Epimetopidae. The Swiss Hydrophiloidea fauna has not been the subject of a synthetic work since Stierlin (1900). The actual study aims to present an updated and annotated checklist of the species present in Switzerland. It is based on a review of the Swiss museum and private collections, as well as the literature and data gathered by naturalists. Resident species are thus distinguished from species mistakenly mentioned for Switzerland or insufficiently documented.

Material and methods

In order to present a complete list of the Swiss fauna, based on all existing information, we performed an exhaustive examination of the relevant material present in Swiss museum collections, as was recently done for other beetle groups (e.g., Chittaro et al. 2021; Sanchez and Chittaro 2022). 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);
HGSB	Musée de l'Hospice du Grand-Saint-Bernard (Jean-Pierre Voutaz);
KMLI	Archäologie und Museum Baselland, Liestal (Marc Limat);
LEBA	Laboratoire d'écologie et de biologie aquatique, Université de Genève (Emmanuel Castella);
MHNF	Musée d'histoire naturelle de Fribourg (Sophie Giriens);
MHNG	Muséum d'histoire naturelle, 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 (Bärbel Koch);
MZL	Musée cantonal de zoologie, Lausanne (Anne Freitag);
MZA	Museum zu Allerheiligen, Schaffhausen (Urs Weibel);
NMAA	Naturama, Aarau (Christian Sprecher);
NMB	Naturhistorisches Museum Basel (Matthias Borer);
NMBE	Naturhistorisches Museum Bern (Hannes Baur);
NMLU	Natur-Museum Luzern (Marco Bernasconi);
NMO	Naturmuseum Olten (Pia Geiger);
NMSG	Naturmuseum St. Gallen (Karin Urfer);
NMSO	Naturmuseum Solothurn (Marc Neumann);
NMTG	Naturmuseum Thurgau, Frauenfeld (Barbara Richner);
NMWI	Naturmuseum Winterthur (Sabrina Schnurrenberger).

We also cited data gathered from three museums outside Switzerland:

MAMU	Manchester Museum, Great Britain;
MCB	Museo civico di Bolzano, Italy;
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. They are classified in alphabetical order. The municipality and the abbreviated canton of residence are indicated in parentheses: Marc Bastardot (Colombier VD), Emil Birnstiel (Zurich ZH), Hansjörg Brägger (Bischofszell TG), Stève Breitenmoser (Givrins VD), Berndt Eismann (Kreuzlingen TG), Michael Gilgen (Bangerten bei Dieterswil BE), Roman Graf (Horw LU), René Hoess (Bern BE), Barbara Huber (Thusis GR), Lea Kamber (Bienne BE), Christian Monnerat (Neuchâtel NE), Alexander Szallies (Wädenswil ZH), Arnaud Vallat (La Chaux-de-Fonds NE) and André Wagner (Le Sentier VD).

All available data from the literature relevant for Switzerland were also considered. The references from these publications are included in the bibliography if they are specifically cited in the text. Publications consulted but not cited in the text are not mentioned.

The nomenclature and systematics followed were those of the "Catalogue of Palaearctic Coleoptera" (Fikáček 2015; Fikáček and Przewoźny 2015; Fikáček et al. 2015a), with the following exceptions:

- Once considered a synonym of *Megasternum concinnum* (Marsham, 1802), *Megasternum immaculatum* (Stephens, 1829) (Fig. 1E) was resurrected by Forster et al. (2014), based on unpublished notes by Hammond P. M., although this case requires taxonomic revision (Fikáček et al. 2015b). *Megasternum immaculatum* has been recorded in Great Britain (Forster et al. 2014), Russia (Ryndevich 2017), France (Salamé 2023), Sweden (Fägerström 2019), Bulgaria (Greń and Lubecki 2017), Poland and Germany (Lillig 2022; Mainda 2022). In Switzerland, both species are present in every biogeographical region (OFEV 2022). We have not dissected all Swiss specimens and most of the occurrences refer to *M. concinnum,* although *M. immaculatum* appears to be more common. A revision of all Swiss specimens of *Megasternum* spp. is necessary but should be performed once the taxonomy of this group is clarified.
- *Hydrobius rottenbergii* Gerhardt, 1872 and *Hydrobius subrotundus* Stephens, 1829 were considered morphological variations of *Hydrobius fuscipes* (Linnaeus, 1758) until Fossen et al. (2016) considered them as valid species. In the present study, we chose to treat all specimens of this group as "*H. fuscipes*", because the morphological differentiation of the three species is ambiguous outside Scandinavia and because many undescribed cryptic species of *Hydrobius* could occur in Europe (Fossen et al. 2016).

The specimens were identified using the following publications (in alphabetical order): Angus (1992), Fikáček (2006), Forster et al. (2014), Freude (2011), Gentili (1975), Hansen (1987), Pirisinu (1981), Queney and Prévost (2021) and Vorst (2009).

When not otherwise specified, general information on species' distributions is taken from the "Catalogue of Palaearctic Coleoptera" (Fikáček 2015; Fikáček and Przewoźny 2015; Fikáček et al. 2015a).

We have also used the relevant literature concerning the countries and regions adjacent to Switzerland, such as Bameul and Queney (2014) for France and regionally Callot (2001, 2018) for Alsace; Köhler and Klausnitzer (1998) for Germany; Pirisinu (1981) and Rocchi (2002) for Italy as well as the regional treatment of Brandstetter and Kapp (1998) for Vorarlberg (Austria) and Liechtenstein; and Kahlen and Hellrigl (1996) for South Tyrol / Alto Adige.

The list of the main synonyms of each taxon is provided in the "Catalogue of Palaearctic Coleoptera" (Löbl and Löbl 2015) and is, therefore, not reported here.

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 as belonging to the Swiss fauna. 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 30 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 in the checklist. When not otherwise specified, all examined material was identified or reviewed by the first author.

There are various genera and species groups in Hydrophiloidea (e.g., *Laccobius* spp. and *Chaetarthria* spp.) for which the most reliable character is the male genitalia. 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, determinator (in the case that the determinator was not one of the authors), collection and official acronym of the institution where the specimen 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 MHNG, 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 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.

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. = determinator, 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, JU = Jura, LU = Lucerne, NE = Neuchâtel, NW = Nidwalden, SG = St. Gallen, SH = Schaffhausen, SZ = Schwyz, TI = Ticino, TG = Thurgau, UR = Uri, VD = Vaud, VS = Valais, ZH = Zurich.

Results

Swiss fauna Hydrophiloidea list

We considered that the 105 species 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. We also considered here several allochthonous species, originating from other regions of the world (sometimes introduced), which maintain (or have maintained) continuous populations in Switzerland during several years.

On the other hand, the 16 species listed in square brackets "[ ]" should not be considered as belonging to the Swiss fauna, until new data can 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 to be doubtful. Other species may eventually be found in the Swiss territory, but currently available data are not sufficient to confirm their establishment in Switzerland.

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 represents 30,434 occurrences within the concerned families.

Updated distribution maps of these species are available on the info fauna cartographic server (https://lepus.infofauna.ch/carto/). All the valid data are also available on http://www.GBIF.org (https://doi.org/10.15468/dl.bw5mfe).

Checklist of the Swiss species

GEORISSIDAE

***Georissus* (*Georissus*) *crenulatus* (P. Rossi, 1794)**
***Georissus* (*Georissus*) *substriatus* Heer, 1841; C1**
[*Georissus* (*Neogeorissus*) *costatus* Laporte, 1840]; **C2**
***Georissus* (*Neogeorissus*) *laesicollis* Germar, 1832**

HELOPHORIDAE

***Helophorus* (*Empleurus*) *nubilus* Fabricius, 1777**
[*Helophorus* (*Empleurus*) *rufipes* (Bosc, 1791)]; **C3**
***Helophorus* (*Empleurus*) *schmidti* A. Villa & G.B. Villa, 1838**
***Helophorus* (*Helophorus*) *aequalis* Thomson, 1868; C4**
***Helophorus* (*Helophorus*) *aquaticus* (Linnaeus, 1758); C4**
***Helophorus* (*Helophorus*) *grandis* Illiger, 1798**
***Helophorus* (*Kyphohelophorus*) *tuberculatus* Gyllenhal, 1808; C5**
***Helophorus* (*Rhopalohelophorus*) *arvernicus* Mulsant, 1846**
***Helophorus* (*Rhopalohelophorus*) *asperatus* Rey, 1885; C6**
***Helophorus* (*Rhopalohelophorus*) *brevipalpis* Bedel, 1881**
[*Helophorus* (*Rhopalohelophorus*) *croaticus* Kuwert, 1886]; **C7**
***Helophorus* (*Rhopalohelophorus*) *dorsalis* (Marsham, 1802); C8**
***Helophorus* (*Rhopalohelophorus*) *fauveli* Ganglbauer, 1901; C9**
***Helophorus* (*Rhopalohelophorus*) *flavipes* Fabricius, 1792**
***Helophorus* (*Rhopalohelophorus*) *glacialis* A. Villa & G.B. Villa, 1833**
***Helophorus* (*Rhopalohelophorus*) *granularis* (Linnaeus, 1760)**
***Helophorus* (*Rhopalohelophorus*) *griseus* Herbst, 1793**
[*Helophorus* (*Rhopalohelophorus*) *longitarsis* Wollaston, 1864]; **C10**
***Helophorus* (*Rhopalohelophorus*) *minutus* Fabricius, 1775; C11**
***Helophorus* (*Rhopalohelophorus*) *montenegrinus* Kuwert, 1885; C12**
[*Helophorus* (*Rhopalohelophorus*) *nanus* Sturm, 1836]; **C13**
***Helophorus* (*Rhopalohelophorus*) *nivalis* Giraud, 1852**
***Helophorus* (*Rhopalohelophorus*) *obscurus* Mulsant, 1844**
***Helophorus* (*Rhopalohelophorus*) *pumilio* Erichson, 1837**
***Helophorus* (*Rhopalohelophorus*) *strigifrons* Thomson, 1868; C14**

HYDROCHIDAE

***Hydrochus angustatus angustatus* Germar, 1824; C15**
[*Hydrochus brevis* (Herbst, 1793)]; **C16**
***Hydrochus crenatus* (Fabricius, 1792)**
***Hydrochus elongatus* (Schaller, 1783)**
***Hydrochus ignicollis* Motschulsky, 1860**

HYDROPHILIDAE
ACIDOCERINAE Zaitzev, 1908

***Helochares* (*Helochares*) *lividus* (Forster, 1771)**
***Helochares* (*Helochares*) *obscurus* (O.F. Müller, 1776)**
***Helochares* (*Helochares*) *punctatus* Sharp, 1869**

CHAETARTHRIINAE Bedel, 1881
Anacaenini M. Hansen, 1991

***Anacaena bipustulata* (Marsham, 1802); C17**
***Anacaena globulus* (Paykull, 1798)**
***Anacaena limbata* (Fabricius, 1792)**
***Anacaena lohsei* Berge Henegouwen & Hebauer, 1989**
***Anacaena lutescens* (Stephens, 1829)**
***Crenitis* (*Crenitis*) *punctatostriata* (Letzner, 1840)**

Chaetarthriini Bedel, 1881

***Chaetarthria seminulum* (Herbst, 1797)**
***Chaetarthria similis* Wollaston, 1864**
***Chaetarthria simillima* Vorst & Cuppen, 2003**

ENOCHRINAE Short & Fikáček, 2013

***Cymbiodyta marginella* (Fabricius, 1792); C18**

Enochrus (_Enochrus_) _melanocephalus_ (Olivier, 1793)
Enochrus (_Lumetus_) _fuscipennis_ (Thomson, 1884)
Enochrus (_Lumetus_) _ochropterus_ (Marsham, 1802)
Enochrus (_Lumetus_) _quadripunctatus_ (Herbst, 1797)
[_Enochrus_ (_Lumetus_) _segmentinotatus_ (Kuwert, 1888)]; **C19**
Enochrus (_Lumetus_) _testaceus_ (Fabricius, 1801)
Enochrus (_Methydrus_) _affinis_ (Thunberg, 1794)
Enochrus (_Methydrus_) _coarctatus_ (Gredler, 1863)
Enochrus (_Methydrus_) _nigritus_ (Sharp, 1873)

Hydrophilinae Latreille, 1802

Berosini Mulsant, 1844

Berosus (_Berosus_) _affinis_ Brullé, 1835; C20
Berosus (_Berosus_) _luridus_ (Linnaeus, 1760)
Berosus (_Berosus_) _signaticollis_ (Charpentier, 1825)
Berosus (_Enoplurus_) _frontifoveatus_ Kuwert, 1888; C21
[_Berosus_ (_Enoplurus_) _guttalis_ Rey, 1883]; **C22**
[_Berosus_ (_Enoplurus_) _spinosus_ (Steven, 1808)]; **C23**

Hydrobiusini Mulsant, 1844

Hydrobius fuscipes (Linnaeus, 1758)
[_Limnoxenus niger_ (Gmelin, 1790)]; **C24**

Hydrophilini Latreille, 1802

Hydrochara caraboides (Linnaeus, 1758)
[_Hydrochara flavipes_ (Steven, 1808)]; **C25**
Hydrophilus (_Hydrophilus_) _aterrimus_ Eschscholtz, 1822; C26
Hydrophilus (_Hydrophilus_) _piceus_ (Linnaeus, 1758)

Laccobiini Houlbert, 1922

Laccobius (_Dimorpholaccobius_) _albescens_ (Rottenberg, 1874)
[_Laccobius_ (_Dimorpholaccobius_) _atrocephalus atrocephalus_ Reitter, 1872]; **C27**
Laccobius (_Dimorpholaccobius_) _bipunctatus_ (Fabricius, 1775)
Laccobius (_Dimorpholaccobius_) _neapolitanus_ Rottenberg, 1874; C28
Laccobius (_Dimorpholaccobius_) _obscuratus obscuratus_ Rottenberg, 1874
Laccobius (_Dimorpholaccobius_) _sinuatus sinuatus_ Motschulsky, 1849
Laccobius (_Dimorpholaccobius_) _striatulus_ (Fabricius, 1801)
[_Laccobius_ (_Hydroxenus_) _femoralis mulsanti_ Zaitzev, 1908]; **C29**
Laccobius (_Laccobius_) _colon_ (Stephens, 1829); C30
Laccobius (_Laccobius_) _minutus_ (Linnaeus, 1758)
Laccobius (_Microlaccobius_) _alternus_ Motschulsky, 1855
Laccobius (_Microlaccobius_) _gracilis gracilis_ Motschulsky, 1855; C31
Laccobius (_Microlaccobius_) _thermarius thermarius_ Tournier, 1878; C32
[_Paracymus aeneus_ (Germar, 1824)]; **C33**
Paracymus scutellaris (Rosenhauer, 1856); C34

Sphaeridiinae Latreille, 1802

Coelostomatini L. Heyden, 1891

Coelostoma (_Coelostoma_) _hispanicum_ (Küster, 1848); C35
Coelostoma (_Coelostoma_) _orbiculare_ (Fabricius, 1775)
Dactylosternum abdominale (Fabricius, 1792); C36

Megasternini Mulsant, 1844

Cercyon (_Cercyon_) _alpinus_ Vogt, 1969; C37
Cercyon (_Cercyon_) _bifenestratus_ Küster, 1851; C38
Cercyon (_Cercyon_) _castaneipennis_ Vorst, 2009; C39
Cercyon (_Cercyon_) _convexiusculus_ Stephens, 1829
Cercyon (_Cercyon_) _granarius_ Erichson, 1837; C40
Cercyon (_Cercyon_) _haemorrhoidalis_ (Fabricius, 1775)
Cercyon (_Cercyon_) _impressus_ (Sturm, 1807)
Cercyon (_Cercyon_) _lateralis_ (Marsham, 1802)
[_Cercyon_ (_Cercyon_) _littoralis_ (Gyllenhal, 1808)]; **C41**
Cercyon (_Cercyon_) _marinus_ Thomson, 1853
Cercyon (_Cercyon_) _melanocephalus_ (Linnaeus, 1758)
Cercyon (_Cercyon_) _nigriceps_ (Marsham, 1802)
Cercyon (_Cercyon_) _obsoletus_ (Gyllenhal, 1808)
Cercyon (_Cercyon_) _pygmaeus_ (Illiger, 1801)
Cercyon (_Cercyon_) _quisquilius_ (Linnaeus, 1760)
Cercyon (_Cercyon_) _sternalis_ Sharp, 1918
Cercyon (_Cercyon_) _tatricus_ Endrödy-Younga, 1967; C42
Cercyon (_Cercyon_) _terminatus_ (Marsham, 1802)
[_Cercyon_ (_Cercyon_) _tristis_ (Illiger, 1801)]; **C43**
Cercyon (_Cercyon_) _unipunctatus_ (Linnaeus, 1758)
Cercyon (_Dicyrtocercyon_) _ustulatus_ (Preyssler, 1790)
Cercyon (_Paracercyon_) _analis_ (Paykull, 1798)
Cercyon (_Paracycreon_) _laminatus_ Sharp, 1873
Cryptopleurum crenatum (Kugelann, 1794)
Cryptopleurum minutum (Fabricius, 1775)
Cryptopleurum subtile Sharp, 1884
Megasternum concinnum (Marsham, 1802)
Megasternum immaculatum (Stephens, 1829)
Pachysternum capense (Mulsant, 1844); C44

Sphaeridiini Latreille, 1802

Sphaeridium bipustulatum Fabricius, 1781
Sphaeridium lunatum Fabricius, 1792
Sphaeridium marginatum Fabricius, 1787
Sphaeridium scarabaeoides (Linnaeus, 1758)
Sphaeridium substriatum Faldermann, 1838; C45

SPERCHEIDAE

Spercheus emarginatus (Schaller, 1783); C46

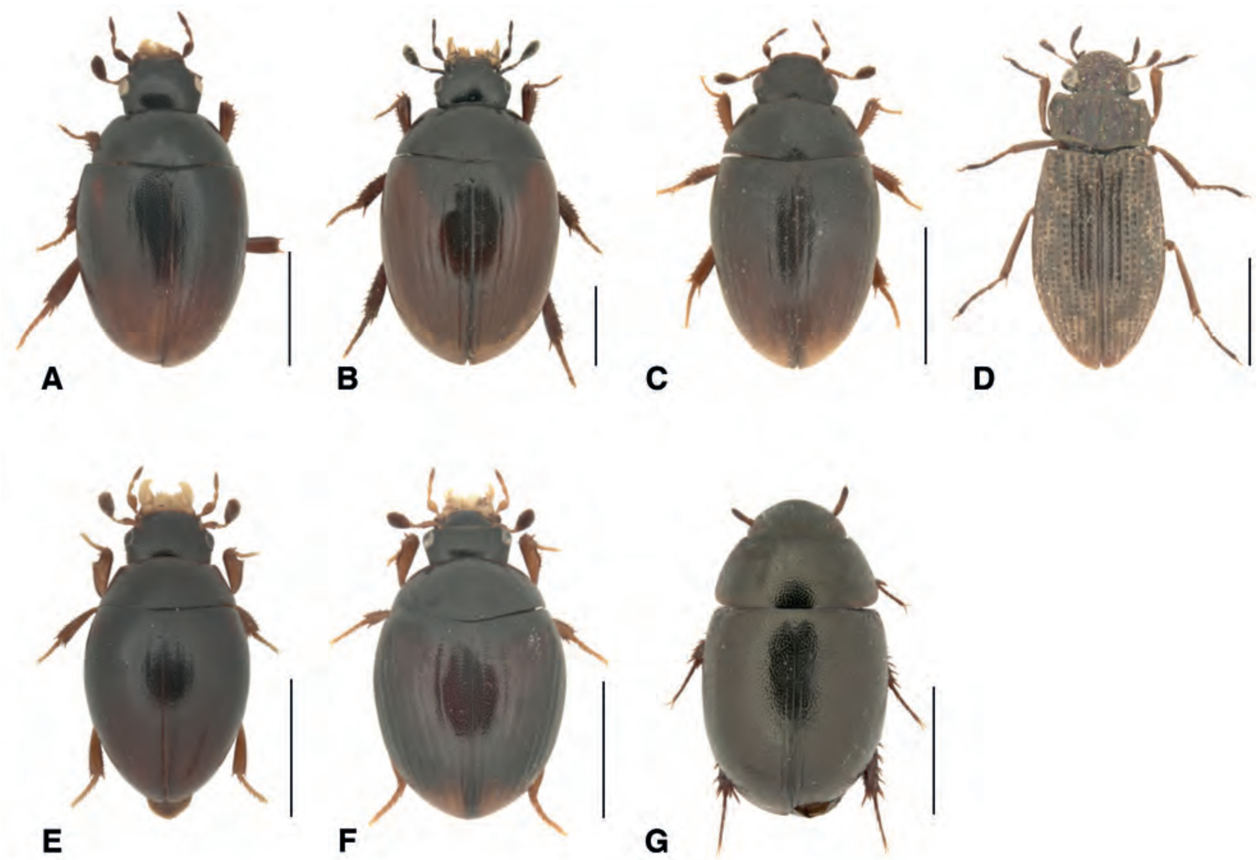


Figure 1. Habitus of the seven species mentioned for the first time in Switzerland. **A.** *Cercyon alpinus*; **B.** *Cercyon castaneipennis*; **C.** *Cercyon tatricus*; **D.** *Helophorus montenegrinus*; **E.** *Megasternum immaculatum*; **F.** *Pachysternum capense*; **G.** *Paracymus scutellaris*. Scale bars: 1 mm. (Photos V. Cosandey).

Commented species

C1) *Georissus* (*Georissus*) *substriatus* Heer, 1841

Examined material. [3)]1 ex., Troinex, leg. Anonymous, MHNG; 4 ex., Büren a. A. [Büren an der Aare], VI.1887, VII.1888, coll. Rätzer A., det. Huber C., NMBE; 1 ex., Chur, VIII.1924, leg. Jörger J. B., det. Besuchet C., NMB; 11 ex., Suisse, Grisons, Untervaz, 11.IX.1924, leg. and coll. Jörger J. B., det. Besuchet C., NMB; 1 ex., Tic., Castione, 5.VII.1943, leg. and coll. Lautner J., MHNG; 1 ex., Locarno, VII.1947, leg. and coll. Linder A., det. Besuchet C., ETH; 1 ex., Rabius, VIII.1953, leg. and coll. Linder A., det. Besuchet C., ETH; 2 ex., Suisse, Berne, Aarberg, VI.1954, leg. and coll. Linder A., det. Besuchet C., ETH, MHNG; 2 ex., Heitenried, VI.1963, leg. and coll. Linder A., det. Besuchet C., ETH; 1 ex., Suisse, Genève, Veyrier, crue de l'Arve, 27.IX.1968, leg. Besuchet C., MHNG; 23 ex., Loderio, 13.VIII.1974, leg. and coll. Scherler P., NMBE; 1 ex., Suisse, Valais, Finges, au bord Rhône, 31.VII.1979, leg. Besuchet C., MHNG.

Published data. [1)]Genf by Chevrier F. (Heer 1841); [1)]Peney bei Genf by Tournier H. (Stierlin and Gautard 1867); Büren by Rätzer A. (Rätzer 1888); Disentis [Rabius] by Linder A. and Untervaz by Jörger J. B. (Linder 1967).

Comment. *Georissus* individuals are rarely collected, probably due to their small size and cryptic habitus. In addition, they have high ecological requirements (Hebauer and Klausnitzer 1998) and are restricted to natural, preserved wetland habitats. The presence of *G. substriatus* in Switzerland is attested by several specimens in collections. However, it has not been observed in the last 40 years. This species, mainly found in southern Europe, should be sought specifically in Switzerland.

C2) [*Georissus* (*Neogeorissus*) *costatus* Laporte, 1840]

Examined material. [3,4,6,8)]1 ex., Alpes, Tessin, leg. Ghidini A., coll. Maerky C., MHNG.

Comment. The only "Swiss" specimen belongs to the problematic collection of C. Maerky (see Monnerat et al. 2015) and was, therefore, not retained as a valid record. This Mediterranean species does not occur in Switzerland.

C3) [*Helophorus* (*Empleurus*) *rufipes* (Bosc, 1791)]

Examined material. [3,8)]1 ex., St-Bernard, coll. Favre E., HGSB; [3,8)]2 ex., St. Bernhard, leg. Venetz I., coll. Dietrich K., ETH; [3,8)]2 ex., Valais, leg. Poncy E., coll. Maerky C., MHNG; [3,8)]1 ex., Waadt, coll. Zschokke A., NMAA; [3,4,6,8)]1 ex., Yverdon, IX.1951, leg. and coll. Sermet A., MZL.

Published data. [1,8)]St. Bernhard ? by Venetz I. (Stierlin and Gautard 1867); [1,8)][Val d'Orvin] by Michaud A. (Michaud 1937).

Comment. This terrestrial species is widespread in Western and Central Europe and North Africa. Since the examined specimens belong to problematic collections and the published data could not be verified, this species is not considered to be part of the Swiss fauna.

C4) *Helophorus* (*Helophorus*) *aequalis* Thomson, 1868 and *Helophorus* (*Helophorus*) *aquaticus* (Linnaeus, 1758)

Comment. *Helophorus aequalis* and *H. aquaticus* have been reported from Switzerland (Fikáček et al. 2015a) with *H. aquaticus* being probably more common (Angus R. comm. pers.). However, we chose not to distinguish these two species since they are virtually impossible to differentiate without the examination of their karyotypes (Angus 1982). Therefore, all Swiss data have been attributed to an aggregate *H. aequalis/aquaticus*.

C5) *Helophorus* (*Kyphohelophorus*) *tuberculatus* Gyllenhal, 1808

Examined material. 1 ex., VD, Ste. Croix, Vraconnaz, X.1969, leg. and det. Toumayeff G., MHNG.

Published data. 1 ex., tourbière de la Vraconne, au-dessus de Ste-Croix, 19.X.1969 by Toumayeff G. (Toumayeff 1980).

Comment. This species is distributed in northern Europe and Asia, as well as in the Nearctic region. In Switzerland, a single specimen was captured in autumn 1969 in a Jura peat bog at 1,100 m a.s.l. (Toumayeff 1980). In France, it has been cited in the Doubs (Bameul and Queney 2014), close to the Swiss locality and was considered not rare in the vicinity of Pontarlier (Sainte-Claire Deville 1935). According to Hansen (1987), this tyrphobiontic species, which could be present in other peat bogs in the Jura Mountains, does not live directly in the water but hides in damp mosses and is generally found in small numbers of individuals.

C6) *Helophorus* (*Rhopalohelophorus*) *asperatus* Rey, 1885

Examined material. [3,4,5,6)]1 ex., Basel, leg. Seiler P., coll. Stöcklin N., NMB; [3,4,5,6)]1 ex., Basel, NMB; 29 ex., Ticino, Monte Bigorio, leg. and coll. Focarile A., MSNL; 1 ex., Ticino, Monte di Medeglia, leg. and coll. Focarile A., MSNL; 1 ex., Nidau, leg. Mathey A., MHNG; 2 ex., K.S. [Katzensee], 9.X.1883, coll. Riss F., ETH; 2 ex., Katzens. [Katzensee], 15.III.1884, coll. Riss F., ETH; 1 ex., ZH, Buchs, 27.III.1948, leg. and coll. Allenspach V., NMB; 2 ex., Kt. Bern, Hindelbank, V.1963, leg. and coll. Linder A., ETH; 14 ex., Ticino, Tesserte, Gola di Lago, VI.1985, leg. and coll. Focarile A., MSNL; 3 ex., Maggia TI, 4.VII.2022, leg. and coll. Chittaro Y.

Published data. [1)]Stein, Hargarten, Brunnentrog, VI.1960, leg. Frey H. T. (Hugentobler 1966); 2 ♂, Marais de Kloten by Gassmann M., det. Angus R. (Gassmann 1974).

Comment. This species is found throughout western and southern Europe. In Switzerland, only a few specimens are known, mainly from the canton of Ticino. This species inhabits grassy pools in open areas (Angus 1992).

C7) [*Helophorus* (*Rhopalohelophorus*) *croaticus* Kuwert, 1886]

Published data. [1)]Portalban-Cudrefin, Grande Cariçaie, 1992 (Mulhauser 1997).

Comment. A single mention in the literature, without any reference specimen, refers to *H. croaticus* in Switzerland. As no specimens belonging to this species have been found in the collections consulted, the species is currently not listed for Switzerland. Since it is widely distributed in the Palaerctic region (Drost 1988) and present in adjacent areas, notably Alsace (Callot 2001, 2018) and southern Germany (Köhler and Klausnitzer 1998), its presence in Switzerland is possible.

C8) *Helophorus* (*Rhopalohelophorus*) *dorsalis* (Marsham, 1802)

Examined material. [3,4,5,6)]1 ex., Basel, coll. Burghold W., NMBE; [3,4,5,6)]1 ex., Basel, leg. Anonymous, NMB; 1 ex., Bienne, leg. Mathey A., NMBE; [3,4,6)]1 ex., Kt. Basel, leg. Täschler M., ETH; 2 ex., Gränch.bg [Grenchenberg], 25.V.1880, coll. Rätzer A., NMBE; 1 ex., Müllheum, IV.1886, coll. Müller-Rutz J., det. Blöchlinger H., NMTG; 1 ex., Fribourg, Schweinsberg, 1934, leg. and coll. Berhaut J., MHNF; 1 ex., BL, Eptingen, VI.1959, leg. Toumayeff G., MHNG; 3 ex., Thurg. [Thurgovie], Pfyn, bord de la Thur, 7.VIII.1979, leg. Besuchet C., MHNG; 1 ex., Péry, Tscharner, 1995, leg. Anonymous, ETH; 2 ♂, Suchy VD, 14.IV.2018, leg. and coll. Cosandey V.; 1 ♂, 1 ♀, Vuisternens-devant-Romont FR, 30.VII.2022, leg. and coll. Cosandey V.

Published data. [1)]Basel by Bischoff-Ehinger A. and Stierlin G. and [1)]Schaffhausen by Stierlin G. (Stierlin and Gautard 1867); [1)][Val d'Orvin] by Michaud A. (Michaud 1937).

Comment. Although widely distributed in Europe and present in Turkey, *H. dorsalis* is rare in Switzerland, where most of the localities are situated on the Plateau. This species colonizes small, often temporary, muddy pools in woodlands (Hansen 1987; Angus 1992). It has also been captured during dispersal using light traps or nets placed on cars ("autokescher") (Gerend 2014). The recent Swiss records involve specimens caught in ruts created by logging machinery, which corresponds to the typical habitat as described in the literature. It is possible that the sporadicity of its occurrences reflects the difficulty of finding these small temporary bodies of water.

C9) *Helophorus* (*Rhopalohelophorus*) *fauveli* Ganglbauer, 1901

Examined material. 2 ex., Wallis, Gr. St. Bernhard, coll. Cerutti N., MHNF; 2 ex., VS, Val Ferret, coll. Rätzer A., NMBE; 5 ex., BE, Gauli-H. [Gauli-Hütte], VII.1928, leg. Mathey A., NMBE; 1 ex., Mt. Camoghè, 6.VIII.1963, leg. and coll. Scherler P., NMBE; 3 ex., Valais, Gd. St. Bernard, VII.1971, leg. Toumayeff G., MHNG; 1 ex., Combe du Barasson, 12.VIII.1977, leg. and coll. Scherler P., NMBE; 1 ex., VS, V. Entremont, P. Lacerandes, IX.1978, leg. Toumayeff G., MHNG; 1 ex., Grisons, Val Bondasca, 11.IX.1985, leg. Besuchet C., MHNG; 1 ex., Vieux Emosson, 25.IX.1985, leg. and coll. Scherler P., NMBE; 6 ex., Zernez GR, 10.VI.2014, leg. Blattner L., det. Nagel P., NMB; 1 ex., Maggia TI, 25.VIII.2017, leg. and coll. Cosandey V.; 1 ex., Lavizzara TI, 26.VIII.2017, leg. and coll. Cosandey V.; 1 ex., Val de Bagnes VS, 19.VII.2022, leg. and coll. Sanchez A.

Published data. 2 ex., au-dessus du Col du Grand-St-Bernard, «Jardins du Valais», 24.7.1972 by Toumayeff G. (Toumayeff 1980).

Comment. *Helophorus fauveli* has been found only sporadically in the Italian and Swiss Alps. Curiously, Pirisinu (1981) did not mention this species in Italy. In Switzerland, *H. fauveli* was first detected by Toumayeff (1980), who collected a few specimens in very humid pastures at 2,600 m a.s.l. Its presence in the southwestern and in eastern Swiss Alps suggests that it may also be present in France and Austria. Targeted surveys should be carried out in these two countries. Today, it is known from a dozen high-altitude localities scattered across the Alps. Potentially, *H. fauveli* may be just aberrant specimens of *H. nivalis* (Shatrovskiy et al. 2023).

C10) [*Helophorus* (*Rhopalohelophorus*) *longitarsis* Wollaston, 1864]

Published data. 2)au-dessus de Dorénaz and 2)Guercet aux Champagnes de Fully by Favre E. (Favre 1890).

Comment. This species was only reported from Switzerland by Favre (1890), under the name (now synonymous) *H. erichsoni* Bach, 1866. The specimens of this species held in the collection of the HGSB, where Favre's collection is housed, happened to be *Helophorus granularis*. Even if its presence remains possible, given its wide distribution, *H. longitarsis* is not included in the Swiss list.

C11) *Helophorus* (*Rhopalohelophorus*) *minutus* Fabricius, 1775

Examined material. 5 ex., Martigny, coll. Rätzer A., NMBE; 3)1 ex., Suisse, Nidau, 5.VII., coll Maerky C., MHNG; 6 ex., Ch. Fully [Champagne de Fully], coll. Cerutti N., MHNF; 1 ex., Kt. Wallis, Martigny, V.1890, leg. Anonymous, coll. Linder A., ETH; 1 ex., Scanfs, VII.1920, leg. and coll. Handschin E., BNM; 1 ex., Kt. Wallis, Martigny, VI.1939, leg. and coll. Linder A., ETH; 2 ex., Klotener Ried, 5.V.1967, 11.VII.1967, leg. Gassmann M., ETH; 1 ex., Vaud, Nyon, Changins, VI.1968, leg. Station fédérale de recherches agronomiques Changins, MHNG; 1 ex., Kt. Thurgau, Frauenfeld, VIII.1970, leg. and coll. Linder A., ETH; 1 ex., GE, Bois de Jussy, 3.VII.1972, leg. Vit S., MHNG; 2 ex., Hochdorf, Siedereiteich, 15.-20.VIII.1979, leg. Rezbanyai-Reser L., det. Herger P., NMLU; 11 ex., Ticino, Bolle di Magadino, 5.VII.1980, 11.VII.1980, 12.VII.1980, 7.VI.1981, 14.VI.1981, leg. Giacinto L., MSNL; 1 ex., SZ, Lauerz, Steinen, VII.1981, leg. Toumayeff G., MHNG; 1 ex., Egg, Litihof, Siedereiteich, 26.-31. VIII.1981, leg. Rezbanyai-Reser L., det. Herger P., NMLU; 2 ex., Valais, Barges près Vouvry, VIII.-X.1985, VII.-IX.1991, leg. Station fédérale de recherches agronomiques Changins, MHNG; 1 ex., Jura, Courtételle, IV.-V.1986, leg. Station fédérale de recherches agronomiques Changins, MHNG; 5 ex., Jura, Bonfol, 22.VII.1998, leg. Carron G., ETH; 51 ex., JU, Neuf Etang, 22.VII.1998, 4.IX.1998, leg. and det. Carron G.; 1)1 ♂., Bernex GE, 13.VI.2006, leg. Anonymous, det. Demierre E.

Published data. 1)Stein, Hargarten, Brunnentrog, VII.1965, leg. Frey H. T. (Hugentobler 1966); 6 ex., Marais de Kloten by Gassmann M., det. Angus R. (Gassmann 1974); 51 ex., Champ de Manche, 1998 by Carron G. (Carron 1999).

Comment. This species is widespread in Europe and North Africa. In Switzerland, it is quite rare but is known from specimens from most regions. It seems restricted to lowland (Queney and Prévost 2021) and relatively thermophilic habitats. It is found mainly in grassy pools (Angus 1992).

C12) *Helophorus* (*Rhopalohelophorus*) *montenegrinus* Kuwert, 1885; Fig. 1D

Examined material. 3,4,6)1 ex., Kt. Zürich, leg. Täschler M., coll. Linder A., ETH; 1 ♂, 1 ♀, Chiasso TI, 22.IV.2018, leg. and coll. Chittaro Y.; 1 ♂, Stabio TI, 21.X.2021, leg. and coll. Cosandey V.; 2 ex., Coldrerio TI, 22.V.2023, leg. and coll. Chittaro Y.; 1 ex., Stabio TI, 22.V.2023, leg. and coll. Chittaro Y.

Comment. This species is new for Switzerland. A few specimens of *H. montenegrinus* were very recently collected in the far south of Switzerland (canton of Ticino). Since it is mainly distributed in the Mediterranean countries of Europe, its presence in southern Switzerland is not surprising. The occurrence from Zurich is doubtful since it concerns a specimen from a problematic collection.

C13) [*Helophorus* (*Rhopalohelophorus*) *nanus* Sturm, 1836]

Published data. 1)am Irchel in Graben by Heer O. and 1)Nyon by Mon. (Heer 1841); 1)Aarau by Frey-Gessner E., 1)Basel by Bischoff-Ehinger A. and 1)Schaffhausen by Stierlin G. (Stierlin and Gautard 1867); 1)Müllheim, IV.1886 by Müller-Rutz J. and 1)Winkeln, Breitfeld, II.1957 by Hugentobler H. (Hugentobler 1966).

Comment. None of the numerous literature citations are reliable, as not one is supported by specimens in any Swiss collection. It is very likely that specimens of *H. pumilio* have been misidentified as *H. nanus*. Although this species is widely distributed in the Palaearctic region outside the Mediterranean (Angus 1992), it is currently not considered to be part of the Swiss fauna. However, it may be present in Switzerland and a future discovery of this species is possible.

C14) *Helophorus* (*Rhopalohelophorus*) *strigifrons* Thomson, 1868

Examined material. 2 ex., Lausanne, 24.VI.1896, coll. Gaud A., MZL; 1 ex., Basel, V.1908, leg. Jörger J. B, NMB; 15 ex., Kt. Bern, Uettligen, V.1932, IV.1934, leg. and coll. Linder A., ETH; 1 ex., Val Milar, 23.VII.1936 leg. and coll. Allenspach V., NMB; 1 ex., VD, Prévondavaux, IX.1961, leg. Toumayef G., MHNG; 2 ex., VD, Gimel, V.1964, leg. Toumayeff G., MHNG; 7 ex., VD, Jura, Lac Ter, VIII.1964, leg. Toumayeff G., MHNG; 5 ex., VD, Ballens, V.1972, VII.1973, leg. Toumayeff G., MHNG; 1 ex., VD, Gimel, Sézeau, III.1979, leg. Toumayeff G., MHNG; 2 ex., Vaud, Le Séchey, Lac Ter, 21.VI.1989, leg. Besuchet C., MHNG; 1 ♂, 1 ♀, Le Chenit VD, 1.XI.2017, leg. and coll. Chittaro Y.; 1 ♂, Le Locle NE, 23.XI.2017, leg. and coll. Chittaro Y.; 1 ♂, Le Chenit VD, 16.VI.2020, leg. and coll. Chittaro Y.; 1 ♂, Les Ponts-de-Martel NE, 23.VI.2020, leg. and coll. Chittaro Y.; 1 ♂, Chavannes-de-Bogis VD, 7.V.2021, leg. and coll. Chittaro Y.; 2 ex., Le Chenit VD, 17.V.2022, leg., det. and coll. Chittaro Y.

Comment. Most of the Swiss specimens come from the west of the country, with the exception of one collected in the canton of Grisons. *Helophorus strigifrons* is widely distributed in Europe but absent from the Mediterranean region (Angus 1992).

C15) *Hydrochus angustatus angustatus* Germar, 1824

Examined material. 3)1 ex., Basel, leg. Anonymous, NMB; 3)1 ex., Verrières, 18.IV.1901, leg. Anonymous, det. Berge Henegowen A. L., MHNG; 6 ex., Versoix, 2002, 7.VI.2003, 2004, 22.V.2005, leg. and det. Carron G., ETH, LEBA; 1 ex., Rances GE, 20.V.2004, leg. and det. Carron G., ETH; 6 ex., Versoix GE, 24.IV.2020, leg. and coll. Cosandey V.; 4 ex., 2 ♂, Versoix GE, 19.V.2020, leg. and coll. Chittaro Y.; 1 ex., 1 ♂, Bernex GE, 19.V.2020, leg. and coll. Chittaro Y.

Published data. 1)Basel by Imhoff L. (Stierlin and Gautard 1867).

Comment. Distributed throughout Western Europe, this species reaches Switzerland in the canton of Geneva, where it is only known from a few specimens. This species is present in pools rich in plants and detritus, often in quarries. It is easiest to find in spring when the water level is high (Hebauer and Klausnitzer 1998). These ecological traits are corroborated by Swiss data.

C16) [*Hydrochus brevis* (Herbst, 1793)]

Published data. 1)Bern by Perty M. (Heer 1841); 1)Basel by Bischoff-Ehinger A. (Stierlin and Gautard 1867).

Comment. The only two Swiss mentions of *H. brevis* originate from very old publications, and no specimens were found in the examined collections. It is likely that the citations refer to misidentified *H. crenatus*. We suggest removing this species from the list of the Swiss fauna, even though its presence in Switzerland remains possible, given its wide Palaearctic distribution and its presence in southern Germany (Köhler and Klausnitzer 1998), Alsace (Callot 2018), and South Tyrol (Kahlen and Hellrigl 1996). This species is becoming rarer in the southern part of its distributional range (Hebauer and Klausnitzer 1998).

C17) *Anacaena bipustulata* (Marsham, 1802)

Examined material. 1 ex., Chiasso, leg. and coll. Fontana P., MSNL; 4,6)1 ex., Marly, leg. Anonymous, coll. Bugnion E., det. Carron G., MZL; 1 ex., Genève, IV., leg. and coll. Toumayeff G., det. Carron G., MHNG; 1 ex., Chiasso, 7.V.1928, leg. and coll. Fontana P., MSNL; 1 ex., Dardagny GE, VI.2009, leg. Dupont N., det. Brancucci M.; 1 ex., Vandoeuvres GE, 2.IV.2012, leg. Anonymous, det. Demierre E.; 2 ex., Russin GE, 18.VIII.2021, leg. and coll. Cosandey V.; 8 ex., Perly-Certoux GE, 24.IX.2021, leg. and coll. Cosandey V.; 5 ex., Russin GE, 28.IV.2022, leg. and coll. Cosandey V.; 2 ex., Versoix GE, 6.IX.2023, leg. and coll. Chittaro Y.

Published data. 1)au dessus de Broccard by Favre E., 1)Jorat près Lausanne and 1)Zürich by Bugnion E. (Favre 1890); 1)Frauenfeld, VI.1956, 2)Wittenbach, Kronbühl, XI.1956, 1)Goldach, Mötteliweiher, X.1957, 2)Altenrhein b. Strandbad, X.1958 and 1)Sulgen, Weinmoos, V.1962 by Hugentobler H. (Hugentobler 1966); bords de l'Aire et de l'Allondon by Cosandey V. (Cosandey 2023).

Comment. This thermophilic species is widespread in Europe and North Africa, being more common in the southwestern part of its distribution (Hebauer and Klausnitzer 1998). Recent prospections have shown that it reaches the southwest of Switzerland in the canton of Geneva (Cosandey 2023), while historical specimens attest its presence in the canton of Ticino. The occurrence from Marly is doubtful, as the locality may refer to one in France and not one on the Swiss Plateau. Most of the published data are not attested by specimens in collections, while the specimens cited by Hugentobler (1966) that could be found in his collection were misindentified specimens of *Anacaea limbata*.

C18) *Cymbiodyta marginella* (Fabricius, 1792)

Examined material. 1 ex., Carouge, leg. Anonymous, MHNG; 1)2 ex., Burgäschi, IV.1944, leg. Peez A., MCB; 1 ex., Hochdorf, Siedereiteich, 15.-20.VIII.1979, leg. Herger P., NMLU; 1 ex., Jura, Bonfol, Champ de manche, 4.IX.1998, leg. and det. Carron G., ETH; 2 ex., Stein am Rhein SH, 11.V.2022, leg. and coll. Chittaro Y.; 1 ex., Ramsen SH, 2.V.2023, leg. and coll. Chittaro Y.; 3 ex., Schaffhausen SH, 3.V.2023, leg. and coll. Chittaro Y.; 1 ex., Bonfol JU, 12.VI.2023, leg. and coll. Chittaro Y.; 1 ex., Marthalen ZH, 12.IX.2023, leg. and coll. Sanchez A.

Published data. 1)Bern by Ougspurger F. and Perty M., 1)Dübendorf by Bremi-Wolf J. J., 1)Katzensee by Heer O., 1)Lausanne by Mellet L., 1)Nyon by Ter. and 1)Pomy by Mellet L. (Heer 1841); 1)Aigle by Heer O., 1)Basel by Bischoff-Ehinger A. and 1)Schaffhausen by Stierlin

G. (Stierlin and Gautard 1867); 1)Buchser-See by Rietmann O. (Täschler 1872); 1)Morges by Bugnion E. (Stierlin 1883); 2)Martigny and 1)Guercet by Favre E. (Favre 1890); 1)Burgäschisee bei Herzogenbuchsee, 2)Villeneuve 1938 and 2)Zollikofen 1938 by Linder A. (Linder 1946); Bonfol, Champ de Manche by Carron G. (Carron 1999).

Comment. *Cymbiodyta marginella* is widely distributed in the Palaearctic region (Smetana 1974; Toussaint and Short 2022) but is only known from a few sparse occurrences in Switzerland. Citations in the literature may, in part, refer to misidentified *Enochrus* species. This is the case with the specimens from Zollikofen and Villeneuve, which turned out to be *Enochrus affinis*, and the specimen from Martigny which is an *E. coarctus*. With the exception of an old occurrence in the canton of Geneva, *Cymbiodyta marginella* has only been recorded in northern Switzerland. Recent targeted surveys have found this species in a few localities in the canton of Jura, Schaffhausen and Zurich.

C19) [*Enochrus* (*Lumetus*) *segmentinotatus* (Kuwert, 1888)]

Examined material. 3,4,6,8)3 ex., Suisse, Argovie, leg. Frey-Gessner E., coll. Maerky C., MHNG; 4,6,8)1 ex., Aïre, 20.III.1920, leg. and coll. van de Gümster J., MHNG.

Comment. The first specimen cited here belongs to C. Maerky's problematic collection (see Monnerat et al. 2015) and is, therefore, not retained as a valid record. Although it does not originate from a notoriously problematic collection, the second specimen cannot be retained either because *E. segmentinotatus* is a Mediterranean species, whose closest occurrences are situated in coastal areas.

C20) *Berosus* (*Berosus*) *affinis* Brullé, 1835

Examined material. 1 ex., Genève, Laconnex, VI.1985, leg. Agroscope, MHNG.

Published data. 1)Yvonand-Estavayer-le-lac, Grande Cariçaie, 1995 (Mulhauser 1997).

Comment. This species is distributed in the Western Palaearctic and is common in the Mediterranean region (Schödl 1993). It reaches southwest Switzerland in the canton of Geneva, where a single specimen was caught in 1985 using a light trap. No specimen could be associated with the literature occurrence, which concerns likely a misidentified specimen of *Berosus*.

C21) *Berosus* (*Enoplurus*) *frontifoveatus* Kuwert, 1888

Examined material. 1 ex., Fully, leg. and coll. Rätzer A., NMBE; 3)1 ex., Genève, leg. Sechehaye A., coll. Maerky C., MHNG; 1 ex., Guercenet [Guercet], coll. Favre E., HGSB; 5 ex., Martigny, coll. Favre E., HGSB; 3,8)1 ex., Murten, leg. Anonymous, NMAA; 3)1 ex., Wallis, leg. Anonymous, MHNG; 5 ex., Ch. Fully [Champagne de Fully], 20.V.1890, coll. Cerutti N., MHNF; 5 ex., Fully, 20.V.1890, coll. Cerutti N., MHNF; 5 ex., Fully, 22.V.1890, coll. Cerutti N., MHNF; 10 ex., Ch. Fully [Champagne de Fully], 24.V.1890, coll. Cerutti N., MHNF; 3 ex., VS, Fully, 24.V.1890, leg. and coll. Rätzer A., NMBE; 8 ex., VS, Fully, 30.V.1890, leg. and coll. Mathey A. and Rätzer A., NMBE; 4 ex., Kt. Wallis, Martigny, V.1890, leg. Anonymous, coll. Linder A., ETH; 2 ex., Suisse, Tessin, Mezzana, 5.VIII.1965, leg. Agroscope, MHNG; 2 ex., CH, TI, Coldrerio-Süd, Molino, V. d. Motta, 21.-31.VII.1988, leg. Rezbanyai-Reser L., NMLU; 2 ex., CH, TI, Monte Albano, San Pietro, 1.-10.VIII.1993, leg. Hächler M., MHNG; 1 ex., CH, TI, Seseglio, Cámpora, 21.-31.VIII.1997, leg. Rezbanyai-Reser L., NMLU.

Comment. *Berosus frontifoveatus* has regularly been misidentified as *B. spinosus* in the Swiss collections (see also the comment under *B. spinosus*). This themophilous species is widely distributed in the Mediterranean region as well as in Central Europe and Asia. In Switzerland, it appears to be restricted to the warmer regions of southern Switzerland, where a few specimens have been found. It may also be present in the Basel region, as suggested by occurrences in Alsace (Callot 2001, 2018).

C22) [*Berosus* (*Enoplurus*) *guttalis* Rey, 1883]

Examined material. 3,4,6,8)1 ♀, Genève, Sionnet, leg. and coll. Maerky C., MHNG.

Published data. 2,8)Champagnes de Fully, 1,8)Econaz près Riddes [Ecône] and 2,8)Guercet by Favre E. (Favre 1890).

Comment. This species is cited from the western Mediterranean region (southern France (Bameul and Queney 2014), Spain, North Africa) and Turkey. On the three occurrences cited by Favre (1890), two turned out to concern misidentified *Berosus frontifoveatus*, while no specimen could not be found for the third one in Favre's collection. The only specimen labelled from Switzerland is a female that must be considered as doubtful as it belongs to the problematic collection of Charles Maerky (see Monnerat et al. 2015). Consequently, *B. guttalis* is not considered to belong to the Swiss fauna.

C23) [*Berosus* (*Enoplurus*) *spinosus* (Steven, 1808)]

Examined material. 3,4,6)1 ex., Schaffhausen ? (written with «?» on the original label), leg. Anonymous, ETH; 2?)1 ♀, Suisse, Tessin, Mezzana, 7.IX.1965, leg. Agroscope, MHNG.

Published data. 1)Aigle by Chavannes D.-A. and 1)Nyon par Ter. (Heer 1841); 1)Martigny by Favre E. (Stierlin 1883); 1)Guercet by Favre E. (Favre 1890); 2)1 ♂, Seseglio, VIII.1997 by Rezbanyai-Reser L. (Herger and Germann 2017).

Comment. This halophilic species (Hebauer and Klausnitzer 1998) is widely distributed in the Palaearctic region and has been recorded in most countries surrounding Switzerland, with the exception of France (Schödl 1991; Bameul and Queney 2014). The published data from Seseglio (TI) (Herger and Germann 2017) corresponds to a misidentified specimen of *B. frontifoveatus*. The only labeled specimen from Switzerland is a female, and its specific identification cannot be confirmed. For the time being, we, therefore, propose to consider this species as absent from Switzerland without further information.

C24) [*Limnoxenus niger* (Gmelin, 1790)]

Examined material. 3,4,6)1 ex., Genève, leg. Anonymous, coll. Maerky C., MHNG; 3,4,6)1 ex., Kt. Genf, leg. Täschler M., coll. Linder A., ETH.

Published data. 1)Genf by Chevrier F. (Heer 1841).

Comment. All specimens examined belong to problematic collections that should not be taken into account, and the very old literature data (under *Hydrobius oblongus* Herbst) cannot be verified. Although this species is widely distributed in the western Palaearctic region, it is absent from Switzerland.

C25) [*Hydrochara flavipes* (Steven, 1808)]

Examined material. 3,4,6,8)2 ex., Genève, leg. Sechehaye A. and Anonymous, coll. Maerky C., MHNG; 3,4,6,8)1 ex., Genève, Onex, leg. Frey-Gessner E., coll. Maerky C., MHNG.

Comment. All the examined specimens belong to Charles Maerky's problematic collection and must, therefore, be considered doubtful. *Hydrochara flavipes* is a species adapted to dry environments. It has a Mediterranean distribution, which extends into Central Asia (Smetana 1980), and does not occur in Switzerland.

C26) *Hydrophilus* (*Hydrophilus*) *aterrimus* Eschscholtz, 1822

Examined material. 1 ex., Bern, leg. and coll. Burghold W., NMBE; 2 ex., Fully, 20.V.1890, coll. Favre E., HGSB; 1 ex., Martigny, leg. Anonymous, MZL; 1 ex., Kt. Wallis, Martigny, leg. and coll. Linder A., ETH; 3)1 ex., Suisse, Martigny, leg. Poncy E., coll. Maerky C., MHNG; 3)1 ex., Suisse, Morat, leg. Fries A., coll. Maerky C., MHNG; 1 ex., Morgins de Loës, leg. and coll. Bugnion E., MZL; 3 ex., Villeneuve, leg. and coll. Gaud A., MHNG, MZL; 1 ex., Dorigny, 8.X.1879, leg. and coll. Bugnion E., MZL; 1 ex., Oerlikon, 9.IV.1884, leg. Anonymous, ETH; 1 ex., Oerlikon, 23.IV.1885, coll. Nägeli A., NMSO; 1 ex., Villeneuve [VD], 4.VI.1888, leg. and coll. Mathey A., NMBE; 1 ex., Villeneuve [VD], VI.1887, leg. Gaud A., coll. Bugnion E., MZL; 4 ex., Fully, 16.V.1890, 20.V.1890, leg. and coll. Rätzer A., NMBE; 1 ex., Ch. Fully [Champagne de Fully], 19.V.1890, coll. Cerutti N., MHNF; 1 ex., Ch. Fully [Champagne de Fully], 20.V.1890, coll. Cerutti N., MHNF; 1 ex., Kt. Wallis, Martigny, V. 1890, leg. Anonymous, coll. Linder A., ETH; 1 ex., Zürich, 1.V.1895, coll. Nägeli A., NMSO; 1 ex., TG, Untersee, 10.V.1910, leg. and coll. Spälti A., MHNG; 3 ex., Zürich, Katzensee, 1910, leg. Rimoldi C., coll. Allenspach V., NMB; 1 ex., Vaud, Roche, 28.V.1944, leg. and coll. Pochon H., MHNF; 1 ex., Vaud, Villeneuve, Gr. Canal, 30.IV.1946, leg. Anonymous, MHNG; 1 ex., Reggenberg, 29.VII.1952, leg. Anonymous, coll. Spälti A., MHNG; 1 ex., Helv., TG, Ermatingen, 16.IX.1961, leg. Sauter W., ETH; 2 ex., Altenrhein, 27.VIII.1968, leg. and coll. Spälti A., MHNG; 1 ex., Oerlikon, 23.IV.1985, leg. Anonymous, MHNG.

Published data. 1)Malans and 1)Ragatz [Bad Ragaz] by Amstein J. G. and 1)Zürichsee by Heer O. (Heer 1841); 1)Basel by Bischoff-Ehinger A. and 1)Schaffhausen by Stierlin G. (Stierlin and Gautard 1867).

Comment. Only old specimens confirm the presence of *H. aterrimus* in Switzerland. It was last recorded in 1985 on the eastern Swiss Plateau, where surveys should be urgently carried out to determine whether the species is still present in Switzerland. This species is declining in Central Europe (Hebauer and Klausnitzer 1998) and may be extinct in France (Bameul and Queney 2014).

C27) [*Laccobius* (*Dimorpholaccobius*) *atrocephalus atrocephalus* Reitter, 1872]

Published data. 2)3 ex., Magadino, X.1966, leg. Linder A. (Allenspach 1978).

Comment. The three specimens listed in Allenspach's publication correspond to *Laccobius albescens*. Known only from Italy and Spain in Europe, *L. atrocephalus atrocephalus* does not belong to the Swiss fauna.

C28) *Laccobius* (*Dimorpholaccobius*) *neapolitanus* Rottenberg, 1874

Examined material. 3 ex., Chiasso, leg. and coll. Fontana P., MSNL; 3)1 ex., Genève, leg. Sechehaye A., coll. Maerky C., MHNG; 3)1 ex., Suisse, leg. Sechehaye A., coll. Maerky C., MHNG; 3 ex., Chiasso, 1.IV., leg. and coll. Fontana P., MSNL; 4 ex., Chiasso, III.1914, leg. and coll. Fontana P., MSNL; 1 ex., Fusio, VII.1923, leg. and coll. Fontana P., MSNL; 1 ex., Fracherets, 23.XI.1947, leg. and coll. Besuchet C., MZL; 1 ex., Suisse, Tessin, Scudellate, leg. and coll. Besuchet C., MZL; 1 ex., GE, L. Baillets, London, 14.VII.1954, leg. and coll. Rehfous M., MHNG; 2 ex., GE, Russin, London, 17.IX.1955, leg. and coll. Rehfous M., MHNG; 1 ex., St. Gallen, Goldach, VI.1956, leg. and coll. Toumayeff G., MHNG; 2 ex., BE, Belp, Au, VI.1958, leg. and coll. Toumayeff G., MHNG; 2 ex., TI, Rancate, VIII.1963, leg. and coll. Toumayeff G., MHNG; 1 ex., Suisse, VD, Jura, Lac Ter, VIII.1964, leg. and coll. Toumayeff G., MHNG; 2 ex., Suisse, VD, Bercher, Mentue, V.1965, leg. and coll. Toumayeff G., MHNG; 1 ex., TI, s/Rovio, VI.1968, leg. and coll. Toumayeff G., MHNG; 2 ex., TI, s/Rovio, VII.1968, leg. and coll. Toumayeff G., MHNG; 1 ex., Rovio, 29.VII.1974, leg. Scherler P., det Carron G., NMBE; 2 ex., Caneggio, 6.VIII.1975, leg. Scherler P., det. Carron G., NMBE; 1 ex., VD, Bavois, Bernoise, VIII.1982, leg. and coll. Toumayeff G., MHNG; 1 ex., TI, Sessa, Bach-Ufer an der Lisora, 17.-22.V.1990, leg. Kiener S., det. Hebauer F., NMBE; 1 ex., TI, Melezza-Ufer zwischen Intragna und Tegna, 4.IV.1991, leg. Kiener S., det. Hebauer F., NMBE; 1 ♂, Chiasso TI, 22.IV.2018, leg. and coll. Chittaro Y.; 1 ♂, Lucens VD, 25.IV.2021, leg. and coll. Cosandey V.; 2 ♂, Zwischbergen VS, 6.VIII.2021, leg. and coll. Sanchez A.;

1 ♂, Plasselb FR, 12.IX.2021, leg. and coll. Cosandey V.; 1 ♂, Lugano TI, 19.X.2021, leg. and coll. Cosandey V.; 1 ♂, Mendrisio TI, 21.X.2021, leg. and coll. Cosandey V.; 1 ♂, Coldrerio TI, 22.V.2023, leg. and coll. Chittaro Y.

Published data. 1)Grangettes, 1960 (Naceur 1997)

Comment. This species is distributed in Central and southern Europe and North Africa. In Switzerland, its presence is mainly attested by specimens from the west and south of the country. Specimens have been caught in small streams and springs. The ecological requirements of *L. neapolitanus* are unclear and sometimes contradictory (Hebauer and Klausnitzer 1998).

C29) [*Laccobius* (*Hydroxenus*) *femoralis mulsanti* Zaitzev, 1908]

Examined material. 3,4,6,8)1 ex., Suisse, Bienne, 6.VI., leg. and coll. Maerky C., MHNG; 3,4,6,8)1 ex., Genève, Rouelbeau, 22.VI., leg. and coll. Maerky C., MHNG; 3,4,6,8)3 ex., Genève, Peney, 7.VII., leg. and coll. Maerky C., MHNG.

Comment. All the examined specimens belong to the problematic collection of Charles Maerky (see Monnerat et al. 2015) and should, therefore, be considered as doubtful. This Mediterranean species does not belong to the Swiss fauna. *Laccobius femoralis* is represented by the nominotypical subspecies in Corsica, Sicily, Sardinia, and Campania (Bameul and Queney 2014), whereas the subspecies *mulsanti* is more widely distributed in the Iberian Peninsula, France, Italy, and North Africa.

C30) *Laccobius* (*Laccobius*) *colon* (Stephens, 1829)

Examined material. 1 ex., Stein a. Rhein, Ufer d. Rhein, leg. and coll. Böschenstein A., NMSH; 1 ex., Büren, V.1894, leg. and coll. Rätzer A., det. Carron G., NMBE; 1 ex., Stein a. Rh., Alm. Hosen, 22.IV.1913, leg. and coll. Böschenstein A., NMSH; 1 ex., Helv., K. Zü., Hänsiried, 17.IV.1932, leg. and coll. Lautner J., NMB; 1 ex., Kt. Berne, Busswil, 23.IV.1938, leg. and coll. Pochon H., MHNF; 3 ex., Zürich Umg., Katzens. [Katzensee], 14.IV.1941, leg. and coll. Wolf J.-P., ETH; 1 ex., Zch., Affoltern, Grube, 10.V.1941, leg. and coll. Wolf J.-P., ETH; 1 ex., CH, VD, Bavois, 15.IV.1989, leg. and coll. Bugnion E., MZL; 1 ex., CH, VD, Chavornay, 15.IV.1989, leg. and coll. Bugnion E., MZL; 4 ex., Chavornay, 19.X.1989, leg. Scherler P., NMBE; 2 ♂, Le Chenit VD, 16.VI.2020, leg. and coll. Chittaro Y.

Published data. 2)Scuol-Sent, 27.VII.1921 by Handschin E., 1)Ravitschana, 5.IX.1934 and 2)Il Fuorn, 13.IX.1934 by Nadig A. (Handschin 1963).

Comment. Widely distributed in the Palaearctic region, this species is rare in Switzerland, where it is known only from a few isolated specimens from the Plateau and the Jura mountains. Two specimens mentioned in the literature were found in the Handschin collection and were misidentified *L. obscuratus* (individual from Scuol-Sent) and *L. albescens* (individual from Il Fuorn). *Laccobius colon* is rare and sporadic in Germany as well (Hebauer and Klausnitzer 1998).

C31) *Laccobius* (*Microlaccobius*) *gracilis gracilis* Motschulsky, 1855

Examined material. 4 ex., Chiasso, leg. and coll. Fontana P., MSNL; 3)1 ex., Helvet. [Helvetia], leg. and coll. Huguenin G., ETH; 3)2 ex., Baden, coll. Killias E., BNM; 3)1 ex., Zürich, leg. Anonymous, MHNG; 2 ex., Greifensee, 3.VIII.1857, leg. and coll. Dietrich K., ETH; 2 ex., im Wasser der Quelle v. Baden, VII.1897, leg. Anonymous, ETH; 1 ex., FR, Marly, 1.V.1944, leg. and coll. Allenspach V., NMB; 8 ex., Russin, Allondon, 18.IX.1955, leg. and coll. Rehfous M., MHNG; 2 ex., Russin, Allondon, 8.X.1955, 5.V.1956, leg. and coll. Rehfous M., MHNG; 3 ex., St. Gallen, Goldach, VI.1956, leg. and coll. Toumayeff G., MHNG; 1 ex., Kt. St. Gallen, St. Gallen, VI.1956, leg. and coll. Linder A., ETH; 2 ex., Lucens, 27.VII.1959, leg. Scherler P., NMBE; 1 ex., TI, Coldrerio-Süd, V. d. Motta, Molino, 21.-31.VII.1988, leg. Rezbanyai-Reser L., NMLU; 24 ex., Genève, Chancy, La Laire, 19.IX.1990, leg. Besuchet C., MHNG; 1 ex., Suisse, Genève, Les Baillets, Allondon, 27.IX.1990, leg. Besuchet C., MHNG; 5 ex., Russin GE, 20.IX.2004, leg. and det. Carron G., ETH; 1 ♂, Russin GE, 8.IV.2020, leg. and coll. Chittaro Y.; 3 ex., Russin GE, 24.IX.2021, leg. and coll. Cosandey V.; 2 ex., Chancy GE, 6.V.2022, leg. and coll. Cosandey V.

Published data. Chiasso by Fontana P. (Fontana 1922); St. Gallen, Goldachgebiet, VI.1956, coll. Toumayeff G. and Linder A. (Hugentobler 1966).

Comment. This rheophilous species seems to have high environmental requirements and has only been found in a few well-preserved rivers in Switzerland. *Laccobius gracilis* is probably more thermophilic than the closely related species *L. alternus*. Both species are widespread in Europe but less common north of the Alps (Hebauer and Klausnitzer 1998).

C32) *Laccobius* (*Microlaccobius*) *thermarius thermarius* Tournier, 1878

Examined material. 3,4,6,8)7 ex., Suisse, Baden, leg. Tournier H., coll. Maerky C., MHNG.

Published data. Thermen von Baden im Aargau (Stierlin 1900); Terme di Baden (Gentili 1975).

Comment. Worldwide, *L. thermarius* is only known from two localities, where it is represented by two subspecies: the nominotypical subspecies *thermarius* described by Tournier in 1878 from specimens collected in Baden (AG) in Switzerland and the subspecies *jelineki* described by Gentili in 1975 based on specimens from Bojnice, in western Slovaquia. Both localities are thermal sites with temperatures above 20 °C (Gentili and Chiesa 1975). The type locality of the nominotypical subspecies is now completely urbanized, and the springs are used for thermal baths. It is not certain that the species still exists in Switzerland.

C33) [*Paracymus aeneus* (Germar, 1824)]

Examined material. [3,4,6)]2 ex., Kt. Genf, leg. Täschler M., coll. Linder A., ETH.

Published data. [1)]Genf [Genève] (Stierlin 1900).

Comment. The two specimens examined belong to Max Täschler's problematic collection (see Monnerat et al. 2015) and are, therefore, not retained as valid records, while the occurrence originating from literature is not verifiable. Although widely distributed in the Palaearctic region, this halobiontic species (Hebauer and Klausnitzer 1998) is not included in the Swiss list.

C34) *Paracymus scutellaris* (Rosenhauer, 1856); Fig. 1G

Examined material. [3)]1 ex., Genève, leg. Anonymous, coll. Maerky C., MHNG; 1 ex., Suisse, Genève, Hermance, 11.X.1961, leg. Besuchet C., MHNG.

Comment. This species is widespread in Europe, North Africa, Cyprus, and Turkey. The presence of *P. scutellaris* in Switzerland is presented here for the first time, based on a single specimen caught "in mosses" (probably by sifting) in the canton of Geneva in 1961. The other examined specimen belongs to the collection of C. Maerky and is, therefore, doubtful.

C35) *Coelostoma* (*Coelostoma*) *hispanicum* (Küster, 1848)

Examined material. [3,5)]1 ex., Genf [Genève], leg. and coll. Lasserre H., ETH; 5 ex., Riva S. Vitale, 8.VI.1928, leg. and coll. Fontana P., MSNL; 1 ex., Melano, 29.VIII.1989, leg. and coll. Scherler P., NMBE; 3 ex., Cartigny GE, 25.-26.V.2020, 18.VIII.2021, leg. and coll. Chittaro Y. and Cosandey V.

Published data. Moulin de Vert, Cartigny, 2021 by Cosandey V. (Cosandey 2023).

Comment. This Mediterranean species reaches the south of Switzerland in the cantons of Geneva and Ticino, where it is rare and localized. Although a few specimens were caught a few decades ago, *C. hispanicum* was only mentioned for the first time in Switzerland very recently (Cosandey 2023).

C36) *Dactylosternum abdominale* (Fabricius, 1792)

Examined material. 2 ex., Genève, Cointrin, X.1950, leg. and coll. Toumayeff G., MHNG; 7 ex., VD, Commugny, 22.IX.1963, 20.X.1963, 14.XI.1963, leg. Steffen J., MHNG; 1 ex., Suisse, Vaud, Bremblens, VIII.1983, leg. Agroscope, MHNG; 3 ex., CH, VS, Conthey, 1.-10.VIII.1988, 11.-20.VIII.1988, 21.-31.VIII.1988, leg. Hächler M., det. Herger P., NMLU; 5 ex., VD, Orny, IX.1988, leg. Toumayeff G., coll. Toumayeff G. and Scherler P., MHNG, NMBE; 1 ex., Genève, Lullier, VIII.1994, leg. Besuchet C., MHNG; 1 ex., Münsterlingen TG, 31.VIII.2014, leg., det. and coll. Eismann B.; 1 ex., Ingenbohl SZ, 29.VII.2018, leg., det. and coll. Graf R.; 1 ex., Signy-Avenex VD, 11.X.2019, leg., det. and coll. Breitenmoser S.; 1 ex., Morges VD, 27.VI.2020, leg. and coll. Chittaro Y.; 25 ex., Essertines-sur-Yverdon VD, 16.IX.2023, leg. and coll. Chittaro Y.

Published data. 2 ex., in der Nähe des Flugplatzes Cointrin-Genf, X.1950, leg. Toumayeff G. (Linder 1953); 3 ex., Conthey, VIII.1988 by Rezbanyai-Reser L. (Herger and Germann 2017).

Comment. This species originated from the Afrotropical region and has now a cosmoplitan distribution (Knisch 1924; Hansen 1999). The first specimens found in Switzerland were collected in 1950. Although generally found in small numbers, the species now appears to be widespread on the Swiss Plateau and arrives in Valais.

C37) *Cercyon* (*Cercyon*) *alpinus* Vogt, 1969; Fig. 1A

Examined material. 1 ex., SZ, Brunnen, VIII., leg. and coll. Toumayeff G., MHNG; 1 ex., Rigi, 13.VI.1912, leg. and coll. Jörger J. B., NMB; 1 ex., Montana, 1934, leg. and coll. Julliard C., MHNG; 5 ex., Kt. Bern, Hasliberg, VIII.1938, leg. and coll. Linder A., ETH; 1 ex., BE, Axalp, VII.1944, leg. and coll. Allenspach V., NMB; 1 ex., Suisse, GR, Bergün, Uglix, VIII.1967, leg. and coll. Toumayeff G., MHNG; 1 ex., CH, LU, Escholzmatt, 15.V.1975, leg. Portmann F., NMLU; 1 ex., Suisse, Obwald, Stöckalp, 2.X.1987, leg. Löbl I., MHNG.

Comment. This species is known from many mountain ranges in Europe (Abruzzi, Alps, Carpathians, Dinaric Alps) (Fikáček 2006). Here, we present the first occurrences of this species in Switzerland, all from the Alps. Most of these specimens were collected a long time ago but had gone unnoticed, confused in collection with other *Cercyon* species.

C38) *Cercyon* (*Cercyon*) *bifenestratus* Küster, 1851

Examined material. 2 ex., CH, BE, Ins, Landw. Schule, 23.VII.1977, leg. Rezbanyai-Reser L., det. Herger P., NMLU.

Published data. [2)]Chiasso, by Fontana P. (Fontana 1922).

Comment. This species is extremely rare in Switzerland and has only been collected once using a light trap in the wetlands of the Seeland, where it is probably associated with the remnants of sand dunes. The specimen announced as *C. bifenestratus* by Fontana (1922), and identified as such in his collection, was in fact *C. haemorrhoidalis*. The species is also rare in France (Bameul and Queney 2014).

C39) *Cercyon* (*Cercyon*) *castaneipennis* Vorst, 2009; Fig. 1B

Examined material. [3)]1 ex., Aarau, leg. Anonymous, NMAA; 1 ex., Chandolin, coll. Cerutti N., MHNF; 1 ex., Martigny, coll. Favre E., HGSB; 1 ex., Susten, leg. and coll. Benteli F., NMBE; 1 ex., Stalden, 25.V.1913, leg. and coll. Mathey A., NMBE; 2 ex., Ajoie, VII.1917, leg.

and coll. Mathey A., NMBE; 1 ex., Ayer, 19.VIII.1959, leg. and coll. Scherler P., NMBE; 3 ex., St-Légier, 10.XII.1960, leg. and coll. Scherler P., NMBE; 1 ex., Zermatt, 16.VIII.1961, leg. and coll. Rehfous M., MHNG; 1 ex., Novazzano, 6.VIII.1974, leg. and coll. Scherler P., NMBE; 1 ex., CH, BE, Lützelflüh-Egg, 12.VII.1995, leg. and coll. Kobel E., NMBE; 1 ex., Scuol GR, 29.IV.2015, leg. and coll. Chittaro Y., det. Büche B.; 1 ex., Vaz/Obervaz GR, 7.V.2016, leg. and coll. Cosandey V.; 1 ex., Bonaduz GR, 8.VII.2016, leg. and coll. Cosandey V.; 1 ex., Valsot GR, 8.VII.2016, leg. and coll. Cosandey V.; 1 ex. Köniz BE, 4.V.2019, leg. and coll. Cosandey V.; 3 ex., Schaffhausen SH, 12.V.2019, leg. and coll. Cosandey V.; 1 ex., Quarten SG, 18.V.2019, leg. and coll. Cosandey V.; 1 ex., S-chanf GR, 14.IX.2019, leg. and coll. Cosandey V.; 2 ex., Ennetbürgen NW, 19.VI.2021, leg. and coll. Cosandey V.; 1 ex., Ayent VS, 18.VI.2022, leg. and coll. Cosandey V.

Comment. This species has only recently been described (Vorst 2009). Previously, *C. castaneipennis* and *C. obsoletus* were grouped together under the nomen *C. lugubris* (Olivier, 1790), which was a misinterpretation of *Dermestes lugubris* Fourcroy, 1775 (Vorst 2009). Despite its presence being attested by old specimens collected before 1950, *C. castaneipennis* is mentioned here for the time in Switzerland, where it is present in most regions. This species may have been expanding recently into Western Europe (Vorst 2009).

C40) *Cercyon* (*Cercyon*) *granarius* Erichson, 1837

Examined material. 2 ex., BE, Nidau, 4.IX.1911, 14.X.1915, leg. and coll. Mathey A., NMBE; 5 ex., Kt. Bern, Aarwangen, III.1928, V.1928, VII.1928, VII.1929, leg. and coll. Linder A., ETH; 1 ex., Lucerne, V.1933, leg. and coll. Toumayeff G., MHNG; 3 ex., Kt. Bern, Uettligen, IX.1940, X.1943, leg. and coll. Linder A., ETH; 1 ex., ZH, Niederglatt, IX.1952, leg. and coll. Toumayeff G., MHNG; 1 ex., Überlingen am Bodensee, 26.III.1961, leg. Horion A., det. Bouwer R., SMNS; 1 ex., Suisse, FG [Fribourg], Lussy, V.1972, leg. and coll. Toumayeff G., MHNG; 2 ex., Lac des Taillères, 25.IX.1977, leg. Scherler P., NMBE; 1 ex., FG [Fribourg], Siviriez, La Pierra, VI.1978, leg. and coll. Toumayeff G., MHNG; 1 ex., VD, Bavois, Bernoise, X.1984, leg. and coll. Toumayeff G., MHNG; 1 ex., Suisse, Genève, Bois de Jussy, marais, 18.V.1989, leg. Besuchet C., MHNG; 1 ex., CH, LU, Wauwilermoos, VI.1996, leg. Rezbanyai-Reser L., NMLU; 1 ex., Hemishofen SH, 31.X.2018, leg. Claude F., coll. Chittaro Y.; 6 ex., Siviriez FR, 22.VI.2021, leg. and coll. Cosandey V.; 1 ♂, Chavannes-de-Bogis VD, 10.IX.2021, leg. and coll. Chittaro Y.

Published data. 1)Genf (Heer 1841); 1)Matzingen, Junkholz, IV.1954 by Hugentobler H. (Hugentobler 1966).

Comment. While this species is widely distributed in the Palaearctic region, it is only known from a few Swiss specimens, almost all from the Plateau. *Cercyon granarius* is found sporadically in wetlands.

C41) [*Cercyon* (*Cercyon*) *littoralis* (Gyllenhal, 1808)]

Examined material. 3,4,6,8)1 ex., Genève, Sionnet, 2.V., leg. and coll. Maerky C., MHNG.

Published data. 1,8)VS, Inden D, 16.IX.1992, leg. Uhlig M. (Uhlig and Uhlig 2006).

Comment. The only examined specimen with "a Swiss label" belongs to the problematic collection of Charles Maerky, which should not be considered (Monnerat et al. 2015). The specimens mentioned in the literature were probably misidentified, but we could not check them. Although widely distributed in the Palaearctic region, this species is restricted to coastal environments (Freude 2011), habitats that obviously do not exist in Switzerland.

C42) *Cercyon* (*Cercyon*) *tatricus* Endrödy-Younga, 1967; Fig. 1C

Examined material. 2 ex., Alp Tablasot, 8.VIII.1918, leg. and coll. Handschin E., BNM; 2 ex., Murtera, Abstieg, 11.VIII.1918, leg. and coll. Handschin E., BNM; 2 ex., Alp Tavrü, 12.VIII.1918, leg. and coll. Handschin E., BNM; 2 ex., Tavrü, 30.VII.1920, leg. and coll. Handschin E., BNM; 2 ex., Davoser Berge, Bergalp, 5.IX.1934, leg. and coll. Wolf J.-P., ETH; 1 ex., Suisse, Grisons, Flüela-nord, 20.IX.1965, leg. Comellini A., MHNG; 2 ex., Suisse, Grisons, s/Samnaun, 26.VIII.1968, leg. Besuchet C., MHNG; 1 ex., Suisse, Grisons, Maloja, Lac de Cavloc, 27.VIII.1968, leg. Besuchet C., MHNG; 6 ex., CH, UR, Klausenpass, Hint. Rustigen, 20.VII.1969, leg. and det. Herger P., NMLU; 8 ex., Suisse, Grisons, s/Pontresina, 9.IX.1985, leg. Besuchet C., MHNG; 1 ex., Suisse, Grisons, Casaccia, 12.IX.1985, leg. Besuchet C., MHNG; 9 ex., Suisse, Uri, Klausen, 25.IX.1985, leg. Besuchet C., MHNG; 1 ex., UR, Klausenpass, Claridenböderli, 29.VII.1995, leg. Kobel E., NMBE.

Comment. This species, described from the High Tatra (Slovakia), is only known from the Carpathian Mountains (Romania, Ukraine), from the Eastern Palaearctic region (Eastern Siberia and Russian Far East) (Fikáček 2006) and now also from Switzerland. In the latter country, *C. tatricus* appears to be restricted to the eastern Alps, mainly between 1800 and 2200 m a.s.l.

C43) [*Cercyon* (*Cercyon*) *tristis* (Illiger, 1801)]

Published data. 2)Chiasso by Fontana P. (Fontana 1947); 1,27)Alp Tavrü, 30.VII.1920 by Handschin E. (Handschin 1963).

Comment. The data mentioned by Fontana (1947) as *C. tristis* (identified as such in his collection) actually turned out to be specimens of *C. analis* (4 ex.) and *C. convexisculus* (2 ex.), and the specimens mentioned by Handschin (1963) were not found in the collections examined, but they probably relate to other species in the genus. *Cercyon tristis* is currently not retained for the Swiss fauna, although it remains potentially present, given its wide Palaearctic distribution.

C44) *Pachysternum capense* (Mulsant, 1844); Fig. 1F

Examined material. 1 ex., Mendrisio TI, 24.X.2015, leg. and coll. Cosandey V.; 2 ex., Chiasso TI, 24.X.2015, leg. and coll. Cosandey V.; 1 ex., Lugano TI, 25.X.2015, leg. and coll. Cosandey V.

Comment. This species is native to sub-Saharan Africa (Lökkös et al. 2014). Now almost cosmopolitan, it has been recorded in many European countries in recent decades: it has been present in Greece since 1997 (Fikáček and Boukal 2004), Italy since 2001 (Hebauer 2006), France since 2005 (Queney 2009), Hungary since 2006 (Lökkös et al. 2014), and Romania since 2009 (Lökkös et al. 2014). The specimens collected in 2015 in the south of the canton of Ticino are the first records for Switzerland.

C45) *Sphaeridium substriatum* Faldermann, 1838

Examined material. 1 ex., Chiasso, leg. and coll. Fontana, MSNL; 1 ex., Martigny, coll. Cerutti N., MHNF; 3)1 ex., Genève, Rouelbeau, 22.VII., leg. and coll. Maerky C., MHNG; 1 ex., Sion, V.1851, leg. Anonymous, MZL; 1 ex., Valais, Niouc, 10.VI.1936, leg and coll. Julliard C., MHNG; 5 ex., Filisur, 21.VII.1937, 15.VIII.1937, 10.VII.1938, leg. and coll. Wolf J.-P., ETH; 1 ex., Les Follaterres [Les Follatères], 2.VIII.1949, leg. Besuchet C., MZL; 1 ex., Valais, Leuk, 5.VI.1958, leg. and coll. Pochon H., MHNF; 1 ♂, Chiasso TI, 24.X.2015, leg. and coll. Cosandey V.; 1 ♂, 1 ♀, Locarno TI, 27.IX.2021, leg. and coll. Sanchez A.

Comment. Althoug widely distributed in the Palaearctic region, this species is only found in the most thermophilic regions of Switzerland. Unlike the other species of the genus *Sphaeridium*, *S. substriatum* is not abundant in Switzerland.

C46) *Spercheus emarginatus* (Schaller, 1783)

Examined material. 3)2 ex., Basel, coll. Benteli F., NMBE; 3)9 ex., Basel, coll. Rätzer A., NMBE; 1 ex., Kt. Waadt, Villeneuve, X.1944, leg. and coll. Linder A., ETH; 1 ex., Egnach, Bodensee, 30.X.1964, leg. Kless J., MHNG; 1 ex., Staad, 7.VIII.1974, leg. and coll. Spälti A., MHNG; 1 ex., Les Grangettes, 19.XI.1987, leg. and coll. Scherler P., NMBE; 3 ex., Noville, Les Grangettes, Grand canal, 27.VIII.1992, leg. Naceur N., MHNG.

Published data. 1)Malans by Amstein J.-G. (Heer 1841); 1 ex., Villeneuve [VD], 10.1944 by Peez A. (Linder 1946); Egnach b. Luxburg, X.1964, leg. Kless J. (Hugentobler 1966); Grangettes, 1992, 1993, 1997 by Naceur N. (Naceur 1997).

Comment. Although widely distributed in the Palaearctic region, this species has been very rarely found in Switzerland. It colonizes eutrophic ponds such as reedbeds and oxbow lakes (Hebauer and Klausnitzer 1998). According to Buhk (1910), it is mainly overlooked because of its cryptic coloration and quiet behavior, with beetles remaining motionless for long periods when caught in a net. In Switzerland, *S. emarginatus* seems to be restricted to lowland areas and has been found mainly near large pieces of water.

Discussion

This study is the first annotated list focusing on the Swiss Hydrophiloidea. Based on a large and robust dataset, the faunal knowledge of this group in Switzerland can now be considered solid. Occurrence maps for the accepted species are available on the info fauna map server (www.infofauna.ch; https://lepus.infofauna.ch/carto), showing the distribution of Hydrophiloidea in Switzerland. All the data have been transmitted to GBIF, making this work part of a global understanding of biodiversity. This study is part of a wider project to update our knowledge of the fauna of aquatic beetles in Switzerland but is also a further step towards a complete comprehension of the beetle fauna of Switzerland (see, for example, Chittaro et al. 2021; Sanchez and Chittaro al. 2022).

According to our results, a total of 105 species of Hydrophiloidea belong to the Swiss fauna. As observed worldwide, Hydrophilidae is the most diverse family of Hydrophiloidea in Switzerland (76 species), followed by Helophoridae (21), Hydrochidae (4), Georissidae (3), and Spercheidae (1). Seven species are mentioned for the first time in the country, while 16 species mentioned from Switzerland in the past have been withdrawn from the species list or considered doubtful. The presence of several species that had gone unnoticed in Switzerland (even though collected specimens had sometimes been deposited in museums for decades) was revealed by an exhaustive revision of collections, as in the case of *Coelostoma hispanicum* (Cosandey 2023). Additional examples provided by this study are found in thermophilic (*Sphaeridium substriatum*) and alpine (*Cercyon alpinus*, *C. tatricus*) Sphaeridiinae. In addition, recent descriptions of *Anacaena lohsei*, another alpine species, based in part on material from Switzerland, and *Cercyon castaneipennis* show the lack of knowledge of this group, even in well-studied regions such as Central Europe (Berge Henegouwen and Hebauer 1989; Vorst 2009). Another new species for Switzerland is *Pachysternum capense*, a now cosmopolitan species like *Cercyon laminatus* and *Cryptopleurum subtile*, which were already known to be in Switzerland. The potential expansion of *Pachysternum capense*, which is well documented in Europe (see comment C44), will be interesting to follow in Switzerland.

Among the species present in Switzerland, several only occur at high altitudes in mountainous habitats (such as *Cercyon alpinus*, *C. tatricus*, *Crenitis punctatostriata*) and some are sub-endemic (*Anacaena lohsei*, *Helophorus fauveli*), underlying the importance of this country for the conservation of some rare, localized, and highly specialized species. On the other hand, a significant part of Swiss wetlands (80% to 88% nationwide) has been destroyed over the last century (Küchler et al. 2018), drained to gain arable land and to extend urban areas, and 90% of wetland types are on the Swiss red list of habitat types (Delarze et al. 2016). It is reasonable to assume that aquatic beetles may have been heavily impacted. Besides the aquatic species, a significant proportion of Hydrophilidae, most of which are Sphaeridiinae, feed on mammal dung. Unlike Scarabaeidae dung beetles (Floate et al. 2005), Sphaeridiinae do not seem to suffer directly from the use of veterinary parasiticides but are mainly affected by the reduction in number of fly larvae in dung patches (Cook and Gerhardt 1977). Although several species appear to be in steep decline (*Berosus* spp., *Hydrophilus piceus*) or may already be extinct (*Hydrophilus aterrimus* or *Laccobius thermarius*), there is no Hydrophiloidea red list for Switzerland, unlike for other aquatic beetle groups such as the Hydradephaga (Brancucci 1994). There is however an urgent need for a better understanding of factors threatening the Hydrophiloidea. The elaboration of a red list based on historical data provided by our study as well as recent and prospective data is the best way to reach this goal.

Acknowledgments

We are thankful to all the Swiss museum curators, who have welcomed us so often and so kindly within their institutions over the past few years, as well as all the active coleopterists whose expertise has enriched our understanding of the distribution of these species in Switzerland. Special thanks are due to the reviewers of this paper Robert Angus and Vojtěch Kolár for their meaningful comments on the manuscript. We also thank Tatiana Zingre for her advice on the manuscript and Giulio Cuccodoro for providing us with the photographic equipment.

References

Angus R (1982) Separation of two species standing as *Helophorus aquaticus* (L.) (Coleoptera, Hydrophilidae) by banded chromosome analysis. Systematic Entomology 7: 265–281. https://doi.org/10.1111/j.1365-3113.1982.tb00444.x

Allenspach V (1978) Fünfter Beitrag zur Coleopteren-Fauna der Schweiz von Arthur Linder. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 51: 407–410.

Angus R (1992) Insecta, Coleoptera, Hydrophilidae, Helophorinae. In: Schwoerbel Z (Ed.) Süßwasserfauna von Mitteleuropa (Vol. 20/10-2). Gustav Fischer Verlag, Stuttgart, Jena, New York, 144 pp.

Bameul F, Queney P (2014) Hydrophiloidea Latreille, 1802a. In: Tronquet M (Ed.) Catalogue des Coléoptères de France. Association Roussillonnaise d'Entomologie, Perpignan, 167–179.

Berge Henegouwen A van, Hebauer F (1989) *Anacaena lohsei*, a new species from Italy and Switzerland (Coleoptera: Hydrophilidae). Bulletin et Annales de la Société Royale Belge d'Entomologie 125: 7–9.

Bloom DD, Fikáček M, Short AEZ (2014) Clade Age and Diversification Rate Variation Explain Disparity in Species Richness among Water Scavenger Beetle (Hydrophilidae) Lineages. PLoS ONE 9(6): e98430. https://doi.org/10.1371/journal.pone.0098430

Bouchard P, Bousquet Y, Davies A, Alonso-Zarazaga M, Lawrence J, Lyal C, Newton A, Reid C, Schmitt M, Slipinski A, Smith A (2011) Family-group names in Coleoptera (Insecta). ZooKeys 88: 1–972. https://doi.org/10.3897/zookeys.88.807

Brancucci M (1994) Liste rouge des hydradéphages menacés de Suisse In: Duelli P (Ed.) Liste rouge des espèces animales menacées de Suisse. Office fédéral de l'environnement, des forêts et du paysage (OFEFP), Berne, 60–63.

Brandstetter CM, Kapp A (1998) Käferinventar von Vorarlberg und Liechtenstein. Insecta: Coleoptera. Eigenverlag des Ersten Vorarlberger Coleopterologischen Vereins, Bürs, 92 pp.

Broun T (1886) Manual of New Zealand Coleoptera. Part III. Colonian Museum and Geological Survey Department, Wellington, 651 pp.

Buhk F (1910) Lebensweise und Entwicklung von *Spercheus emarginatus* Schall. Entomologische Rundschau 27: 127–128.

Callot H (2001) Catalogue et Atlas des Coléoptères d'Alsace. Tome 12, Hydrophilidae, Hydraenidae, Hydrochidae, Spercheidae, Georissidae, Colonidae, Leiodidae, Scydmaenidae, Ptiliidae, Corylophidae, Clambidae. Société Alsacienne d'Entomologie, Musée zoologique de l'Université et de la ville de Strasbourg, 111 pp.

Callot H (2018) Liste de référence des Coléoptères d'Alsace. Société Alsacienne d'Entomologie, 107 pp. http://soc.als.entomo.free.fr [version du 30-IX-2018]

Carron G (1999) Les Coléoptères aquatiques de quelques étangs d'Ajoie (Commune de Bonfol, JU). Bulletin Romand d'Entomologie 17: 127–146.

Chittaro Y, Sanchez A, Geiser M (2021) An updated checklist of the Cantharidae and Lycidae of Switzerland (Coleoptera, Elateroidea). Alpine Entomology 5: 77–94. https://doi.org/10.3897/alpento.5.67808

Cook CW, Gerhardt RR (1977) Selective mortality of insects in manure from cattle fed Rabon and Dimilin. Environmental Entomology 6: 589–90. https://doi.org/10.1093/ee/6.4.589

Cosandey V (2023) Bilan de trois années de captures de Coléoptères aquatiques dans le canton de Genève. Entomo Helvetica 16: 107–121.

Delarze R, Eggenberg S, Steiger P, Bergamini A, Fivaz F, Gonseth Y, Guntern J, Hofer G, Sager L, Stucki P (2016) Liste rouge des milieux de Suisse. Abrégé actualisé du rapport technique 2013 sur mandat de l'Office fédéral de l'environnement (OFEV), Berne, 33 pp.

Drost MBP (1988) *Helophorus croaticus* and *H. pumilio* in The Netherlands with description of their larvae (Coleoptera; Hydrophilidae). Entomologische Berichte Amsterdam 49(1): 1–7.

Esser J, Mainda T (2022) Elfter Nachtrag zum Verzeichnis der Käfer (Coleoptera) Brandenburgs und Berlins. Märkische Entomologische Nachrichten 24(1): 1–22.

Fägerström C (2019) Några för Sverige nya skalbaggar [Some beetle species new to the Swedish fauna]. Entomologisck Tidskrift 140(1): 73–79.

Favre E (1890) Faune des Coléoptères du Valais et des Régions Limitrophes. Zurcher, Furrer, 448 pp.

Fikáček M (2006) Taxonomic status of *Cercyon alpinus*, *C. exorabilis*, *C. strandi* and *C. tatricus* and notes on their biology (Coleoptera: Hydrophilidae: Sphaeridiinae). Annalen des Naturhistorischen Museums in Wien 107(B): 145–164.

Fikáček M (2015) Spercheidae. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera (Vol. 2). Hydrophiloidea, Staphylinoidea. Revised and Updated Edition. Brill, Leiden Boston, 36–37.

Fikáček M, Angus RB, Gentili E, Jia F, Minoshima YN, Prokin A, Przewoźny M, Ryndevich SK (2015a) Helophoridae, Hydrochidae, Hydrophilidae. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera (Vol. 2). Hydrophiloidea, Staphylinoidea. Revised and Updated Edition. Brill, Leiden Boston, 25–33, 35–36, 37–76.

Fikáček M, Ryndevich SK, Minoshima YN, Prokin A (2015b) New Nomenclatural and Taxonomic Acts, and Comments. Hydrophilidae. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera (Vol. 2). Hydrophiloidea, Staphylinoidea. Revised and Updated Edition. Brill, Leiden Boston, 1 pp. https://doi.org/10.1163/9789004296855_002

Fikáček M, Boukal M (2004) *Pachysternum capense*, a new genus and species for Europe, and updated key to genera and subgenera of European Sphaeridiinae (Coleoptera: Hydrophilidae). Klapalekiana 40: 1–12.

Fikáček M, Przewoźny M (2015) Georissidae Laporte, 1840. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera (Vol. 2). Hydrophiloidea, Staphylinoidea. Revised and Updated Edition. Brill, Leiden Boston, 33–35.

Floate (2005) Fecal Residues of Veterinary Parasiticides: Nontarget Effects in the Pasture Environment. Annual Review of Entomology 50: 153–179. https://doi.org/10.1146/annurev.ento.50.071803.130341

Fontana P (1922) Contribuzione alla Fauna coleotterologica ticinese. Bolletino della Società Ticinese di Scienza Naturali 19: 35–48.

Forster GN, Bilton DT, Friday LE (2014) Keys to adults of the water beetles of Britain and Ireland (Part 2). Handbooks of the Identification of British Insects (Vol. 4, Part 5b). Royal Entomological Society, Londres, 126 pp.

Foster GN, Friday LE (2011) Keys to adults of the water beetles of Britain and Ireland (Part 1). Handbooks of the Identification of British Insects (Vol. 4, Part 5) (2nd edn.). Royal Entomological Society, Londres, 144 pp.

Fossen EI, Ekrem T, Nilsson AN, Bergsten J (2016) Species delimitation in northern European water scavenger beetles of the genus *Hydrobius* (Coleoptera, Hydrophilidae). ZooKeys 564: 71–120. https://doi.org/10.3897/zookeys.564.6558

Freude H (2011) Die Käfer Mitteleuropas, Band 3. Adephaga II, Palpicornia. Spektrum Akademischer Verlag, Heidelberg, 367 pp. https://doi.org/10.1007/978-3-8274-2211-8

Gassmann M (1974) La faune des Coléoptères aquicoles du Marais de Kloten. Etude faunistique et écologique considérant principalement les relations entre la faune et la végétation. Thèse EPFZ N°5232, Zürich, 166 pp.

Gentili E, Chiesa A (1975) Revisione dei *Laccobius* Palearctici (Coleoptera Hydrophilidae). Estratto dale memorie della Società entomologica italiana volume 54. Fratelli Pagano, Genova, 187 pp.

Gerend R (2014) Updating the water beetle fauna of Luxembourg, with notes on the habitat of *Enochrus fuscipennis* (Thomson, 1884) in Luxembourg, Lorraine and Switzerland (Coleoptera: Dytiscidae, Helophoridae, Hydrophilidae, Dryopidae). Bulletin de la Société des Naturalistes Luxembourgeois 115: 211–225.

Greń C, Lubecki K (2017) Water beetles (Coleoptera: Adephaga, Hydrophiloidea, Byrrhoidea) in Bulgaria: new records. Annals of the Upper Silesian Museum in Bytom, Entomology 26: 1–20.

Handschin E (1963) Die Coleopteren des schweizerischen Nationalparkes und seiner Umgebung. Ergebnisse der wissenschaftlichen Untersuchungen im schweizerischen Nationalpark. Band VIII. Lüdin, Liestal, 302 pp.

Hansen M (1987) Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica (Vol. 18). E.J. Brill/ Scandinavian Science Press ltd., Leiden, Copenhagen, 254 pp. https://doi.org/10.1163/9789004273429

Hansen M (1999) Hydrophiloidea (s. str.) (Coleoptera). World Catalogue of Insects (Vol. 2). Apollo Books, Stenstrup, 416 pp. https://doi.org/10.1163/9789004629042_004

Hebauer F (2006) *Pachysternum capense* (Mulsant, 1844). In: Rocchi S, Bordoni A, Bramanti A (Eds) Ricerche sulla Coleotterofauna delle zone umide della Toscana. VII. Lago di Porta (Lucca-Massa Carrara) (Coleoptera). Frustula Entomologica, Pisa, 140–142.

Hebauer F, Klausnitzer B (1998) Insecta: Coleoptera: Hydrophiloidea (exkl. *Helophorus*). Süsswasserfauna von Mitteleuropa. Bd. 20/10-2, 134 pp.

Heer O (1841) Fauna coleopterorum helvetica. Pars 1. Turici: Impensis Orelii, Fuesslini et Sociorum, 652 pp.

Herger P, Germann C (2017) Käfer aus Lichtfallenfängen in Conthey (VS) und in Seseglio (TI) (Coleoptera). Entomo Helvetica 10: 87–92.

Hudson GV (1934) New Zealand Beetles and their Larvae. An Elementary Introduction to the Study of our Native Coleoptera. Fergusson and Osborn, Wellington, 236 pp.

Hugentobler H (1966) Beitrag zur Kenntnis der Käfer der Nordostschweiz. Naturwissenschaftlichen Gesellschaft St. Gallen, 248 pp.

Jäch MA (1998) Annotated check list of aquatic and riparian/littoral beetle families of the world (Coleoptera). In: Jäch MA, Ji L (Eds) Water Beetles of China (Vol. II). Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien, 25–42.

Jäch MA, Balke M (2008) Global diversity of water beetles (Coleoptera) in freshwater. Hydrobiologia 595: 419–442. https://doi.org/10.1007/s10750-007-9117-y

Kahlen M, Hellrigl K (1996) Ordnung Coleoptera-Käfer. In: Hellrigl K (Ed.) Die Tierwelt Südtirols. Naturmuseum Südtirol, Bozen, 393–511.

Knisch A (1924) Hydrophilidae. Coleopterorum Catalogus. Pars 79. W. Junk, Berlin, 306 pp.

Köhler F, Klausnitzer B (1998) Entomofauna Germanica. Verzeichnis der Käfer Deutschlands. Entomologische Nachrichten und Berichte, Dresden, Beiheft 4: 1–185.

Küchler M, Küchler H, Bergamini A, Bedolla A, Ecker K, Feldmeyer-Christe E, Graf U, Holderegger R (2018) Moore der Schweiz. Haupt, Bern, 258 pp.

Lillig M (2022) Die Gattung *Megasternum* Mulsant, 1844 im Saarland (Coleoptera: Hydrophilidae, Megasternini). Delatinia 47: 11–21.

Linder A (1946) 2. Beitrag zur Coleopteren-Fauna der Schweiz. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 20: 197–207.

Linder A (1953) 3. Beitrag zur Coleopteren-Fauna der Schweiz. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 26(1): 63–71.

Linder A (1967) Nachtrag zum Verzeichnis der Bündner Coleopteren von Dr. E. Killias. Jahresbericht der Naturforschenden Gesellschaft Graubünden 93: 78–108.

Löbl I, Löbl D [Eds] (2015) Catalogue of Palaearctic Coleoptera. Volume 2. Hydrophiloidea – Staphylinoidea. Revised and Updated Edition. Brill, Leiden Boston, 1702 pp. https://doi.org/10.1163/9789004296855

Lökkös A, Boukal M, Fikáček M (2014) The hydrophilid beetle *Pachysternum capense* (Mulsant, 1844) (Coleoptera: Hydrophilidae) became a worldwide adventive species: a summary of distribution with new records from Europe, Australia, and South America. North-western Journal of Zoology 10(2): 333–336.

Michaud A (1937) Observations sur la Faune entomologique du Val d'Orvin. Bulletin de la Société Neuchâteloise des Sciences Naturelles 62: 84–98.

Monnerat C, Chittaro Y, Sanchez A, Gonseth Y (2015) Critères et procédure d'élaboration de listes taxonomiques nationales: le cas des Buprestidae, Cerambycidae, Lucanidae et Cetoniidae (Coleoptera) de Suisse. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 88: 155–172.

Mulhauser B (1997) Inventaire de la faune de la Grande Cariçaie. Grande Caricaie, Yverdon, 356 pp.

Naceur N (1997) Synthèse du suivi scientifique des invertébrés aquatiques dans les mares des réserves gérées par la Fondation: Bilan 1992–1996. Etude et gestion du site marécageux de Noville. Fondation des Grangettes, rapport 13, 23 pp.

OFEV (2022) Les régions biogéographiques de la Suisse. 1ère édition actualisée 2022. 1ère parution 2001. Connaissance de l'environnement n° 2214. Office fédéral de l'environnement, Berne, 28 pp.

Pirisinu Q (1981) Palpicorni (Coleoptera: Hydraenidae, Helophoridae, Spercheidae, Hydrochidae, Hydrophilidae, Sphaeriididae). Guide per il riconoscimento delle specie animali delle acque interne italiane 13. Consiglio Nazionale delle Ricerche, Verona, 97 pp.

Queney P (2009) Localités récentes et nouvelles pour des Coléoptères aquatiques et un Hydrophilidae terrestre de la faune de France peu connus ou de distribution incertaine (Coleoptera Sphaeriusidae, Dytiscidae, Haliplidae, Helophoridae, Hydrochidae, Hydrophilidae, Spercheidae, Hydraenidae, Dryopidae, Heteroceridae, Limnichidae). L'Entomologiste 65(1): 27–33.

Queney P, Prévost P (2021) Clés d'identification des coléoptères aquatiques de France métropolitaine. Myxophaga, Polyphaga Hydrophiloidea (adultes). Association des entomologistes de Picardie (Adep), Compiègne, Office pour les insectes et leur environnement (Opie), Guyancourt, 190 pp.

Rätzer A (1888) Nachträge zur Fauna coleopterorum Helvetiae besonderes aus dem Gebiete des berner Seelandes, des Jura und der Walliseralpen. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 8: 20–42.

Rocchi S (2002) Reperti inediti di Hydrophiloidea in Italia (Insecta Coleoptera Helophoridae, Hydrochidae, Hydrophilidae). Quaderno di Studi e Notizie di Storia Naturale della Romagna, Cesena, 16 suppl.: 43–48.

Ryndevich SK (2017) New faunistics records of hydrophilid beetles (Coleoptera: Hydrophiloidea) from Eurasia. BarSU Herald. Series of Biological Sciences (General Biology), Agricultural Sciences (Agronomy) 5: 65–70.

Sainte-Claire Deville J (1935) Catalogue raisonné des coléoptères de France. L'Abeille, Journal d'Entomologie 36: 1–160.

Salamé F (2023) Découverte de *Megasternum immaculatum* (Stephens, 1829), espèce nouvelle pour la faune de France (Coleoptera Hydrophilidae Sphaeridiinae). L'Entomologiste 79(1): 41–44.

Sanchez A, Chittaro Y (2022) Annotated checklist of the Coccinellidae (Coleoptera, Coccinelloidea) of Switzerland. Alpine Entomology 6: 111–127. https://doi.org/10.3897/alpento.6.89476

Schödl S (1991) Revision des Gattung *Berosus* Leach, 1. Teil: Die paläarktischen Arten der Untergattung *Enoplurus* (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 61: 111–135.

Schödl S (1993) Revision des Gattung *Berosus* Leach, 3. Teil: Die paläarktischen un orientalischen Arten der Untergattung *Berosus* s.str. (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 63: 189–233.

Shatrovskiy AG, Angus RB, Jäch MA (2023) Notes on the *Helophorus guttulus* group (Coleoptera: Helophoridae). Koleopterologische Rundschau 92: 139–151.

Short AEZ, Fikáček M (2011) World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). Acta Entomologica Musei Nationalis Pragae 51: 83–122.

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38: 723–752. https://doi.org/10.1111/syen.12024

Smetana A (1974) Revision of the genus *Cymbiodyta* Bed. (Coleoptera: Hydrophilidae). The Memoirs of the Entomological Society of Canada 106(Supplement 93): 1–113. https://doi.org/10.4039/entm10693fv

Smetana A (1980) Revision of the genus *Hydrochara* Berth. (Coleoptera: Hydrophilidae). The Memoirs of the Entomological Society of Canada 112(Supplement S111): 1–100. https://doi.org/10.4039/entm112111fv

Spangler PJ (1962) A new species of the genus *Oosternum* and a key to the U.S. species (Coleoptera: Hydrophilidae). Proceedings of the Biological Society of Washington 75: 97–100.

Stierlin G (1883) Zweiter Nachtrag zur Fauna coleopterorum helvetica. Neue Denkschriften der schweizerischen Gesellschaft für die gesammten Naturwissenschaften 8(3): 1–98.

Stierlin G (1900) Fauna coleopterorum helvetica. Die Käfer-Fauna der Schweiz nach der analytischen Methode. I. Theil. Bolli & Böcherer, Schaffhausen, 667 pp.

Stierlin G, Gautard VV (1867) Fauna Coleopterorum Helvetica. Die Käfer-Fauna der Schweiz. Schaffhausen und Vevey, 372 pp.

Täschler M (1872) Beitrag zur Coleopteren-Fauna der Kantone St. Gallen und Appenzell. Berichte der Tätigkeiten der St. Galler Naturwissenschaftlichen Gesellschaft, 39–249.

Toumayeff G (1980) De quelques Coléoptères dont la présence en Suisse est contestée ou ignorée. Mitteilungen der Entomologischen Gesellschaft Basel 30(4): 211–212.

Toussaint EFA, Short AEZ (2022) Historical Biogeography of Holarctic *Cymbiodyta* Water Scavenger Beetles in the Times of Cenozoic Land Bridge Dispersal Routes. Insect Systematics and Diversity 3(5): 1–7. https://doi.org/10.1093/isd/ixz017

Uhlig M, Uhlig B (2006) Zur Käferfauna der Schweiz (Coleoptera ohne Staphylinidae). Entomologische Berichte Luzern 56: 1–20.

Vorst O (2009) *Cercyon castaneipennis* sp. n., an overlooked species from Europe (Coleoptera: Hydrophilidae). Zootaxa 2054: 59–68. https://doi.org/10.11646/zootaxa.2054.1.4

Zhou Y-L, Caterino MS, Ren D, Slipinski A (2020) Phylogeny and evolution of Mesozoic and extant lineages of Histeridae (Coleoptera), with discovery of a new subfamily Antigracilinae from the Lower Cretaceous. Cladistics 36: 521–539. https://doi.org/10.1111/cla.12418

Alpine Entomology 7 2023, 185–194 | DOI 10.3897/alpento.7.109855

PENSOFT.

Alpine
Entomology

Taxonomic study of the alpine carabid beetle *Nebria* (*Falcinebria*) *taketoi* Habu, 1962 (Coleoptera, Carabidae)

Kôji Sasakawa[1]

[1] *Laboratory of Zoology, Department of Science Education, Faculty of Education, Chiba University, 1-33 Yayoi-cho, Inage-ku, Chiba-shi, Chiba, 263-8522 Japan*

https://zoobank.org/D86CC411-147C-43DF-8394-337CB9CC6341

Corresponding author: Kôji Sasakawa (ksasa@chiba-u.jp)

Academic editor: Andreas Sanchez ♦ **Received** 21 July 2023 ♦ **Accepted** 3 October 2023 ♦ **Published** 12 October 2023

Abstract

The carabid beetle *Nebria taketoi* Habu, 1962 is endemic to the high-altitude mountains of Honshu, Japan; due to its rarity, it is one of the least taxonomically studied species among Japanese *Nebria*. This study taxonomically revised *N. taketoi* based on morphological comparisons, mainly of the endophallus in males, and geometric morphometrics of the pronotum, a taxonomically useful external character. Specimens previously identified as *N. taketoi* were found to belong to at least two species: *N. taketoi*, with a currently confirmed distribution in the northern Hida Mountains (type locality: Mikurigaike, Mount Tateyama), and *N. kobushicola* **sp. nov.** from the Okuchichibu and Yatsugatake mountains (type locality: Mount Kobushigatake). Species identities in populations from other localities could not be determined, as male specimens for endophallus examinations were unavailable. However, some populations may consist of species distinct from *N. taketoi* and *N. kobushicola*, based on their distribution and morphometric features. Based on comparative morphology of the endophallus, *N. kobushicola* shares features more similar to *N. niohozana* Bates, 1883 and *N. dichotoma* Sasakawa, 2020 than to *N. taketoi*.

Key Words

endophallus, Japan, male genitalia, new species description, taxonomy

Introduction

Nebria taketoi Habu, 1962 is a Japanese endemic species of the beetle family Carabidae found in high-elevation areas in the mountains of central Honshu. It is one of the least studied Japanese species of the genus *Nebria*, mainly due to its rarity. To date, there are only a few collection records, and public collections contain a limited number of specimens (e.g., Yoshitake et al. 2011; Yoshimatsu et al. 2018). Moreover, studies of *N. taketoi* have been hindered by the complicated nomenclatural history of this species and the resulting misunderstandings. Specifically, two of the three papers on the taxonomy of this species were written in Japanese (Uéno 1953; Nakane 1974), such that the nomenclature has been incorrectly understood by researchers outside Japan (Farkač and Janata 2003; Ledoux and Roux 2005; Huber 2017).

This study performed a taxonomic revision of *N. taketoi* based on two types of analyses that have been performed in some *Nebria* taxa but not in *N. taketoi*: a comparative morphology of the endophallus (the membranous inner sac everted from the aedeagus) of the male genitalia, which when fully inflated often have a complex shape that provides taxonomic information; and geometric morphometrics, which can quantitatively evaluate subtle morphological differences that are difficult to detect via traditional morphometrics (e.g., aspect ratios). The utility of these two approaches in species- and supra-species-level taxonomies has been demonstrated in some *Nebria* taxa (e.g., Huber et al. 2010; Sasakawa 2016; Huber and Schnitter 2020), including *Nebria reflexa* Bates, 1883 and its relatives, which belong to the same subgenus as and are closely related to *N. taketoi*

(Sasakawa 2000; Sasakawa and Itô 2021). Therefore, the two analytical approaches were employed in this study to clarify the taxonomy of *N. taketoi*.

Materials and methods

Materials

Specimens treated as *Nebria taketoi* or *N. nakanei* Uéno, 1953 and housed in the collections of the following institutions or individuals in Japan were examined: Gifu Prefectural Museum, Seki-shi, Gifu Prefecture (**GPM**); the Hokkaido University Museum, Sapporo, Hokkaido (**HUM**); Kenta Sawada, Toyama-shi, Toyama (**KSWD**); the National Agriculture and Food Research Organization, Tsukuba-shi, Ibaraki (**NARO**); and Tateyama Caldera Sabo Museum, Tateyama-machi, Toyama (**TCSM**). Label data of the *N. taketoi* holotype were provided in the original notation without any modification; a slash (/) was used to separate lines on the same label, and a double slash (//) to separate different labels. Label data (i.e., locality and collection date) of other specimens, which were often written in a simplified, older notation, were modified to be compatible with the more-detailed, currently used notation whenever possible.

Among the collection sites, Murôdodaira is only 70 m from the type locality, Mikurigaike, and was therefore regarded as being virtually the same site as the type locality. In total, 10 male and 17 female specimens from 14 sites, ranging from the Iide Mountains in the north to Mount Kitadake (Akaishi Mountains) in the south and Mount Ontakesan in the west, were examined (Fig. 1).

Comparative morphology

Body length was measured from the mandible apices to the elytral end based on scaled dorsal-view photographs taken with a digital camera, using the software ImageJ ver.

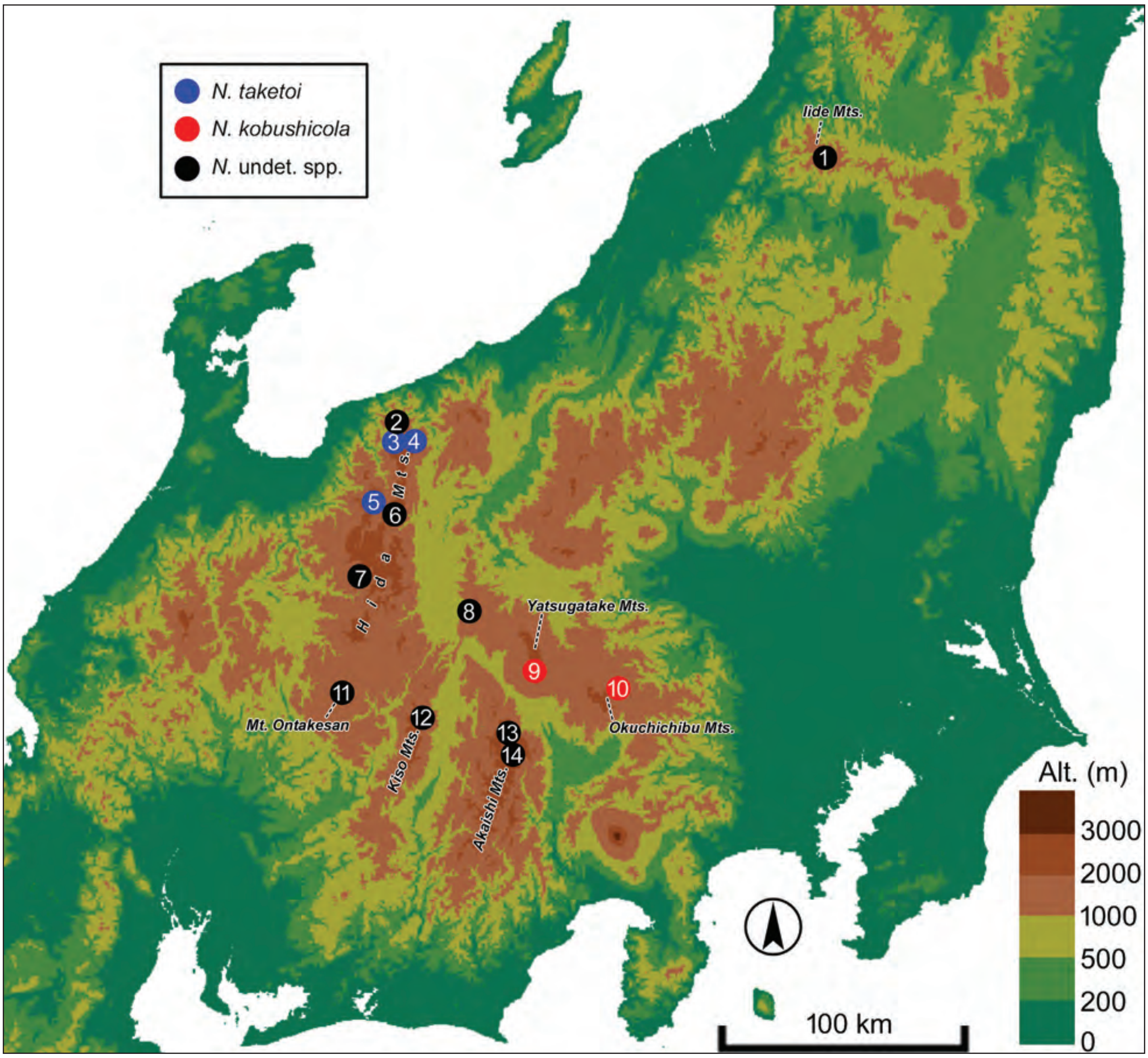


Figure 1. Collection sites of the examined specimens. Locality numbers correspond to those in Fig. 6.

1.50i (Rasband 2016). Measurements and subsequent calculations [mean and standard deviation (SD)] were performed using values with an accuracy of 0.001 mm, but values with an accuracy of 0.01 mm are reported in the species descriptions. The endophallus was everted and fully inflated by injecting toothpaste from the base of the aedeagus. In some specimens, toothpaste injection into the gonopore protrusion and some lobes was difficult, such that these structures could not be fully everted. This was also the case in consubgeneric *N. reflexa* and allied species, and particularly for their gonopore protrusion (Sasakawa 2020). To prevent damage to these structures by toothpaste injection, the endophallus of the respective specimens was observed with the gonopore protrusion and lobes not fully everted. The homology and terminology of the endophallus structures were adopted from Sasakawa (2020).

Morphometric analyses

Geometric morphometrics were performed for the dorsal view of the pronotum. The utility of the shape of pronotum for species-level taxonomy has already been demonstrated in various groups of *Nebria* (Huber et al. 2010; Roggero et al. 2013; Sasakawa 2016, 2020; Huber and Schnitter 2020). Scaled digital images were obtained using a digital camera attached to a microscope. The pronotum was maintained with the apices of anterior and posterior angles of both lateral sides in the same horizontal plane when taking photographs. Using the software tpsDig version 2.17 (Rohlf 2013a), four points were plotted as landmarks, and 42 points distributed along the contour at regular intervals between landmarks were plotted as semi-landmarks (Fig. 2). The landmarks are as follows: 1, anterior end along the median line; 12, apex of anterior angle of the left side; 35, apex of hind angle of the left side; and 46, posterior end along the median line. The semi-landmarks are as follows: 2–11, between landmarks 1 and 12; 13–34, between landmarks 12 and 35; and 36–45, between landmarks 35 and 46. Using the software tpsRelw version 1.53 (Rohlf 2013b), the raw coordinates were converted into Procrustes coordinates, in which variations due to rotation, position and size were removed with semi-landmarks being ‘slid’ along the contours. Relative warp analysis and visualization of shape differences were also performed using this software. The raw data used in the analysis are provided in Suppl. material 1.

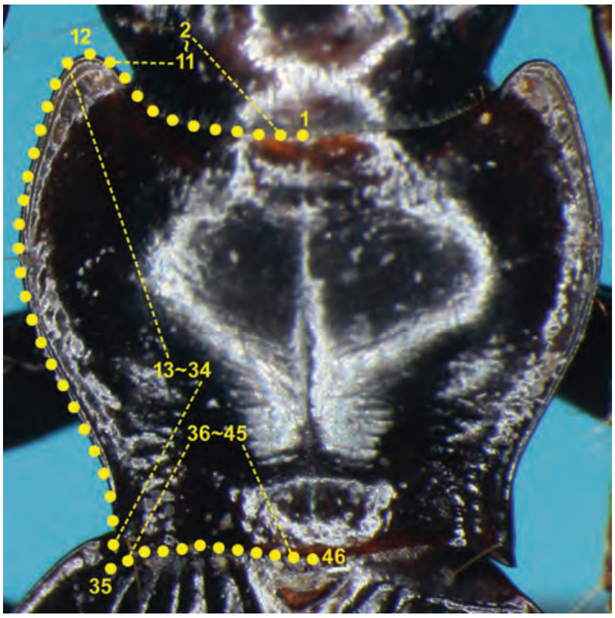


Figure 2. Positions of landmarks (1, 12, 35, and 46) and semi-landmarks (the others) on a pronotum.

Results

Comparative morphology revealed that specimens previously treated as *N. taketoi* included at least two different species (Fig. 1): *N. taketoi*, the currently confirmed distribution of which is the type locality (Mount Tateyama) and two high-altitude mountains in the northern Hida Mountains (Mount Shiroumadake and Mount Yukikuradake), and a species from Mount Kobushigatake (Okuchichbu Mountains) and Akadakekousen (Yatsugatake Mountains), described below as the new species *N. kobushicola*. These two species are distinguished by their external morphologies (Fig. 3) and by the morphology of the endophallus (Figs 4, 5).

The identities of the following specimens (2♂9♀) could not be determined due to the unavailability of male specimens from the same collection site, thus prohibiting endophallus examinations (male specimens were either absent or unsuitable for dissection): 2♀ (NARO), Iide Mountains, Niigata Prefecture, 21.vii.1976, K. Terada leg.; 1♀ (NARO), Mount Asahidake, Itoigawa-shi, Niigata Prefecture, 27.vii.1961, K. Baba leg.; 1♀ (NARO), “Ogawara”, Mount Harinokidake, on the border between Tateyama-machi, Toyama Prefecture and Omachi-shi, Nagano Prefecture, 3.viii.1958, M. Kurata leg.; 1♀ (GPM), Kuriyadani Valley, 1600–2000 m, on the eastern side of Mount Shakujôdake, Takayama-shi, Gifu Prefecture, 22.viii.1985, K. Suzuki leg.; 1♀ (HUM), Iriyamabe, Matsumoto-shi, Nagano Prefecture, 28.vii.1943, K. Takahashi leg.; 1♀ (NARO), Mount Ontakesan, on the border between Nagano and Gifu prefectures, 19.vii.1961, S. Imafuku leg.; 1♀ (NARO), Kitagoshodani Valley, Miyada-mura, Nagano Prefecture, 5.viii.1960, Oobori leg.; 1♂ (NARO), Kitazawatôge Pass, Minamiarupusu-shi, Yamanashi Prefecture, 15.viii.1956, K. Fujii leg.; 1♂1♀ (NARO), Mount Kitadake, Minamiarupusu-shi, Yamanashi Prefecture, 15.viii.1956, K. Fujii leg.

In the geometric morphometrics (Fig. 6), the first relative warp scores (RW1) accounted for 32.8% of the total variance and was mainly associated with the contour of overall shape; positive and negative values indicated square and cordate shapes, respectively. The second relative warp scores (RW2) accounted for 20.5% of the total variance and was mainly associated with the shape of anterior angle; positive value indicated narrowly- and strongly-protruding anterior angle, whereas negative value indicated widely-rounded and barely-protruding anterior angle. In the scatterplot of RW1 and RW2, the areas representing *N. taketoi* and the new species *N. kobushicola* did not overlap. None of the specimens with undetermined species identity were included in the areas of either *N. taketoi* and *N. kobushicola*, with the exception of the male specimen from Kitazawatôge Pass, which was just barely included in the male *N. taketoi* area.

In the following, a redescription of *N. taketoi* and a description of the new species, *N. kobushicola*, considered to be distinct based on the morphology of its endophallus, the external morphology, and a morphometric analysis, are provided.

Descriptions

N. taketoi and *N. kobushicola* are similar to each other and adults share the following morphology.

***Habitus*:** Dorsal surface of body glossy, not opaque; mouthpart appendages, legs, except for femora, reddish brown to brownish black; vertex with reddish brown patch; other body parts almost black.

***Head*:** Widest at mid-eye level. Mandibles stout, with the length between the apex and posterolateral end of the left mandible 1.5 times longer than the anterior width of the clypeus; apices of both left and right mandibles sharp; apex of the left mandible bent inward at a right angle, with the length of the apical part as long as the width of the apical end of the maxillary palp; inner margin of left mandible, except the apical part, only slightly arcuate; apex of right mandible not bent like the left one; inner margin of the right mandible arcuate, with a more arched curvature than the left mandible; one seta on the dorsolateral side. Labrum usually with three pairs of setae at the anterior margin, with additional one to two setae in some individuals; anterior margin slightly wavy, with anterolateral corners protruding anteriorly; area at the second outermost pair of setae concave, and area at the innermost pair of seta protruding anteriorly; middle of the anterior margin shallowly concave. Clypeus with a pair of setae. Frontal impressions shallow, wider than antennomere 1, reaching the supraorbital seta. Tempora short, not swollen. Eyes convex, with the anterior–posterior length twice as long as the width at the widest part as seen on dorsal view; width between apices of left and right eyes 1.4–1.5 times as wide as that between the inner margins of the eyes; posterior end of eyes behind the supraorbital seta, with the longitudinal length between the level of the supraorbital seta and that of the posterior end of the eye less than one-third the anterior–posterior length of the eye. Reddish brown patch on vertex slightly behind the level of the supraorbital setae. Antennomere 1 with one or two setae on apical quarter; antennomere 2 as long as half the length of antennomeres 1 and 3, without setae; antennomeres 3–10 with six setae on the subapical to apical part; antennomeres 5–11 with pubescence.

***Pronotum*:** Cordate-shaped, widest at apical one-third on the anteroposterior length between the levels of the anterior and hind angle apices. Dorsal surface smooth except for anterior, posterior, and lateral margins, which are more or less punctate. Lateral margin arcuate on apical seven eighths, with a contour more strongly arched than the curvature of the anterior and posterior margins and posterior one-eighth of the lateral margins; posterior one-eighth almost straight or only slightly sinuate. Anterior margin almost straight or only slightly arched anteriorly, except for lateral areas, which near the anterior angles are directed anterolaterally, at an angle of ~45°. Posterior margin almost straight or only slightly arched posteriorly; lateral areas near the posterior angles directed posterolaterally, at an angle of < 45° from the lateral direction. Anterior angles prominent anteriorly, with widely rounded apices. Hind angles with both sides almost straight, forming an acute angle; apices not denticulate. Anterior transverse impression grooved, but without a distinct line. Lateral margins narrow, with the width equal to or less than the length of antennomere 2. Median line distinctly impressed in the middle area, nearing but not connecting with the anterior and posterior margins. Laterobasal impressions single, deep, with the degree of concavity greater than that of the convexity of the median area of the pronotum; end of the anterior part reaching the apical half of the pronotum; impressions of both sides connected by a transverse groove; the degree of concavity of which is weaker than that of the laterobasal impressions and greater than that of the pronotum median line. Two marginal setae on each lateral side, anterior setae at widest pronotal point and posterior setae in front of hind angle.

***Elytra*:** Oblong, widest almost at the middle, convex. Shoulders indistinct, with elytral anterior and lateral margins smoothly connected, forming an arc. Elytral apices rounded, not denticulate. Distinct basal transverse line connecting anterior ends of elytral intervals. Scutellar stria present, not connected to stria 1; posterior end behind the posterior end of the scutellum. Stria distinct, impressed as strongly as the median line of the pronotum; intervals less convex; microsculpture transverse. Setigerous puncture either absent on stria 1 or present at or behind the level of the posterior end of the scutellum. Five or six setigerous punctures on interval 3, all adjoining or near stria 3. Around ten marginal setigerous punctures on interval 9. Hind wings atrophied.

***Ventral side*:** Ventral side of head smooth, except for gena in some specimens, in which ventrolateral sides of the gena have more than five shallow, somewhat indistinct transverse wrinkles. Mentum with three pairs of setae, one near the tooth, one at the middle part near the posterior margin, and one at the posterolateral margins; mentum tooth shallowly bifid; submentum with > 16 setae along the anterior margin. Ventral side of pronotum almost smooth except for prosternum and pleuron; prosternum near the anterior margin and anterolateral corners and the pleuron punctate. Mesepisternum, mesepimeron, and metepisternum, more or less punctate in all specimens. Sternites II–III punctate in some specimens. Sternites IV–VII almost smooth in all specimens. Metepisternum subparallelogram, with lateral margins > 1.7 times as long as the basal width. Metacoxa with two setae; medial seta absent. Metatrochanter without setae. Sternites IV–VI with two to six setae on each lateral side. Sternite VII with two to three setae on each lateral side in males, three to four setae in females.

***Legs*:** Slender, with hind tibia about twice as long as the width of the pronotal posterior margin. Apical outer end of hind tarsomere 4 distinctly protruding posteriorly but short; length difference between the inner and outer ends on ventral view equal to or less than the width of the basal end of hind tarsomere 5. Hind tarsomere 5 with four to five setae on ventrolateral margins.

***Male genitalia*:** Aedeagus stout and strongly arcuate; apex short and widely rounded. Endophallus with five lobes on the surface in both species, two on the laterobasal surface (laterobasal lobes), two on the lateroapical surface (lateroapical lobes), and one on the dorsoapical surface (dorsoapical lobe); surface around the gonopore protruding (gonopore protrusion). Both right and left parameres spatulate, with the former larger than the latter.

Nebria (*Falcinebria*) *taketoi* Habu, 1962

Figs 3A, B, E, F, I, J, 4

Nebria taketoi Habu: Habu (1962): 2 (original description, type locality “Mikurigaike, Mt. Tateyama, Toyama Prefecture”, subgenus *Paranebria*); Nakane (1974): 15 (part, subgenus not specified); Farkač and Janata (2003): 94 (subgenus *Paranebria*); Ledoux and Roux (2005): 831 (misidentified type locality “Japon, mont Yatsuga-take”, subgenus *Falcinebria*); Yoshitake et al. (2011): 4 (subgenus *Paranebria*); Yoshitake et al. (2011): 34 (part, subgenus *Falcinebria*); Huber (2017): 50 (misidentified type locality “Yatsudatake Mts.”, subgenus *Falcinebria*); Yoshimatsu et al. (2018): 38 (part, subgenus *Falcinebria*).

Nebria nakanei Uéno: Uéno (1953): 58 (unavailable name under International Code of Zoological Nomenclature (ICZN) article 8.3, specimen(s) from “the Azusagawa River, Kamikôchi”, subgenus *Paranebria*); Nakane (1963): 19 (part, subgenus *Paranebria*); Ledoux and Roux (2005): 832 (subgenus *Falcinebria*); Huber (2017): 50 (synonym of *taketoi*).

Notes. In his brief review of Japanese *Nebria*, Uéno (1953) reported on a species of *Nebria* referred to as *Nebria nakanei* based on specimen(s) from Kamikôchi in the Hida Mountains, with a comment that the species would later be formally described as a new species. However, a description of *N. nakanei* was never published. Habu (1962) described *Nebria taketoi* based on a male from Mount Tateyama in the Hida Mountains; this species is apparently identical to *N. nakanei*. In his brief review of Japanese *Nebria*, Nakane (1974) treated this species under the name *N. taketoi* and stated that it is most likely conspecific with *N. nakanei*. That report included a line drawing of the pronotum of an individual from the Yatsugatake Mountains. This complicated nomenclatural history was not correctly understood by researchers outside Japan, in part because the reports by Uéno (1953) and Nakane (1974) were written in Japanese. In Ledoux and Roux (2005), the type locality of *N. taketoi* was described as the Yatsugatake Mountains, and *N. nakanei* was treated as a related species of *N. taketoi*. This was probably due to the misidentification of the Yatsugatake Mountains, whose specimen was described by Nakane (1974), as the same as the type locality of *N. taketoi*. In the Catalogue of Palaearctic Coleoptera, which is widely accepted by experts, *N. taketoi* and *N. nakanei* are treated as the same species under the name of *N. taketoi*, but the reason for this classification is not provided (Farkač and Janata 2003; Huber 2017). The type locality was again given as the Yatsugatake Mountains. Since Uéno (1953) himself did not intend to describe this species in his publication, the nomenclature of *N. nakanei* used in that report was not accepted according to ICZN article 8.3, such that *N. nakanei* remains an unavailable name. Therefore, *N. taketoi* should be used as the name of this species, and its type locality is “Mikurigaike, Mt. Tateyama,” as stated in Habu (1962).

Materials examined. ***Holotype*** ♂ (NARO), “VIII. 5, 1961 / Mikurigaike / Mt. Tateyama / Toyama P. / A. TAKETO // Holotype / Nebria. / taketoi / HABU”; 2♂5♀ [1♂3♀ (KSWD), 1♂2♀ (TCSM)], Murodôdaira, alt. 2390 m, Ashikuraji, Tateyama-machi, Nakaniikawa-gun, Toyama Prefecture, Japan (36°34'43"N, 137°36'6"E), 27.viii.2019, Kenta Sawada leg.; 1♂1♀ (NARO), Renge-Onsen, Mount Shiroumadake, Itoigawa-shi, Niigata Prefecture, Japan, 29.vii.1977, K. Baba leg.; 1♂ (NARO), Mount Yukikuradake, Itoigawa-shi, Niigata Prefecture, 26.vii.1961, K, Baba leg.

Diagnosis. *Nebria taketoi* is distinguished from the new species described below by less protruded anterior angles of the pronotum, more densely punctated pronotal margin and the ventral sides of some of its notal and abdominal segments, and not bifurcated apices of lateroapical and dorsoapical lobes of the endophallus. Among specimens previously treated as *N. taketoi*, the absence of setigerous punctures on elytral stria 1 is a character found only in individuals of *N. taketoi*. However, due to individual variation, in which setigerous punctures are seen in a few individuals, the presence of this character does not provide a definitive diagnosis at the individual level.

Description. ***Body length*:** ♂, 10.29–10.94 mm (mean ± SD: 10.62 ± 0.28 mm, n = 5); ♀, 10.42–12.16 mm (mean ± SD: 11.31 ± 0.65 mm, n = 6).

***Head*:** Dorsal surface smooth, except for frontal impressions, the surfaces of which are more or less wrinkled. Antennomere 1 usually with one seta, rarely two setae.

***Pronotum*:** Surface near and in front of anterior transverse impression moderately punctate but clearly lacking punctations near the anterior margin; surfaces of lateral margins, laterobasal impressions, and area between the transverse groove and the posterior margin moderately punctate.

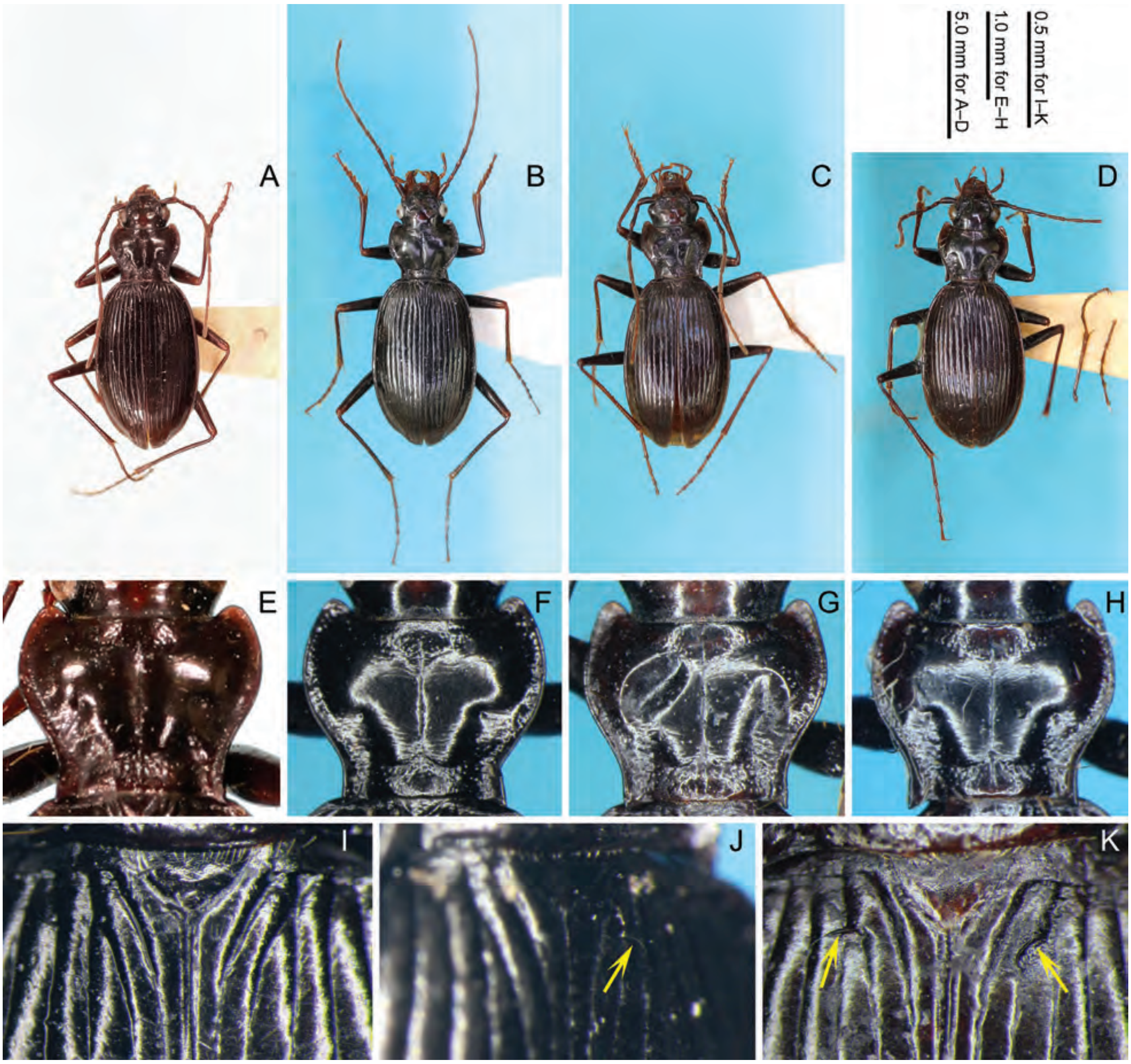


Figure 3. External structures of *Nebria taketoi* and *N. kobushicola* sp. nov. **A, E.** *N. taketoi* holotype male from Mikurigaike; **B, F, J.** *N. taketoi* male from Murodôdaira; **I.** *N. taketoi* female from Murodôdaira; **C, G, K.** *N. kobushicola* holotype male from Mount Kobushigatake; **D, H.** *N. kobushicola* paratype male from Mount Aka; **A–D.** Habitus, in dorsal view; **E–H.** Pronotum, in dorsal view; **I–K.** Elytral base around the median line in dorsal (**I, K**) and left dorsolateral (**J**) views, showing the variation [present (yellow arrows) or absent (no arrow)] in setigerous puncture on stria 1.

***Elytra*:** Anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellar stria more than twice as long as the anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellum. Setigerous punctures on stria 1 variable at the individual level, including one on both sides, one on either side, and absent on both sides.

***Ventral side*:** Submentum with 16–25 setae. Surface punctations of prosternum near the anterior margin and anterolateral corners and pleuron sparser than those at the pronotal laterobasal impressions. Mesosternal, metasternal, and abdominal surface almost smooth, except for mesepisternum, mesepimeron, metepisternum, metasternum, and metacoxa for all specimens examined, and sternite II for some specimens. All surfaces of the mesepisternum, mesepimeron, and metepisternum, and the lateral side of the metasternum until the metepisternum punctate to the same degree as pronotal laterobasal impressions. Metacoxae punctate at lateral sides, with the degree of punctation varying among individuals, ranging from only a few punctations to the same degree as the metepisternum; in all cases, punctures weaker than those of the mesepisternum, mesepimeron, and metepisternum. Punctures of sternite II varying from absent to punctation as extensive as on other notal parts. Sternites IV–VI with three to six setae on each lateral side. Male sternite VII with two setae on each lateral side.

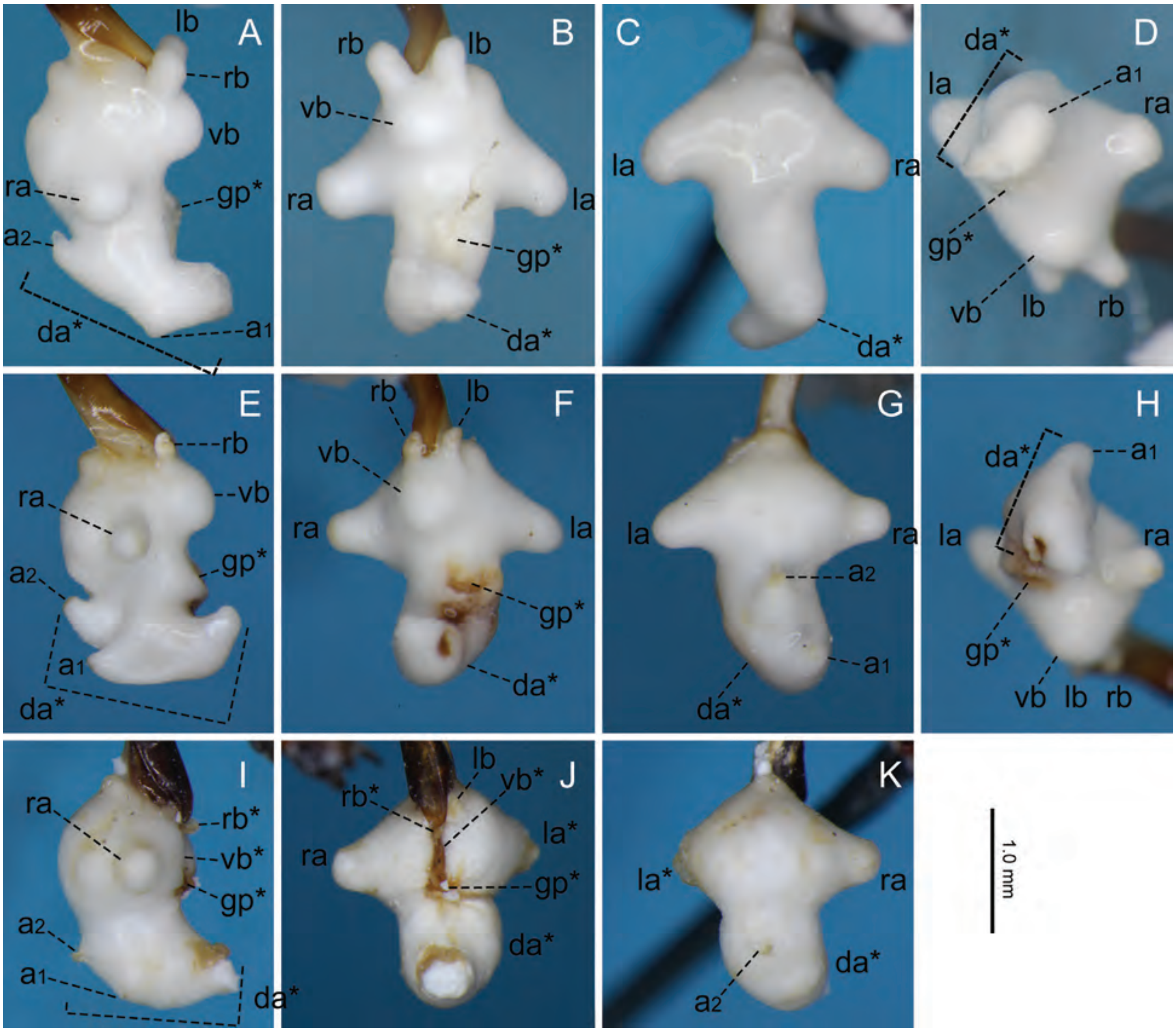


Figure 4. Endophallus of *Nebria taketoi*. **A–D.** Male from Murodôdaira; **E–H.** Male from Mount Yukikuradake; **I–K.** Male from Renge-Onsen. Right lateral view (**A, E, I**), ventral view (**B, F, J**), dorsal view (**C, G, K**), and ventroapical view (**D, H**), showing a dorsal view of the dorsoapical lobe. Abbreviations: da. dorsoapical lobe, gp. gonopore protrusion, la. left lateroapical lobe, lb. left laterobasal lobe, ra. right lateroapical lobe, rb. right laterobasal lobe, vb. ventrobasal swelling. a_1 and a_2 denote apices of the dorsoapical lobe. Asterisk indicates that the gonopore protrusion or lobes is not fully everted.

***Male genitalia*:** Laterobasal lobes semi-ellipsoid, with the basal diameter smaller than the height; inflated lobes directed ventrobasally, covering the aedeagal apex on lateral views. Lateroapical lobe broadly rounded at apex, directed lateroapically, not bent, and larger than the laterobasal lobes. Dorsoapical lobe with two protrusions on dorsobasal and dorsomedian parts; protrusions weakly bent, directed basally, and smaller than the lateroapical lobes; apex of the protrusions narrowly rounded; in the specimens examined, the dorsoapical lobe apex was not fully inflated, but its shape is probably broadly rounded or slightly widened. Ventrobasal swelling large and semi-spherical on lateral views; basal diameter larger than that of laterobasal lobes. Dorsobasal surface near the ostium with a lobe smaller than the ventrobasal swelling. Gonopore protrusion probably present, but unsuccessfully inflated in the specimens examined.

***Nebria* (*Falcinebria*) *kobushicola* Sasakawa, sp. nov.**

https://zoobank.org/F38997DD-D669-4E26-8134-C97F43FFB284

Figs 3C, D, G, H, K, 5

Nebria taketoi Habu: Nakane (1974): 15 (part, subgenus not specified); Yoshitake et al. (2011): 34 (part, subgenus *Falcinebria*).

Types. ***Holotype*:** ♂ (NARO), Mount Kobushigatake, Chichibu-shi Saitama Prefecture, 3.viii.1963, S.-I. Uéno leg. Paratypes: 1♂2♀ (NARO), same data as the holotype; 1♂ (HUM), Akadakekousen, alt. ca. 2240 m, the Yatsugatake Mountains, Chino-shi, Nagano Prefecture, 25.vii.1956, F. Motoyoshi leg.

Diagnosis. This new species is distinguished from *N. taketoi* by more protruded anterior angles of the pronotum, less punctated pronotal margin and ventral sides of some notal and abdominal segments, and bifurcated apices of lateroapical and dorsoapical lobes of the endophallus.

Description. ***Body length*****:** ♂, 10.78–11.08 mm (mean ± SD: 10.88 ± 0.17 mm, n = 3); ♀, 11.11–11.82 mm (mean ± SD: 11.47 ± 0.51 mm, n = 2).

Head**:** Dorsal surface smooth; antennomere 1 with one seta.

Pronotum**:** Surfaces of anterior transverse impression, lateral margins, laterobasal impressions, and area between the transverse groove and posterior margin only sparsely punctate.

Elytra**:** Anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellar stria > 4 times longer than the anteroposterior length between the level of the basal transverse line and that of the posterior end of the scutellum. One setigerous puncture on stria 1.

Ventral side**:** Submentum with 16–20 setae. Punctations of prosternum surfaces near anterior margin and anterolateral corners and pleuron denser than or as dense as those at the pronotal laterobasal impressions. Mesosternal, metasternal and adominal surface almost smooth except for mesepisternum, mesepimeron, and metepisternum for all specimens examined, and metasternum and sternite II for some specimens. All surfaces of mesepisternum, mesepimeron, and metepisternum punctate to the same degree as or more densely than the pronotal laterobasal impressions. Punctures of metasternum (lateral sides) and sternite II (anterolateral sides) varying among individuals, ranging from absent to the same as on other notal parts. Sternites

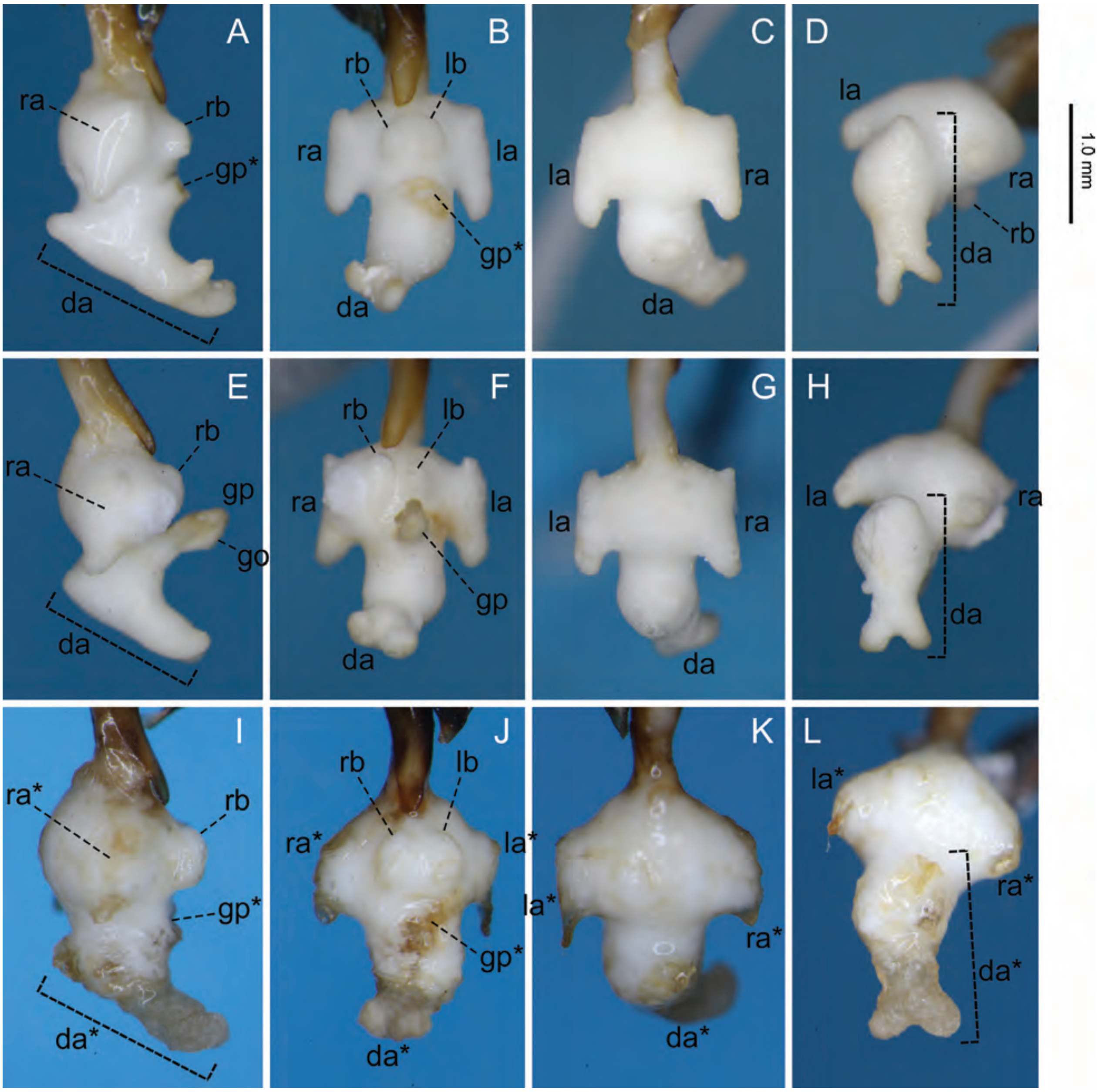


Figure 5. Endophallus of *Nebria kobushicola* sp. nov. **A–D.** Holotype male from Mount Kobushigatake; **E–H.** Paratype male from Mount Kobushigatake; **I–L.** Paratype male from Akadakekousen. Right lateral view (**A, E, I**), ventral view (**B, F, J**), dorsal view (**C, G, K**), and dorsoapical view (**D, H, L**), showing a dorsal view of the dorsoapical lobe. Abbreviations: go, gonopore; others are the same as in Fig. 4.

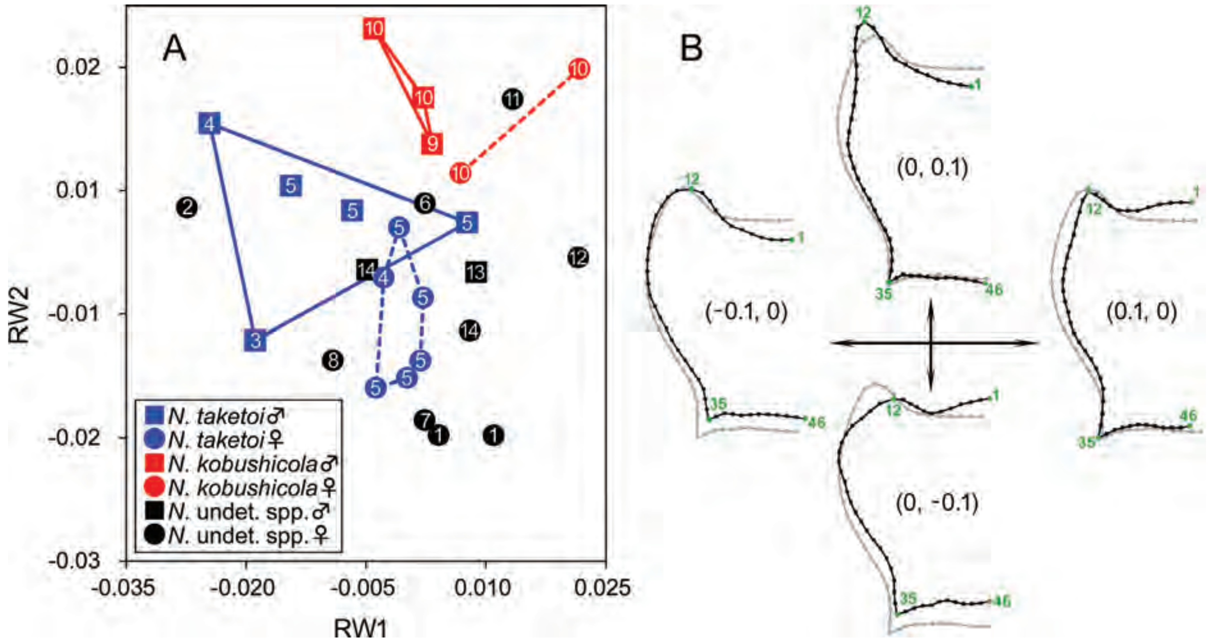


Figure 6. Scatterplot of RW1 and RW2 for the pronotum (**A**) and representations of extreme shape along each axis (**B**). In (**A**), numbers within the symbols indicate that the respective specimen was obtained from the collection site with the same number in Fig. 1. In (**B**), each shape with coordinates in parentheses is shown on the mean shape, which is shown in gray.

IV–VI with two to three setae on each lateral side. Male sternite VII with two to three setae on each lateral side.

***Male genitalia*:** Laterobasal lobes semi-spherical; inflated lobes directed ventrally, not covering the aedeagal apex on lateral views. Lateroapical lobe markedly wide on dorsal view, with the base as wide as or slightly wider than the width of the base of the dorsoapical lobe; anterior and posterior corners protruding in apical and basal directions, respectively, resulting in T-shaped dorsoapical lobes on dorsal view. Dorsoapical lobe with a protrusion on the dorsobasal part; the protrusion directed dorsobasally, not bent; apex of the dorsoapical lobe in a Y-shaped bifurcation on dorsal view; each of the bifurcated apices larger than the protrusion on the dorsobasal part. Dorsobasal surface near the ostium only slightly or not at all swollen. Gonopore protrusion directed ventrally.

Discussion

This study demonstrates the utility of the endophallus in species- and subgenus-level taxonomies of the focal species. Based on this genital morphology, a new species could be distinguished from specimens previously treated as *N. taketoi*. This determination was consistent with the external morphology of the specimens and the results of the morphometric analysis. The results also provide insights into the autapomorphy of the subgenus *Falcinebria*, to which *N. taketoi* and *N. kobushicola* belong. This subgenus was established by Ledoux and Roux (2005), with *N. reflexa* as the type species, but its morphological definition was unclear. Most morphological characters listed as common to members of the subgenus are shared by many species of other *Nebria* subgenera. However, the gonopore protrusion is a feature found only in *N. reflexa* and related *Nebria* species in which the endophallus was examined (e.g., Ledoux and Roux 2005; Sasakawa and Kubota 2006; Sasakawa 2020). In this study, the gonopore protrusion was successfully inverted in one specimen of *N. kobushicola*. Although it could not be successfully everted in the *N. taketoi* specimens examined in this work, the similarity around the gonopore protrusion between the endophallus of *N. taketoi* (Fig. 4F) and the unsuccessfully everted endophallus of *N. kobushicola* (Fig. 5B) implies that *N. taketoi* also has the gonopore protrusion. Thus, the gonopore protrusion can probably be considered an autapomorphy of *Falcinebria*. Future studies should examine the endophallus of other members of the subgenus, especially species from Taiwan and mainland China (Ledoux and Roux 2005).

It is noteworthy that *N. kobushicola* shares two putative apomorphic characters of endophallus with *N. niohozana* Bates, 1883 and *N. dichotoma* Sasakawa, 2020, species previously treated as *N. reflexa*, but not with *N. taketoi*. The first is the T-shaped laterobasal lobes reported in *N. niohozana* and *N. dichotoma*; among *Nebria* species in which the endophallus was examined, T-shaped lobes were found only in *N. niohozana* and *N. dichotoma* and were therefore considered a synapomorphy uniting the two species (Sasakawa 2020). The second character is a dorsoapical lobe with a largely bifurcated apex, reported only in *N. dichotoma*. One possible interpretation of this result is that these morphological similarities reflect phylogenetic relationships among species. If so, the ancestor of species previously regarded as *N. taketoi* (i.e., *N. taketoi*, *N. kobushicola*, and specimens treated as *N. taketoi*) was morphologically similar to *N. kobushicola*, having evolved from a clade containing *N. niohozana* and *N. dichotoma*. This assumption is consistent with the reports of Habu

(1962) and Nakane (1974), which note that *N. taketoi* is morphologically most similar to *N. niohozana*, based on the character states of the male genital right paramere, setae on the abdominal sternites, and the external appearance. Another possible interpretation is that the similar endophallus structures evolved independently. If the observed character states have an advantage for reproductive success, then morphological convergence of endophallus could occur as a result of sexual selection. Future molecular phylogenetic studies of this group will provide insights into this issue.

Some of the specimens with undetermined species identities were obtained from high-altitude mountains, which are separated from the Hida Mountains and the Okuchichibu and Yatsugatake mountains, where *N. taketoi* and *N. kobushicola* occur (Fig. 1). The collection sites at the Iide Mountains are > 200 km away from the other localities. Consequently, some of these specimens may be species other than *N. taketoi* and *N. kobushicola*, but this remains to be confirmed in additional studies.

Acknowledgements

I thank M. Ôhara and R. Satô (HUM), K. Sawada (Toyama), K. Setsuda (GPM), T. Shiraishi (TCSM), and J. Yamasako (NARO) for the loan of specimens under their care. Thanks are also due to H. Ikeda (Kashihara City Museum of Insect, Nara) and T. Iwata (Toyama Science Museum, Toyama), who examined the museum collections for the current study. This study was partly supported by JSPS KAKENHI (no. 17K15171).

References

Farkač J, Janata M (2003) Tribe Nebriini Laporte, 1834. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera (Vol. 1). Archostemata – Myxophaga – Adephaga. Apollo Books, Stenstrup, 79–96.

Habu A (1962) A new species of *Nebria*, and preliminary notes on the variation in *Nebria* (*Paranebria*) *sadona* Bates (Coleoptera, Carabidae). Akitu 10: 1–7.

Huber C (2017) Tribe Nebriini Laporte, 1834 (except genus *Leistus*). In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera. Vol. 1. Archostemata – Myxophaga – Adephaga. Revised and Updated Edition. Brill, Leiden, 31–60.

Huber C, Schnitter PH (2020) *Nebria* (*Pseudonebriola*) *tsambagarav* sp. nov., a new alpine species from the Mongolian Altai (Coleoptera, Carabidae). Alpine Entomology 4: 29–38. https://doi.org/10.3897/alpento.4.50408

Huber C, Szallies A, Baur H, Giachino PM (2010) *Nebria* (*Nebriola*) *gosteliae* sp. nov. from the Penninian Alps near Biella, Piemonte, Italy (Coleoptera: Carabidae, Nebriinae). Contributions to Natural History 15: 9–27.

Ledoux G, Roux P (2005) *Nebria* (Coleoptera, Nebriidae) Faune Mondiale. Société Linnéenne de Lyon, Bossuet, Lyon, 976 pp.

Nakane T (1963) The Family Carabidae. In: Nakane T et al. (Eds) Iconographia Insectorum Japonicorum, Colore naturali edita (Vol. 2) (Coleoptera). 3–54, plates 3–27. Hokuryukan, Tokyo, Japan. [In Japanese]

Nakane T (1974) The beetles of Japan (5). The Nature and Insects 9(2): 13–18. [In Japanese]

Rasband WS (2016) ImageJ, Version 1.50i. National Institutes of Health (US) U.S, Bethesda, MD. https://imagej.nih.gov/ij/

Roggero A, Giachino PM, Palestrini C (2013) A new cryptic ground beetle species from the Alps characterised via geometric morphometrics. Contributions to Zoology 82: 171–183. https://doi.org/10.1163/18759866-08204002

Rohlf FJ (2013a) tpsDid, Version 2.17. Department of Ecology and Evolution, State University of New York at Stony Brook, NY. http://life.bio.sunysb.edu/morph/

Rohlf FJ (2013b) tpsRelw: relative warps analysis, Version 1.53. Department of Ecologyand Evolution, State University of New York at Stony Brook, NY. http://life.bio.sunysb.edu/morph/

Sasakawa K (2016) Two new species of the ground beetle subgenus *Sadonebria* Ledoux & Roux, 2005 (Coleoptera, Carabidae, *Nebria*) from Japan and first description of larvae of the subgenus. ZooKeys 578: 97–113. https://doi.org/10.3897/zookeys.578.7424

Sasakawa K (2020) Taxonomic studies of the ground beetle subgenus *Falcinebria* Ledoux & Roux, 2005 (Coleoptera, Carabidae, *Nebria*) from Honshû, Japan. ZooKeys 902: 37–60. https://doi.org/10.3897/zookeys.902.46531

Sasakawa K, Itô H (2021) A new species and distribution record of the ground beetle subgenus *Falcinebria* Ledoux & Roux, 2005 (Coleoptera: Carabidae: *Nebria*) from central Honshu, Japan. Biogeography 23: 30–32. https://doi.org/10.3897/zookeys.902.46531

Sasakawa K, Kubota K (2006) *Nebria tenuicaulis* sp. nov., a sympatric species with *Nebria sadona ohdaiensis* Nakane, with studies on the phylogeny of the subgenus *Sadonebria* Ledoux & Roux (Coleoptera: Carabidae). Zootaxa 1306: 41–50. https://doi.org/10.11646/zootaxa.1306.1.3

Uéno S (1953) The Coleoptera of Japan (6). Shin Konchû 6: 55–60. [In Japanese] https://doi.org/10.12935/jvma1951.6.55

Yoshimatsu S, Ito N, Nakatani Y, Yoshitake H (2018) A list of ground beetles (Insecta: Coleoptera: Caraboidea) in Dr. Kazuo Tanaka Collection preserved in the Insect Museum of Institute for Agro-Environmental Sciences, NARO. Bulletin of the NARO, Agro-Environmental Sciences 39: 15–191. [In Japanese with English summary]

Yoshitake H, Kurihara T, Yoshimatsu S, Nakatani Y, Yasuda K (2011) A list of carabid specimens (Insecta: Coleoptera) collected by the late Dr. Akinobu Habu preserved in the Insect Museum of the National Institute for Agro-Environmental Sciences. Bulletin of the National Institute of Agricultural Sciences, Series C 28: 1–327.

Supplementary material 1

Supplementary information

Author: Kôji Sasakawa
Data type: rtf
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/alpento.7.109855.suppl1

Alpine Entomology 7 2023, 195–200 | DOI 10.3897/alpento.7.111490

Anchonidium selvanum sp. nov. (Coleoptera, Curculionidae, Molytinae) from northern Portugal

Christoph Germann[1,2], Carlo Braunert[3]

1 Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel, Switzerland
2 Naturhistorisches Museum Bern, Bernastrasse 15, CH-3005 Bern, Switzerland
3 Musée National d'Histoire Naturelle de Luxembourg, 25 rue Münster, L-2160 Luxembourg, Luxembourg

https://zoobank.org/D92E8495-535C-4E18-82BC-DE08526128D7

Corresponding author: Christoph Germann (germann.christoph@gmail.com)

Academic editor: Yannick Chittaro ♦ **Received** 22 August 2023 ♦ **Accepted** 11 October 2023 ♦ **Published** 24 October 2023

Abstract

The fourth species of *Anchonidium* sensu stricto from Western Europe is described, photographed and compared with its congeners; an updated key of the genus is given. The habitat in the northern mountain chains in Portugal in the native *Quercus* mountain forests is characterized and illustrated.

Key Words

Molytinae, Typoderini, morphology, taxonomy, ancient forest, *Quercus* forest

Introduction

The genus *Anchonidium* Bedel, 1884 comprises at present five species. Three of them in Western Europe (*A. unguiculare* (Aubé, 1850), *A. braunerti* Germann, 2020 and *A. spathiferum* Germann, 2020) belonging to *Anchonidium* sensu stricto. Furthermore, two morphologically deviating species from the Caucasus region (*A. caucasicum* (Motschulsky, 1845), *A. perpensum* Faust, 1886) recently re-defined by Hlaváč (2020) are clearly belonging to another genus within the Tribe Typoderini, and they were therefore termed preliminarily as *Anchonidium* sensu lato by Germann (2020). *Anchonidium* had also been used as a wastebasket to harbor superficially similar species from Africa. Grebennikov (2018) started clarifying descriptions by Hoffmann (1965, 1968) and Hlaváč and Borovec (2022) erected the genus *Oberprielerius* Hlaváč & Borovec, 2022 (Cyclominae) to accommodate the former *Anchonidium uniforme* Voss, 1974 from South Africa.

We here focus on a new species of *Anchonidium* s. str. from northern Portugal, morphologically most closely related to *Anchonidium spathiferum* Germann, 2020 from Serra do Estrela. Germann (2020) already assumed that four specimens from Serra do Marão might belong to a new species. A collecting excursion into the northern mountain chains in Portugal finally allowed to study the variability of the new species, and helped understanding of the distribution patterns of *A. unguiculare* and *A. selvanum* sp. nov.

Material and methods

We provide the description of the new species in a condensed form. For details, we refer to the exhaustive redescription of the genus sensu stricto by Germann (2020). Main emphasis is set on the illustrating photos taken with a Keyence VHX-6000 photosystem at the Naturhistorisches Museum Basel (NMB). Photos of the genitalia were taken from objects embedded in glycerol. Body length was measured dorsally from the anterior margin of the pronotum to the apex of elytra.

For the collection methodology of specimens, all details are given in Germann (2020). Label data for all specimens are printed. All type specimens are labelled with red printed name labels. Locality data for the map was taken from Germann (2020).

Acronyms are as follows: **NHML** Natural History Museum London; **NMB** Naturhistorisches Museum Basel; **NMBE** Naturhistorisches Museum Bern, Switzerland; **NMPC** National History Museum Prague, Czech Republic; **SDEI** Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; **cCB** collection Carlo Braunert, Mensdorf, Luxembourg; **cCG** collection Christoph Germann, Rubigen, Switzerland; **cLB** collection Lutz Behne, Müncheberg, Germany.

Description

Anchonidium selvanum sp. nov.

https://zoobank.org/2E634368-2E7C-4640-B9D6-216D0368AB73

Material. ***Holotype*** ♂ 413_23.2 Portugal, Vila Real, Sra do Alvão, Bilhó, Bobal, 41°23'56''N, 7°49'48''W, 880m, *Quercus cerris*, *Q. pyrenaica*, *Erica umbellata*, 31.5.2023, leg. C. Germann (NMB).

***Paratypes*:** 1 ♀ Portugal, Vila Real, Serra do Marão, 750 m, 21.05.1997, leg. W. Starke (cLB). – 1 ♂, 1 ♀ Portugal, Vila Real, Serra do Marão, 750 m, June 1997, leg. Th. Aßmann (cLB). – 1 ♂ Portugal, Vila Real, Serra do Marão, 750 m, 10.06.1997 (SDEI). – 27 ♂, 9 ♀ 413_23.2 PORTUGAL, Vila Real, Sra do Alvão, Bilhó, Bobal, 41°23'56''N, 7°49'48''W, 880 m, *Quercus cerris*, *Q. pyrenaica*, *Erica arborea*, 31.5.2023, leg. C. Germann (cCG, NHML, NMB, NMBE, NMPC). – 33 ex. dito, leg. C. Braunert (cCB). – 15 ♂, 6 ♀ 413_23.3 Portugal, Vila Real, Sra do Alvão, Bilhó, Bobal, 41°23'54''N, 7°49'42''W, 941 m, 31.5.2023, leg. C. Germann (cCG, NMB). – 6 ex. dito, leg. C. Braunert (cCB). – 9 ♂, 3 ♀ 413_23.4 Portugal, Vila Real, Sra do Alvão, 2km NW Lamas de Olo, 41°22'56''N, 7°49'01''W, 1056 m, 31.5.2023, leg. C. Germann (cCG). – 9 ♂, 9 ♀ dito, leg. C. Braunert (cCB). – 1 ♂, 1 ♀ 413_23.10 Portugal, Porto, Sra do Marão, 5 km E Ansiães, 41°14'55''N, 7°53'44''W, 1330 m, 2.6.2023, leg. C. Germann (cCG). – 1 ex. 413_23.11 Portugal, Porto, Sra do Marão, 5km NE Ansiães, 41°16'10''N, 7°54'21''W, 1180 m, GS [sifted] *Quercus*, 2.6.2023, leg. C. Braunert (cCB).

Diagnosis. (Figs 1–3, 7–14) Body length (without rostrum): 2.1–3.3 mm. Body colour auburn. Pronotum: Anterior margin of prosternum lacking rostral notch or channel. Metacoxae separated from mesocoxae by distance slightly superior to diameter of metacoxae; length of metaventrite as long as diameter of mesocoxae; first ventrite inbetween metacoxae coarsely punctuate with especially large, roundish-oval punctures, but not confluent to form deep grooves as in *A. unguiculare*. Elytra L/W: 1.5–1.6, elongate, parallel sided, widest shortly behind middle. Striae coarsely and regularly punctuate, counting 15–17 punctures from elytral base to declivity.

***Male genitalia*:** Penis tube-like, in dorso-ventral view laterally diverging just before apex, almost rectangular, apical margin weakly rounded (Figs 7, 8); in lateral view bowed (Fig. 9).

***Female genitalia*:** Sternite 8 with plate drop-shaped, apodeme shorter than plate, apex thickened and laterally strongly protruding (Fig. 10). Spermatheca c-shaped with tip of cornu pointed, base roundish, ramus and nodulus not protruding (Fig. 11). Sclerotized bursal atrium in dorso-ventral view ear-shaped, in lateral view with protruding basal appendix (Figs 12–14).

Derivation of name. *Anchonidium selvanum* sp. nov. is named after the native oak-forest in Portugal, characterised below, the name is taken from the Portuguese “la selva” which means the primeval forest. Unfortunately, this native habitat is severely threatened by the intensive wood logging, the reforestation with *Eucalyptus* and *Mimosa* trees from Australia or *Pinus halepensis* Mill. which all grow fast and the short time yield per square meter tempts the forest owners to plant them (Garcia et al. 2008; Queirós 2012). Finally, the natural forest habitats are severely threatened by wildfires, often lighted on purpose and tolerated or even enhanced by the fire-tolerant invading tree species.

Ecology. We found most numerous specimens per locality in remains of the native oak forests – 69 at the type locality in two sifting samples, and 57 at localities just nearby where the forest had been cut supposedly years before – (Figs 15, 16). This typical forest is similar to a subtropical cloud forest and is composed of the two indigenous species *Quercus pyrenaica* Willd. and *Q. cerris* L. with *Erica umbellata* L. and a wide variety of mosses, lichens and fern species on the tree’s branches, growing on granite stone. The deep and humid leaf litter is a good indicator for individual rich occurrences of *Anchonidium selvanum* sp. nov.

Adapted key from Germann (2020) on *Anchonidium* sensu stricto in Western Europe

2A Ventral side of pronotum at anterior margin with faint and shallow rostral notch or channel. First ventrite with oval groove between metacoxae; elytra laterally rounded, shorter, 1.4–1.5 times as long as wide; 10 to 13 punctures on elytral disc from base to declivity; widest in first third; aedeagus thin (lateral view), slender and flattened with almost rectangular apex and rounded sides; apex dorsally with well visible setae. Sclerotized bursal atrium helmet-like with bubble on top. Great Britain (Cornwall), W- and NW-France, N-, NW- and S-Spain, N-Portugal, N-Morocco (Fig. 4) .... *A. unguiculare* (Aubé, 1850)

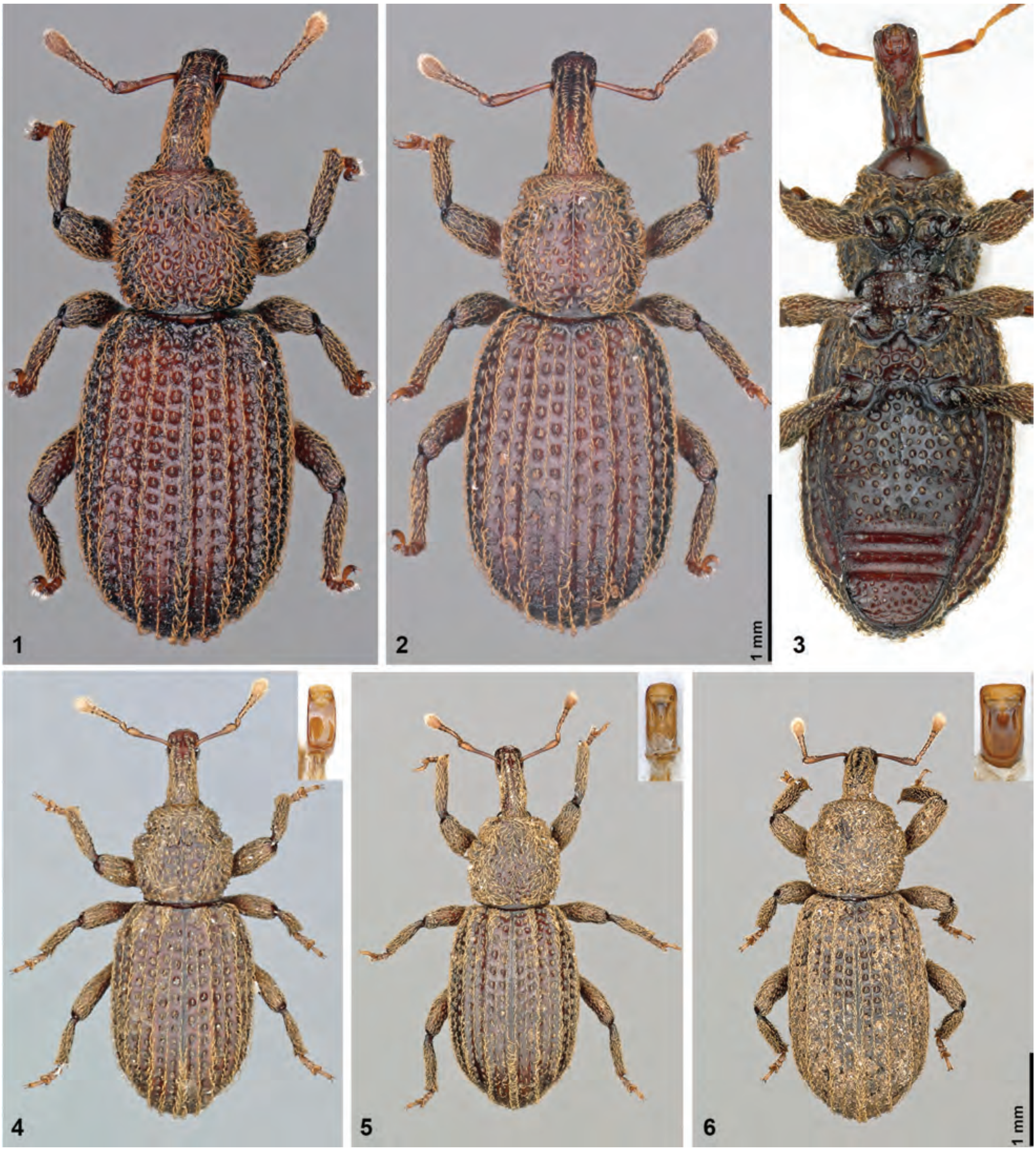
2B Ventral side of pronotum at anterior margin only sinuate, no rostral notch or channel detectable. First ventrite without groove, but with very coarse oval punctures between metacoxae; elytra parallel sided, longer, 1.5–1.8 times as long as wide; 14 to 17 punctures on elytral disc from base to declivity; widest in or behind middle; aedeagus shorter, tube shaped, blunt and thick in lateral view; apex without well visible setae 3

3A Elytra widest in middle, 1.6–1.8 times as long as wide; Aedeagus parallel sided, apex in dorsal view evenly rounded. Portugal (Serra de Monchique) (Fig. 5) ....*A. braunerti* Germann, 2020

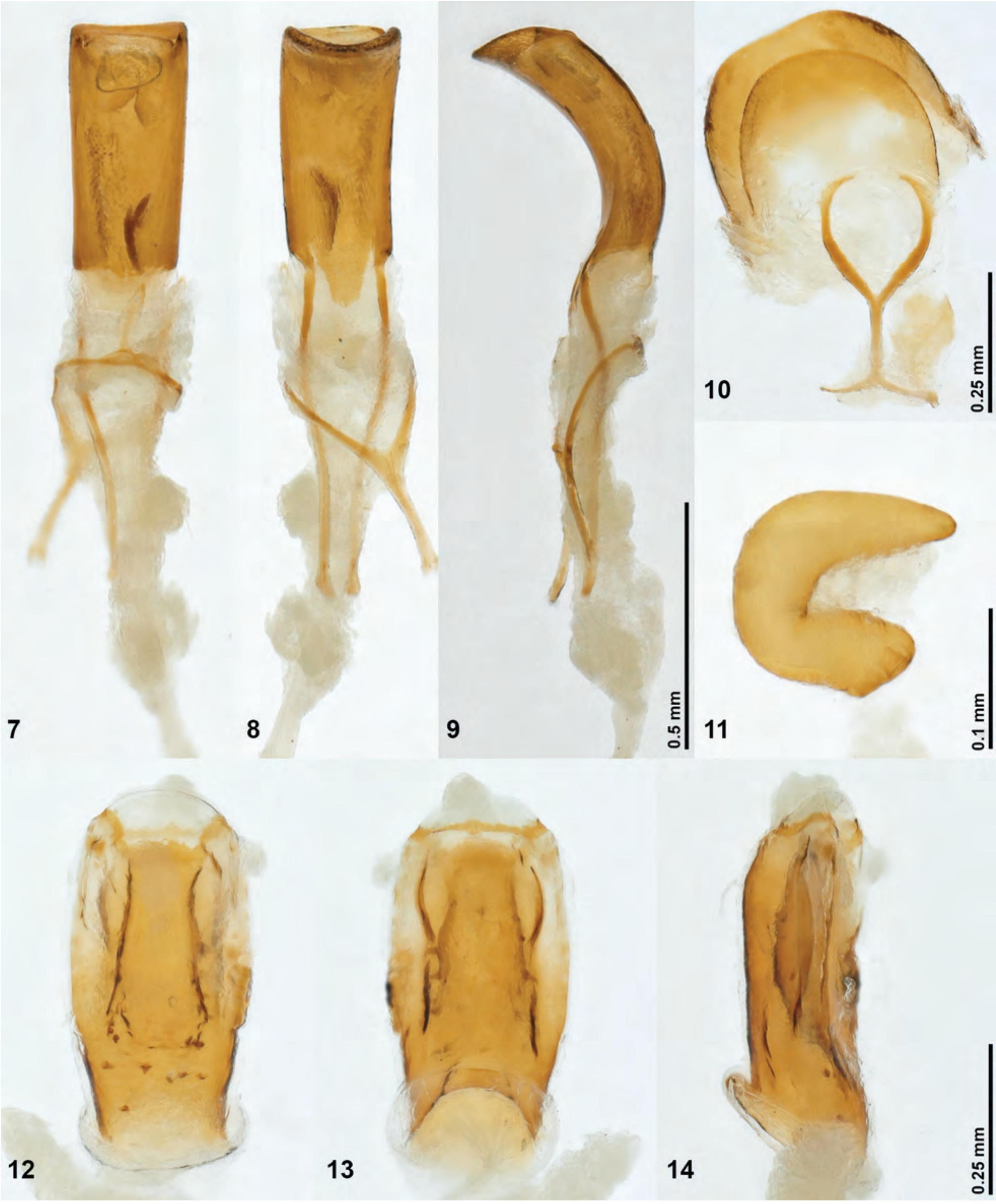
3B Elytra widest behind middle, 1.5–1.6 times as long as wide. Aedeagus slightly expanded to apex, apex in dorsal view straight 4

4A Body robust. Apex of aedeagus very broad, spatula-shaped with sinuate apical margin. Bursal atrium sclerotized, frog shaped. Portugal (Serra da Estrela) (Fig. 6) ....*A. spathiferum* Germann, 2020

4B Body slender. Apex of aedeagus narrower, apex weakly rounded, not sinuate (Figs 7, 8). Bursal atrium sclerotized, ear shaped (Figs 12, 13). Portugal (Serra do Marão, Serra do Alvão) (Figs 1–3, 7–14)...........................*A. selvanum* sp. nov.



Figures 1–6. 1–3. *Anchonidium selvanum* sp. nov. **1.** Male; **2.** Female; **3.** Male underside; **4–6.** Habitus and penis (medianlobus, dorsal view) of **4.** *Anchonidium unguiculare* (Spain, Alto Campoo). **5.** *A. braunerti* (Portugal, Serra de Monchique). **6.** *A. spathiferum* (Serra da Estrela). Photos: C. Germann).



Figures 7–14. 7–9. Aedeagus of *Anchonidium selvanum* sp. nov, holotype. **7.** Dorsal view; **8.** Ventral view; **9.** Lateral view; **10–14.** Female genitalia of a paratype; **10.** Tergites 8 and 7 and Sternite 8; **11.** Spermatheca; **12.** Sclerotized bursal atrium; **12, 13.** Dorso-ventral views; **14** Lateral view (Photos: C. Germann).

Discussion

The distribution of the four *Anchonidium* s. str. species in Portugal follows the mountain chains and river valleys (Fig. 17). *Anchonidium braunerti* in the most southern Serra de Monchique on 890 m a.s.l. with the Rio Tajo as the northern barrier. *A. spathiferum* in the Serra da Estrela on 1290 m a.s.l. with the Douro valley in between the hereby described *A. selvanum* sp. nov. in both, the Serra do Marão and Serra do Alvão on 750–1180 m a.s.l. The specific excursions into the most northern Serras revealed that *A. unguiculare* is not only distributed in the

Figure 15. Habitat at type locality of *A. selvanum* sp. nov. at Bobal, 880 m a.s.l., Serra do Alvão. A small remaining part of the ancient Oak forest with mosses, lichens and a deep leaf litter layer at ground where the new species lives in remarkable densities (Photo: C. Braunert).

Figure 16. Remains and replantation of Oak forest in the Serra do Marão close to Ansiães. A good example for small remains of the ancient forests where we found only few individuals of *A. selvanum* sp. nov. (Photo: C. Braunert).

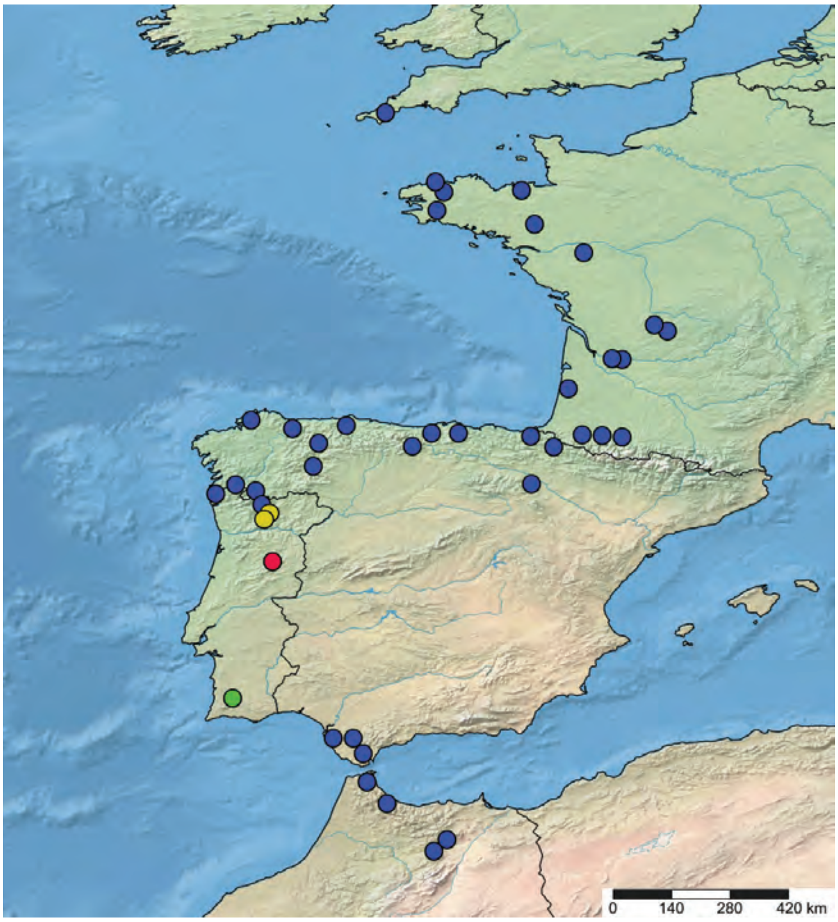


Figure 17. Records from *Anchonidium* sensu stricto in Western Europe. *A. unguiculare* (blue dots), *A. braunerti* (green dot), *A. spathiferum* (red dot) and *A. selvanum* sp. nov. (yellow dots). Background map by https://www.simplemappr.net/.

Serras Peneda and Gerez, but reaches also the Serra do Barroso (two sampled localities: 10 km NE Cabeceiras de Basto, 41°35'26"N, 7°56'12"W, and 11 km NE Cabeceiras de Basto, 41°35'45"N, 7°56'26"W), and even crosses the Rio Tâmega valley. In the northernmost edge of the Serra do Alvão, we collected *A. unguiculare* from scrubland at the following locality: 1 km northeast of Macieira, 41°25'53"N, 7°48'34"W, 970 m a.s.l. just four kilometers north of the type locality of the new species. Hence, we did not directly observe a sympatric occurrence, but it is likely.

Due to the constant loss of its characteristic habitat, *Anchonidium selvanum* sp. nov. must be considered as threatened. The relict character of those forests and the new species is of special importance, and we need to address this observation here. These ancient oak forests are tiny relicts of a habitat type, which had a much wider distribution in ancient times; surely these forests covered a considerable part of those mountain chains. Nevertheless, due to exceptionally redundant wildfires in Portugal (Nunes and Duarte 2006), and a severe loss of natural habitats due to overexploitation followed by plantations of the above-mentioned Australian trees, which even enhance the chance of severe wildfires, this habitat type strongly declined. Even in the Parque Natural do Alvão, we found only small remains of this ancient forest type. *Anchonidium selvanum* sp. nov. has to be considered as an excellent indicator for these ancient woodlands. We observed spectacular differences in individual numbers collected, when comparing disturbed habitats with more intact ones.

The observed ecological demands of the *Anchonidium* s. str. species investigated differ to a certain extent. We collected all species under humid and shaded conditions. *A. unguiculare* accepts larger varieties of forests, from mediterranean Oak forests in the south of Spain and in Morocco, to the oceanic influenced deciduous forests along the Atlantic coast of Spain, France and Great Britain. *A. braunerti* seems to be restricted to the highest elevations of Serra de Monchique in a habitat type where heather and mosses dominate nowadays. We collected *A. spathiferum* in a very similar habitat, where, however, the absence of an ancient Oak forest might explain the rareness of specimens found. Here, with the discovery of *A. selvanum* sp. nov. it is obvious that this new species is restricted to the ancient Oak forests, and as we could show with specifically prospected localities, the more northern situated mountain chains are populated by *A. unguiculare*. The latter species also occurred in much larger numbers in more ancient forests, rather comparable with *A. selvanum* sp. nov.

Acknowledgements

Many thanks to all our friends joining the successful Portugal excursion, Michael Balkenohl (Bonstetten), Ruedi Bryner (Biel) and Salome Steiner (Bern). Many thanks to Mandy Schröter (SDEI Müncheberg) for the prolonged loan of specimens from Serra do Marão; those specimens initiated the present excursion.

References

Garcia C, Sérgio C, Jansen J (2008) The bryophyte flora of the natural park of Serra da Estrela (Portugal): Conservation and Biogeographical approaches. Cryptogamie Bryologie 29(1): 49–73.

Germann C (2020) On *Anchonidium* Bedel, 1884 sensu stricto, with descriptions of two new species from the Iberian peninsula (Coleoptera, Curculionidae: Molytinae). Revue Suisse de Zoologie 127(1): 27–41. https://doi.org/10.35929/RSZ.0004

Grebennikov V (2018) Re-defined *Aparopionella* from Afrotropical forest floors comprises 20 poorly known nominal species (Coleoptera, Curculionidae, Molytinae). Entomologische Blätter und Coleoptera 114: 219–231.

Hlaváč P (2020) Review of the tribe Typoderini (Coleoptera: Curculionidae) from Caucasus with the description of a new species of *Caulomorphus* from Armenia. Acta Entomologica Musei Nationalis Pragae 60(2): 629–638. https://doi.org/10.37520/aemnp.2020.044

Hlaváč P, Borovec R (2022) *Oberprielerius*, a new genus for *Anchonidium uniforme* Voss, 1974, a microphthalmic species of Rhythirrinini (Coleoptera: Curculionidae: Cyclominae) from South Africa. Zootaxa 5196(1): 128–134. https://doi.org/10.11646/zootaxa.5196.1.6

Hoffmann A (1965) Curculionides nouveaux du Tanganyika (Coleoptera). Annales de la Société Entomologique de France (Nouvelle Série) 1: 393–409.

Hoffmann A (1968) The scientific results of the Hungarian soil zoological expedition to the Brazzaville-Congo. 32. Espèces de la famille Curculionidae (Coleoptera). Opuscula Zoologica, Budapest 8: 11–29.

Nunes A, Duarte J (2006) In: Viegas DX (Ed.) V International Conference on Forest Fire Research. Assessment of forest fire risk in the Serra da Estrela Natural Park (Portugal): methodological application and validation, 1–10.

Queirós M (2012) Natural Parks in Portugal: A way to become more ecologically responsible? Special places and protected spaces: Historical and Global Perspectives on Non-National Parks in Canada and Abroad 18(4): 585–611. https://doi.org/10.3197/096734012X13466893037189

Alpine Entomology 7 2023, 201–204 | DOI 10.3897/alpento.7.110958

PENSOFT.

Alpine Entomology

Planning insect surveys in alpine ecosystems

Jérôme Pellet[1,2]

1 *n+p wildlife ecology, Place St-François 6, CH-1003 Lausanne, Switzerland*
2 *Department of Ecology and Evolution, University of Lausanne, Lausanne CH-1015, Switzerland*

https://zoobank.org/032B0AE3-92C0-43C3-AE98-9EBB41AD434E

Corresponding author: Jérôme Pellet (jerome.pellet@nplusp.ch)

Academic editor: Claudia Buser ♦ **Received** 12 August 2023 ♦ **Accepted** 25 October 2023 ♦ **Published** 30 October 2023

Abstract

Most biological survey programs rely on multi-species inventories (e.g. birds, amphibians, butterflies, dragonflies). These programs usually rely on multiple visits during pre-defined time windows. The implicit goal of this popular approach is to maximize the observed species richness. Here, we present a novel method to optimize the timing of survey windows using a framework maximizing the detectable species pool. We present a proof of concept using 20 years of entomological records in Switzerland using butterflies, dragonflies, and grasshoppers. The general framework presented can potentially be applied to a wide range of biological survey schemes. It offers a new practical tool for adaptive entomological monitoring under climate change.

Key Words

Lepidoptera, Odonata, Orthoptera, altitudinal levels, phenology, adaptive monitoring

Introduction

Standing at the core of complex ecological food webs, insects provide insights into the health and stability of ecosystems. They are thus widely used as bioindicators at local, regional, and international scales (McGeogh 1998; Thomas 2005; Buckland and Johnston 2017; Chowdhury et al. 2023). By surveying and monitoring insect diversity, we gain a better understanding of the intricate relationships between species and their habitats across time, enabling us to develop environmentally sound conservation strategies and evaluate the efficiency of public policies (Yoccoz et al. 2001).

Many of the ongoing entomological survey programs aim at estimating species richness among taxa. Even though recent technologies (e.g. computer vision, acoustic monitoring, radar, and molecular methods) offer new perspectives (van Klink et al. 2022), visual encounters remain the most widespread approach. This is especially true for several popular taxa that are widely surveyed in alpine ecosystems, such as butterflies/day-flying moths, dragonflies/damselflies, and crickets/grasshoppers, all of which can be readily identified or photographed in the field. Even though these taxa do not contain an overwhelming number of species compared to other taxa, surveying them remains a costly endeavor.

Entomological visual surveys are usually based on repeated visits across the activity period of the focal taxon. This is necessary because individual species fluctuate in abundance asynchronously during a year (the adult activity or flight periods of various species of insect typically only partly overlap within a focal taxon, see Pellet 2008). These multiple visits aim to maximize the chance of encountering all potentially present species. Monitoring schemes therefore very often rely on pre-defined time windows surveys that are assumed to maximize the observed species richness of the community under scrutiny.

Here, we present a novel approach to identify the best time windows for surveying alpine entomological communities by optimizing the encounter probabilities of every species with as few visits as possible. Using 20 years of observations for three popular taxa, we provide evidence-based, data-driven, guidance for alpine insect survey planning.

Material and methods

We first extracted all observations of Lepidoptera (limited to butterflies and day-flying moths), Odonata (dragonflies and damselflies), and Orthoptera (crickets and grasshoppers) from info fauna, the Swiss biological records center (www.infofauna.ch) for the period spanning 2003–2022. The data was then organized into three matrices (one for each taxon) containing (i) the species name, (ii) the year the observation was made, (iii) the altitudinal levels of the observation, (iv) 52 columns corresponding to the weeks of the calendar year. These weekly columns were then filled with the total number of adult individuals of a given species that had been observed each year at a given altitudinal level.

Species detectability in a given week at a given altitudinal level was first assumed to follow $P(X_{s,t}) \cong 1 - e^{-N_{s,t}}$, where $P(X_{s,t})$ is the probability of detecting species s during week t and $N_{s,t}$ is the number of observations of species s during week t. That is, the more abundant a species is, the more likely it is that a single individual of that species will be observed. In short, we ended up with an expected number of species being potentially observed at every altitudinal level, week, and year.

Our optimization algorithm then worked through the following steps, iterating years and altitudinal levels, finding - by exhaustion of all possibilities - the combination of survey weeks maximizing the sum of $P(X_{s,t})$ (i.e. the number of species likely to be detected). For convenience, we tested 5 scenarios representing an increasing number of annual surveys (from 1 to 5). We then used this data to plot the best time windows - from a single week to a combination of 5 different weeks - that maximize the species richness likely observed by an observer.

The first draft of the introduction, discussion, and abstract of this paper has been adapted with PerplexityAI (2023). Prompts included the first version of the texts along with requests to (i) shorten paragraphs, (ii) improve clarity and (iii) correct any grammatical errors. All outputs from PerplexityAI (2023) were then reviewed and edited before being taken into consideration.

Results

The optimized survey windows for 3 taxa and 3 altitudinal levels are described in Fig. 1. Each of the 9 sub-figures illustrates the best periods to maximize detectable species richness under 5 survey intensity scenarios (from a single annual survey to 5 annual surveys).

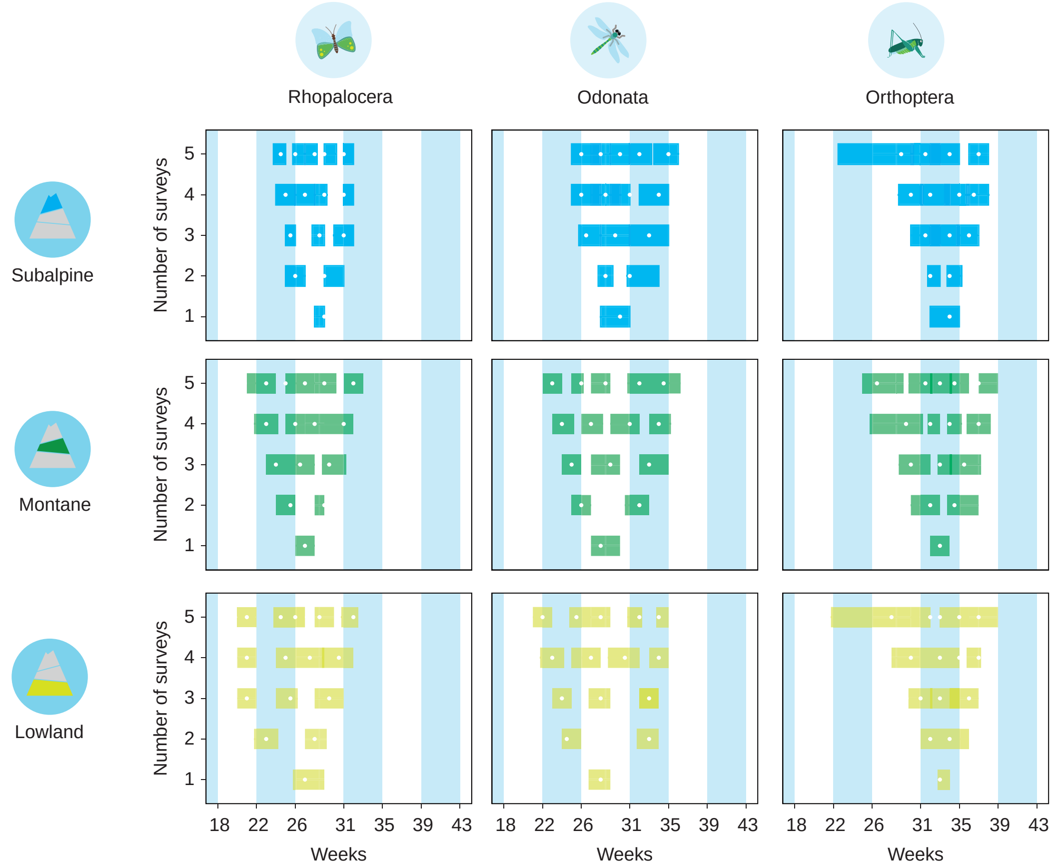


Figure 1. Optimal time windows to maximize potential species richness in entomological surveys for 3 taxa at 3 altitudinal levels assuming between 1 and 5 surveys each. The mean of the 2003–2022 period is represented with a white dot, the colored bars represent the standard deviation. A single survey aiming at maximizing the potential species richness of butterflies in the lowland (lower left sub-figure) would have to take place between weeks 26 and 30 of the year (first half of July). If two surveys are planned, then they should ideally take place on week 23 (early June ±1 week) and on week 28 (mid-July ±2 weeks).

For Odonata at the subalpine level (top middle sub-figure), a single visit should be made on the last week of July (the white dot representing the median best week). Depending on yearly variability, this best week can span anywhere between mid-July and the end of August. If two surveys are envisioned, then the first one should occur in mid-July and the second one in early August.

As expected, higher elevations translate into later survey windows, the amplitude of the shift being about 2 weeks between the lowland and the subalpine levels. Fig. 1 also shows, with little surprise, that Orthoptera tend to be more detectable later in the year than Odonata and Rhopalocera, the latter two groups having a larger spring/early summer species pool.

Running the algorithm for the 1983–2022 period (data not represented in Fig. 1) yielded valuable insights into changes in the timing of the optimal survey windows between the two 20-year periods. On average, all groups showed an advance of the best time windows of 0.9 weeks. That is, the best time windows moved about one week early between the two time periods. More specifically, Rhopalocera and Orthoptera showed a bigger advancement (1.1 week) than Odonata (0.6 week). The advancement of the timing was also larger at the subalpine level (1.6 weeks) than at lower elevations (0.9 and 1.2 week for the lowland and mountain levels respectively). There was, however, no significant change in the standard deviations of the best time windows for any taxon or altitudinal level.

Discussion and conclusion

Insect surveys represent technically and logistically challenging operations that can prove costly (Field et al. 2007). In a world of limited financial resources, optimizing survey periods allows for a better balance of resources between monitoring investments and management actions, which constitute the final aim of most natural resources public policies (Field et al. 2007). This approach requires that the goals and scope of the surveys be explicitly formulated (Anderson 2001). In our case, we postulated, as in many ongoing programs, that maximizing observed species richness was the objective. Maximizing species cumulative detection probabilities across multiple surveys increases the chance of obtaining relevant species community data, as well as identifying species/habitat relationships or detecting trends in occupancy (Pollock et al. 2002; MacKenzie and Royle 2005; Mourguiart et al. 2020). This optimization approach focusing on both detection probability and estimates of occupancy has proven useful in other groups in the past (e.g. amphibians, Barata et al. 2017 or mammals, Baumgardt et al. 2019). In short, our approach potentially increases the return on investment for multiple species survey schemes.

By using a large 20-year-long dataset across multiple altitudinal levels, we closed the loop of active adaptive monitoring, where data collected in the past is used to improve future efforts (Lindenmayer et al. 2011). This is especially important under climate changes that shift both habitat suitability and phenological periods of insects and other cold-blooded species (Vitasse et al. 2021; Buckley 2022). As we have shown here, the overall phenological shift in 20 years is about 1 week. It is consequently a necessity to regularly adapt existing survey programs (Halsch et al. 2021; Hill et al. 2021). Further optimization could consider not only changes in emergence timing but also changes in voltinism or shifts in altitudinal ranges.

Acknowledgments

Gerard Maze and Marine Bugnon provided help with the construction of the model and its implementation in both Python (parsing and optimization algorithms) and R (summary statistics and figure production). DO! L’agence prepared the pictograms of Fig. 1. Yves Gonseth, Benedikt Schmidt, and Christian Monnerat provided feedback during the initial stages of this project.

References

Anderson DR (2001) The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29: 1294–1297.

Barata IM, Griffiths RA, Ridout MS (2017) The power of monitoring: optimizing survey designs to detect occupancy changes in a rare amphibian population. Nature Scientific Reports 7: 16491. https://doi.org/10.1038/s41598-017-16534-8

Baumgardt JA, Morrison ML, Brennan LA, Pierce BL, Campbell TA (2019) Development of multispecies, long-term monitoring programs for resource management. Rangeland Ecology & Management 172: 168–181. https://doi.org/10.1016/j.rama.2018.07.010

Buckland ST, Johnston A (2017) Monitoring the biodiversity of regions: Key principles and possible pitfalls. Biological Conservation 214: 23–34. https://doi.org/10.1016/j.biocon.2017.07.034

Buckley LB (2022) Temperature-sensitive development shapes insect phenological responses to climate change. Current Opinion in Insect Science 52: 100897. https://doi.org/10.1016/j.cois.2022.100897

Chowdhury S, Dubey VK, Choudhury S, Das A, Jeengar D, Sujatha B, Kumar A, Kumar N, Semwal A, Kumar V (2023) Insects as bioindicators: A hidden gem for environmental monitoring. Frontiers in Environmental Science 11: 1146052. https://doi.org/10.3389/fenvs.2023.1146052

Field SA, O’Connor PJ, Tyre AJ, Possingham HP (2007) Making monitoring meaningful. Austral Ecology 32: 485–491. https://doi.org/10.1111/j.1442-9993.2007.01715.x

Field SA, Tyre AJ, Possingham HP (2005) Optimizing allocation of monitoring effort under economic and observational constraints. Journal of Wildlife Management 69: 473–582. https://doi.org/10.2193/0022-541X(2005)069[0473:OAOMEU]2.0.CO;2

Hill GM, Kawahara AY, Daniels JC, Bateman CC, Scheffers BR (2021) Climate change effects on animal ecology: butterflies and moths as a case study. Biological Reviews 96: 2113–2126. https://doi.org/10.1111/brv.12746

Halsch CA,Shapiro AM, Fordyce JA, Nice CC, Thorne JH, Waetjen DP, Forister ML (2021) Insects and recent climate change. PNAS 118(2): e2002543117. https://doi.org/10.1073/pnas.2002543117

Lindenmayer DB, Likens GE (2010) The science and application of ecological monitoring. Biological Conservation 143: 1317–1328. https://doi.org/10.1016/j.biocon.2010.02.013

Lindenmayer DB, Likens GE, Haywood A, Miezis L (2011) Adaptive monitoring in the real world: proof of concept. Trends in Ecology and Evolution 26: 641–646. https://doi.org/10.1016/j.tree.2011.08.002

McGeogh MA (1998) The selection, testing, and application of terrestrial insects as bioindicators. Biological Reviews 73: 181–201. https://doi.org/10.1111/j.1469-185X.1997.tb00029.x

MacKenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42: 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

Mourguiart B, Couturier T, Braud Y, Mansons J, Combrisson D, Besnard A (2020) Multi-species occupancy models: an effective and flexible framework for studies of insect communities. Ecological Entomology 46: 163–174. https://doi.org/10.1111/een.12991

Pellet J (2008) Seasonal variation of butterflies' detectability in Pollard walks. Journal of Insect Conservation 12: 155–162. https://doi.org/10.1007/s10841-007-9075-8

PerplexityAI (2023) Perplexity [Large language model]. https://www.perplexity.ai

Pollock KH, Nichols JD, Simons TR, Farnsworth GL, Bailey LL, Sauer JR (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13: 105–119. https://doi.org/10.1002/env.514

Possingham HP, Wintle BA, Fuller RA, Joseph LN (2012) The conservation return on investment from ecological monitoring. In: Lindenmayer DB, Gibbons P (Eds) Biodiversity monitoring in Australia. CSIRO, Collingwood, 49–62.

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Proceedings of the Royal Society B, Biological Sciences 360: 339–357. https://doi.org/10.1098/rstb.2004.1585

Vitasse Y, Ursenbacher S, Klein G, Bohnenstengel T, Chittaro Y, Delestrade A, Monnerat C, Rebetez M, Rixen C, Strebel N, Schmidt BR, Wipf S, Wohlgemuth T, Yoccoz NG, Lenoir J (2021) Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. Biological Reviews 96: 1816–1835. https://doi.org/10.1111/brv.12727

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. Trends in Ecology & Evolution 16: 446–453. https://doi.org/10.1016/S0169-5347(01)02205-4

Alpine Entomology 7 2023, 205–212 | DOI 10.3897/alpento.7.109021

PENSOFT.

Alpine Entomology

Description of the larva of *Isoperla orobica* Ravizza, 1975 (Plecoptera, Perlodidae), with notes on ecology and distribution in Switzerland

Verena Lubini-Ferlin[1], Pia Teufl[2], Christoph Novotny[2], Laurent Vuataz[3,4]

1 *Eichhalde 14, CH-8053 Zürich, Switzerland*
2 *Institute of Hydrobiology and Aquatic Ecology Management, University of Natural Resources and Life Sciences, Gregor Mendel Strasse 33, A-1180 Vienna, Austria*
3 *Muséum cantonal des sciences naturelles, Département de zoologie, Palais de Rumine, Place de la Riponne 6, CH-1005 Lausanne, Switzerland*
4 *University of Lausanne (UNIL), Department of Ecology and Evolution, CH-1015 Lausanne, Switzerland*

https://zoobank.org/2922E5D9-5FC0-40E1-89BC-2AC742B70F42

Corresponding author: Verena Lubini-Ferlin (lubini@sunrise.ch)

Academic editor: Dávid Murányi ◆ **Received** 5 July 2023 ◆ **Accepted** 21 October 2023 ◆ **Published** 2 November 2023

Abstract

The larva of *Isoperla orobica* Ravizza, 1975, an endemic Alpine species, is described with information about the distribution and ecology in Switzerland. New barcodes were generated to support the association between life stages. The species is associated with springs and spring brooklets. In Switzerland, the species occurs almost exclusively on the southern slopes of the Alps in the cantons Valais, Ticino and Grisons.

Key Words

Stoneflies, morphology, COI, Alps, endemism, taxonomy, larval description

Introduction

Isoperla Banks, 1906 is the most species-rich genus among the stonefly family Perlodidae, with at least 190 valid species recognized from the Holarctic and Oriental Realms (DeWalt et al. 2023). Sixty-three species are reported in Europe, with most of them in the Mediterranean region (DeWalt et al. 2023). Eight species are reported from Switzerland (Roesti 2021), belonging to five different species groups: *acicularis*: *Isoperla carbonaria* (Aubert, 1953), *I. lugens* (Klapálek, 1923); *grammatica*: *I. grammatica* (Poda, 1761), *I. felderorum* (Roesti, 2021); *obscura*: *I. obscura* (Zetterstedt, 1840); *oxylepis*: *I. orobica* (Ravizza, 1975), *I. oxylepis* (Despax, 1936); *rivulorum*: *I. rivulorum* (Pictet, 1841) (Muranyi 2011). *Isoperla lugens* and *I. orobica* are endemic species to the Alps (Gtraf et al. 2009). In Switzerland, all but two species (*I. orobica*, *I. felderorum*) are well known also in terms of their larval stage (Lubini et al. 2012). This study aims to newly describe the larva of *I. orobica*, which is currently only known in the adult stage. This will enhance our knowledge of the distribution of *Isoperla* species in the context of the Swiss monitoring project of aquatic insects. Furthermore, the distribution and ecology of the species in the Alps are discussed.

Materials and methods

All specimens were caught by hand, the larvae by kicknet sampling or by picking specimens directly from the substrate, and the adults by sweep net or “Japanese umbrella” (beating sheet). The specimens were stored in 80% ethanol and deposited in the collection of the Muséum cantonal des sciences naturelles, Lausanne, Switzerland. Mouthparts, abdominal tergites and cerci were mounted on slides and photographed. To distinguish *I. orobica* from sympatric species such as *I. carbonaria* and *I. rivulorum*, we examined comparative material, refering to Lubini et al. (2012) regarding most morphological characters. The terminology of the maxilla follows Sandberg (2011). Local and altitudinal distribution as well as the phenological data were provided by the National Center for Wildlife Data and Information in Switzerland (https://infofauna.ch), the Italian distribution by R. Fochetti (Tuscia University).

To provide additional evidence supporting the association between larvae and adults, we conducted genetic sequencing of a 658 bp fragment from the mitochondrial gene cytochrome oxidase subunit 1 (COI hereafter), which corresponds to the standard animal barcode region. We conducted this sequencing on three specimens of *I. orobica*, consisting of two larvae and one adult male (Table 1), using the non-destructive DNA extraction procedure described in Vuataz et al. (2011). The Polymerase Chain Reaction (PCR), purification and sequencing steps were conducted according to the methodology described in El Alami et al. (2022). Forward and reverse sequencing reads were assembled and edited in Codon Code Aligner 10.0.2 (Codon-Code Corporation, Dedham, MA), and aligned in Jalview 2.11.2.7 (Waterhouse et al. 2009). To tentatively augment our dataset, we searched for COI sequences associated with *I. orobica* in the GenBank and Barcode of Life Data System (BOLD) databases as of September 21, 2023, but no additional sequences were available.

Material examined

Isoperla orobica: Switzerland: 6 larvae, spring brooklet, tributary to river Taferna (VS), 46°15'53"N, 8°02'09"E, 1580 m, 6.VII.2017, leg. Verena Lubini, 1 larva DNA, GBIFCH00658280; 8 larvae, same locality, same date, leg. Remo Wüthrich; 4 larvae, same locality, 7.VII.2022, leg. Verena Lubini; 4 larvae, tributary to Fiume Bello, Alpe Rompiago (TI), 46°05'25"N, 8°59'44"E, 1131 m, 28.VI.2018, leg. Verena Lubini; 4 larvae, tributary to Riale Vadina, Alpe di Neggia (TI), 46°06'46"N, 8°50'55"E, 1289 m, 27.VI.2018, leg. Remo Wüthrich; 1 larva, 3 ♂, tributary to Riale Vadina, Rotiscia (TI), 46°07'05"N, 8°51'01"E, 996 m, 27.VI.2018, leg. Remo Wüthrich, 1 ♂ DNA, GBIFCH00658286; 6 larvae, same locality, 29.VI.2022, leg. Verena Lubini and Viviane Uhlmann; 1 larva DNA, GBIFCH00658284, tributary to Riale Vadina, Alpe di Neggia (TI), 46°06'47"N, 8°51'11"E, 1250 m, 29.VI.2022, leg. Verena Lubini; spring brooklet, tributary to river Laggina, Alte Staful (VS), 46°09'30"N, 8°03'24"E, 1550 m, 7.VII.2017, leg. Remo Wüthrich. Italy: 1 larva, 1 ♂, spring brooklet, Valchiusella, 45°32'4"N, 7°40'48"E, 1200 m, 6.VIII.2016, leg. Verena Lubini.

Isoperla carbonaria: Switzerland: 3 larvae, Val Giona, Büèe (TI), 46°06'18"N, 8°50'18"E, 1135m, 5.VI.2000, leg. Verena Lubini; 1 larva, Val Muggio (TI), 45°53'53"N, 9°02'32"E, 544 m, 5.VI.2000, leg. Verena Lubini; 1 larva, Valle Verzasca, Gerra (TI), 46°19'37"N, 8°48'08"E, 819 m, 14.IV.2023, leg. Paola Gandolfi.

Isoperla rivulorum: Switzerland: 1 larva, Alp Prüma, Val Roseg (GR), 46°27'29"N, 9°52'52"E, 1913 m, 27.III.2000, leg. Verena Lubini; 1 larva, spring brooklet, tributary to Rigiaa, Gruonholz (SZ), 47°02'25"N, 8°30'22"E, 1176 m, 19.VI.2022, leg. Emil Birnstiel; 1 larva, Munt San Franzesch (GR), 46°22'45"N, 10°06'03"E, 2150 m, 27.IV.2001, leg. Verena Lubini; 1 larva, river Landquart, Grüsch (GR), 46°58'27"N, 9°38'02"E, 593 m, 30.III.1993, leg. Verena Lubini.

Results

The alignment of the three COI sequences was 100% complete, with no missing data, and all sequences were identical, except for a single site that was ambiguous in the GBIFCH00658280 sequence (Table 1). These findings strongly support the conspecificity of the sequenced larvae and adult. As of September 21, 2023, a BLAST search on our sequences showed the closest match to be a sequence with a 94.1% similarity, originating from a specimen collected in Croatia and identified as *I. rivulorum* (Hlebec et al. 2021), while all other results were less than 94% similar, confirming that our sequences are the first *I. orobica* barcodes to be publicly deposited.

Description of the mature larva

Body length 8.9–11.3 mm (n = 14). General colour light brown, abdomen notably darker than head and thorax (Fig. 1A, B, 6C), ventral coloration pale (Fig. 1D, E). Pilosity typical of the genus, thoracic segments covered by dark brown clothing hairs and blunt marginal spines.

Head light brown with indistinct pale markings; defined pale interocellar area lacking; frontoclypeus anterior to M-line pale; sometimes two darker sublateral markings at anterior margin of frontoclypeus; pale sublateral occipital spots posterior to epicranial suture; head trapezoid shaped with frontal area slightly elongated (Fig. 2A). Scape, pedicel and following antennomeres pale; palpi and mouthparts pale (Fig. 2B).

Lacinia bidentate, sub-quadrate shaped with only slightly rounded inner margin; subapical tooth slightly longer than half of the length of apical tooth; 1 group A submar-

Table 1. Newly sequenced *Isoperla orobica* specimens from Switzerland, including collection details and GenBank accession numbers.

Specimen catalogue nb	Stage	GPS Coordinates	Altitude	Date	Collector	GenBank ID
GBIFCH00658280	Larva	46°15'53"N, 8°02'09"E	1580 m	6.VII.2017	V. Lubini	OR600533
GBIFCH00658284	Larva	46°06'47"N, 8°51'11"E	1250 m	29.VI.2022	V. Lubini	OR600534
GBIFCH00658286	Adult male	46°07'05"N, 8°51'01"E	996 m	27.VI.2018	R. Wüthrich	OR600535

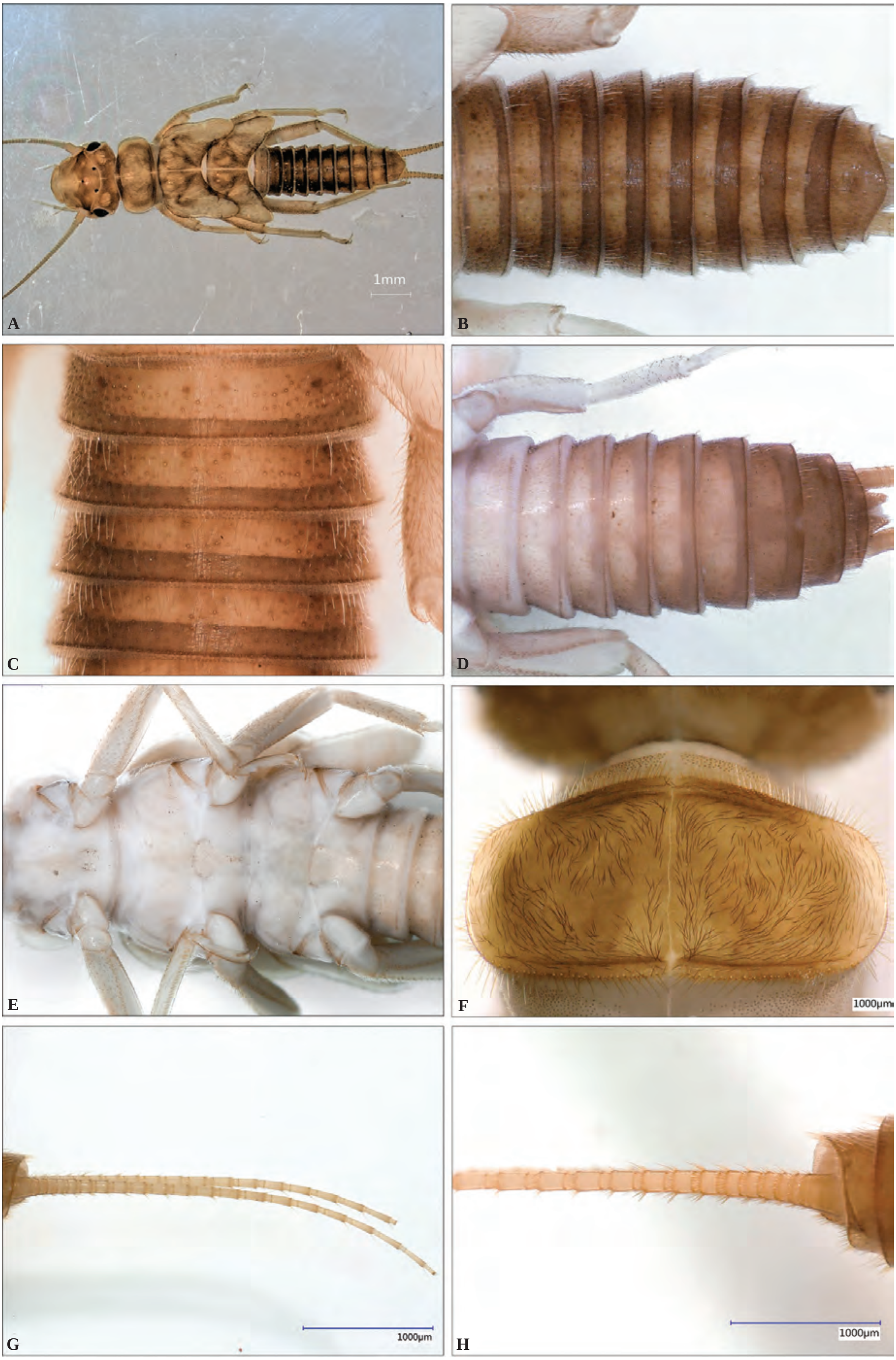


Figure 1. *Isoperla orobica*, larval morphology. **A.** Habitus dorsal; **B.** Abdomen dorsal; **C.** Tergite 1–4; **D.** Abdomen ventral; **E.** Furcasternites; **F.** Pronotum; **G.** Left cercus lateral; **H.** Right cercus detail lateral. (Photos: Pia Teufl, Christoph Novotny).

Figure 2. *Isoperla orobica*, larval morphology. **A.** Head and pronotum dorsal; **B.** Head ventral; **C.** Left lacinia and galea dorsal view; **D.** Right lacinia dorsal view; **E.** Right mandible dorsal view; **F.** Right mandible ventral view (Photos: Pia Teufl, Christoph Novotny).

ginal setae present, below apical tooth and adjacent to subapical tooth; 1 thin marginal seta below apical tooth and 1 thin marginal seta proximal to subapical tooth; 6–10 stout marginal setae, space between setae continuously decreasing towards base, almost all stout marginal setae of equal length except for the most proximal setae, which are shorter; sparse row of thin marginal setae (9–12) along proximal half of inner lacinial margin (Fig. 2C, D); scattered, sparse ventral surface setae on inner basal palm. Galea with four apical setae; inner and outer margin with sparse setae; galea reaching base of apical tooth. Mandible with one incisor and three molars, molar brush dense and long; dense seate dorsally and ventrally at inner margin; small area of setae laterally at the base of mandibles (Fig. 2E, F).

Pronotum light brown, lateral margins of disc lighter in colour; anterior and posterior margin of pronotum slightly darker; half as long as wide (ratio 1:2); spines on protonal margin distinct; longest spines as long as one fifth of the pronotal width with shorter spines in between (Fig. 1F).

Mesonotum and metanotum with indistinct darker markings; wingpads pale; outer margin of wingpads slightly concave (Fig. 1A). Thoracic sternites pale; furcasternites and furcal pits hardly contrasting (Fig. 1E).

Abdominal terga mostly brown with variable dark median marking; first tergite lighter; posterior margin of tergites 1–10 with long blunt spines, longest spines longer than half of tergal lengths (Fig. 1C). Sternites pale, distal segments slightly darker.

Legs light brown; dense row of acute spines covering dorsal margin of femur; spines short on proximal third and longer (length: half of femur width) on two distal thirds of femur; long silky setal fringe (almost as long as femur width) covering dorsal margin of femur (Fig. 3B); spines and setae on surface of femur (Fig. 3A).

Double row of dense spines (length: one third of tibia width) on dorsal margin of tibia (Fig. 3C) with longer ones towards distal third; dorsal side of tibia with sparse and long setal fringe (length: as long as tibia width). Tarsi with sparse setal fringe on dorsal margin (Fig. 3D). All claws with one basal tooth each.

Cercus pale yellow with a thin brown ring on proximal 1/4 of cercomeres; cercomeres cylindrical; medial cercomeres twice as long as wide. Cercal apical fringes dense, circumferential setae on medial cercomeres approximately one fourth of segment length, dorsomedial and ventromedial setae longer (length: more than half of segment length); cercus without dorsal setal fringe (Fig. 1G, H). Paraproct blunt with widely rounded apex.

Figure 3. *Isoperla orobica*, larval morphology. **A.** Front left femur; **B.** Front left femur, dorsal margin; **C.** Front left tibia; **D.** Front left tarsus (Photos: Pia Teufl, Christoph Novotny).

Distribution and ecology

Isoperla orobica is an endemic rheophilic species from the western and central Alps (Graf et al. 2009; Fochetti 2020), distributed only in northern Italy (Consiglio 1979; Ravizza 2023) and Switzerland (Fig. 4). In Switzerland, the species is predominantly observed along the southern slopes of the Alps, with its current distribution primarily centered on the Simplon Pass, as well as in certain mountainous regions within the canton Ticino (Val Colla, Valle di Vira, Val Serdena) and the canton Grisons (Val Mesocco) (https://infofauna.ch). Apart from the southern slopes of the Alps there is only one location in the central Alps, which is situated in the catchment of the river Rhone in the canton Valais, Switzerland.

Figure 4. Present distribution of *I. orobica* in Switzerland and Italy. Only one location is in the drainage area of the river Rhone (red star), all other locations (red squares) are in the drainage basin of the river Po. The Swiss locations represent areas of 5×5 km with a total of 30 sampling stations (https://infofauna.ch).

The larvae were found in springs, spring brooklets and in brooks of the epirhithral zone mainly between 900 m and 1500 m, rarely above 2000 m. The substrate varies from organic to coarse stony bottoms in moderate to steep slopes (Fig. 5). The flight periods of the adult insects extend from late June to October at altitudes ranging from 900 m to 2030 m. The accompanying fauna consists of *Dictyogenus fontium* (Ris, 1896), *Chloroperla susemicheli* (Zwick, 1967), *Siphonoperla italica* (Aubert, 1953), *Leuctra insubrica* (Aubert, 1949), *L. armata* (Kempny, 1899), *L. braueri* (Kempny, 1898), *L. caprai* (Festa, 1939), *L. dolasilla* (Consiglio, 1955), *L. schmidi*

Figure 5. Habitat of *I. orobica* in Switzerland, upstream views. **A, B.** Spring brook, tributary to river Taferna (Rhone basin, canton Valais); **C.** River Vadina, tributary to Lake Maggiore (canton Ticino); **D.** Brook in Simplon pass, near Stalde (canton Valais) (Photos: Verena Lubini).

(Aubert, 1946), *L. vinconi* (Ravizza & Ravizza Dematteis, 1993), *Nemoura sinuata* (Ris, 1902) and *Protonemura lateralis* (Pictet, 1836).

Diagnosis

For comparison between *I. orobica* and the two sympatric species *I. rivulorum* and *I. carbonaria*, body coloration patterns and characteristics of the maxillae were considered (Table 2). In terms of coloration, *I. orobica* differs from both other species (Fig. 6, Lubini et al. 2012) in having a uniformly brown colour and lacking a pale interocellar area on the head.

The lacinia of all three species is bidentate and generally sub-quadrate, but differences in the number of thin marginal setae on the lacinia and pilosity of the galea can aid in distinguishing these taxa. *Isoperla orobica* has 9–12 thin marginal setae compared to 25–35 in *I. rivulorum* (Table 2, Fig. 7). Additionally, *I. orobica* has setae on both the inner and outer margins of the galea; whereas *I. carbonaria* only has setae on the outer margin. Furthermore, *I. orobica* lacks the dense setal fringes on the tibiae, as is the case in the other two species.

Table 2. Verification table of morphological characters for *Isoperla orobica*, *I. rivulorum* and *I. carbonaria* (SMS = stout marginal setae; TMS = thin marginal setae).

Species	Body color	Interocellar area	Lacinia SMS	Lacinia TMS	Galea setae
Isoperla orobica	uniform	indistinct	6–10	9–12	inner & outer
Isoperla rivulorum	contrasting	distinct	7–8	25–35	inner & outer
Isoperla carbonaria	contrasting	distinct	7–8	10–16	outer

Figure 6. Larval habitus. **A.** *I. carbonaria*; **B.** *I. rivulorum*; **C.** *I. orobica* (Photos: Verena Lubini).

Figure 7. Lacinial morphology. **A.** *I. carbonaria*; **B.** *I. rivulorum* (Photos: Laurent Vuataz).

Acknowledgments

We are grateful for the photos of Figures 1 to 3 provided by the Institute of Hydrobiology and Aquatic Ecology Management, University of Natural Resources and Life Sciences, Vienna. Remo Wüthrich and Viviane Uhlmann helped collect larvae and adults, and Céline Stoffel conducted the laboratory work for COI sequencing. The National Center for Wildlife Data and Information in Switzerland (https://infofauna.ch) provided the Swiss data, Romolo Fochetti the Italian data. We further thank Wolfram Graf for expert advice. Finally, we express our sincere gratitude to the reviewer, Chris Verdone, for his valuable comments which helped to improve our manuscript.

References

Consiglio C (1979) La distribuzione dei Plecotteri italiani. Biogeographia – The Journal of Integrative Biogeography 6(1): 383–393. https://doi.org/10.21426/B66110071

DeWalt RE, Maehr MD, Hopkins H, Neu-Becker U, Stueber G (2023) Plecoptera Species File Online. Version 5.0/5.0. http://Plecoptera.SpeciesFile.org/

El Alami M, Benlasri M, Sartori M, Vuataz L, Ghamizi M (2022) A new species of the genus *Prosopistoma* Latreille, 1833 (Ephemeroptera, Prosopistomatidae) from Morocco. ZooKeys 1117: 203–218. https://doi.org/10.3897/zookeys.1117.83539

Fochetti R (2020) Endemism in the Italian stonefly-fauna (Plecoptera). Zootaxa 4722(4): 381–388. https://doi.org/10.11646/zootaxa.4722.4.7

Graf W, Lorenz AW, Tierno de Figueroa JM, Lücke S, López-Rodrígues MJ, Davies C (2009) Distribution and Ecological Preferences of European Freshwater Organisms. Vol. 2. Plecoptera. Pensoft Publishers. Sofia, Bulgaria, 262 pp.

Hlebec D, Sivec I, Podnar M, Skejo J, Kučinić M (2021) Morphological and molecular characterisation of the Popijač's Yellow Sally, *Isoperla popijaci* sp. nov., a new stenoendemic stonefly species from Croatia (Plecoptera, Perlodidae). ZooKeys 1078: 85–106. https://doi.org/10.3897/zookeys.1078.66382

Lubini V, Knispel K, Vinçon G (2012) Die Steinfliegen der Schweiz. Bestimmung und Verbreitung. Les plécoptères de Suisse. Identifcation et distribution. Fauna Helvetica 27. CSCF & SEG, Neuchâtel, 270 pp.

Muranyi D (2011) Balkanian species of the genus *Isoperla* Banks, 1906 (Plecoptera: Perlodidae). Zootaxa 3049(1): 1–46.

Ravizza C (2023) The Stonefly communities of three brooks of the Soana Valley (Graian Alps), (Insecta Plecoptera). Rivista piemontese di Storia naturale 44: 87–101.

Roesti C (2021) Die Steinfliegen der Schweiz. Haupt Verlag, Bern, 631 pp.

Sandberg JB (2011) The *Isoperla* of California (Plecoptera: Perlodidae); larval descriptions and a key to 17 western Nearctic species. Illesia 7(22): 202–258.

Vuataz L, Sartori M, Wagner A, Monaghan MT (2011) Toward a DNA Taxonomy of Alpine *Rhithrogena* (Ephemeroptera: Heptageniidae) Using a Mixed Yule-Coalescent Analysis of Mitochondrial and Nuclear DNA. PLoS ONE 6(5): e19728. https://doi.org/10.1371/journal.pone.0019728

Waterhouse AM, Procter JB, Martin DMA, Clamp M, Barton GJ (2009) Jalview Version 2—a multiple sequence alignment editor and analysis workbench. Bioinformatics 25(9): 1189–1191. https://doi.org/10.1093/bioinformatics/btp033

Alpine Entomology 7 2023, 213–217 | DOI 10.3897/alpento.7.109422

Zu Biologie und Identität von *Donus proximus* (Capiomont, 1876) comb. nov. (Coleoptera, Curculionidae, Hyperinae)

On biology and identity of *Donus proximus* (Capiomont, 1876) comb. nov. (Coleoptera, Curculionidae, Hyperinae)

Christoph Germann[1,2]

1 *Curator Biosciences, Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel, Switzerland*
2 *Naturhistorisches Museum Bern, Bernastrasse 15, CH-3005 Bern, Switzerland*

https://zoobank.org/2097221F-A4DE-4950-8768-4E242FC2C983

Corresponding author: Christoph Germann (germann.christoph@gmail.com)

Academic editor: Thibault Lachat ♦ **Received** 12 July 2023 ♦ **Accepted** 2 November 2023 ♦ **Published** 9 November 2023

Zusammenfassung

Anlässlich einer Exkursion in die Gebirgszüge im Norden Portugals konnten Imagines und Larven der wenig bekannten *Donus*-Art vom Doldenblütigen Heidekraut (*Erica umbellata* L.) auf submontaner Lage gesammelt werden. Bisher waren Heidekrautgewächse (Ericaceae) als Wirtspflanzen für Hyperinae gänzlich unbekannt. Eine durchgeführte Zucht bestätigte diese Wirtspflanzenbindung. Die nomenklatorische Änderung *Donus proximus* (Capiomont, 1876), **comb. nov.** von *Brachypera* wird eingeführt, Imago, Larve und der Kokon werden vorgestellt, und das Habitat wird charakterisiert.

Abstract

During an excursion into the mountain chains in northern Portugal, adults and larvae of this largely unknown *Donus*-species were collected at submontane altitudes from *Erica umbellata* L. At present, the Ericaceae are not known as host plants of any Hyperinae. A subsequent breeding allowed to confirm this host-plant relationship. The taxonomically relevant change *Donus proximus* (Capiomont, 1876), **comb. nov.** from *Brachypera* is introduced, adults, larvae and the cocoon are presented, and the habitat is characterized.

Key Words

larval instars, Ericaceae, Iberian Peninsula, Taxonomy, new combination

Einleitung

Wie bereits mehrfach angetroffen, sind die ektophag lebenden Larvalstadien der Hyperinae im Frühsommer immer eine gute Gelegenheit, die Wirtspflanzenbindungen dieser Gruppe zu untersuchen (Dieckmann 1989; Skuhrovec 2005; Curculio Team East 2010; Germann 2011a, 2011b; Germann 2016, 2021a). Vorliegend wird die Entdeckung der Wirtspflanze einer weiteren *Donus*-Art vorgestellt – *Donus proximus* – welche in Nordwestspanien und Nordportugal vorkommt, jedoch wenig bekannt ist und auch in gut assortierten Sammlungen in nur wenigen Belegtieren vertreten ist.

Material und Methoden

Die Funde von *Donus proximus* stammen von folgenden vier Fundorten (alle leg. C. Germann): Vila Real, Serra do Alvão, Bilhó, Bobal, 41°24'05"N, 7°50'02"W, Waldrand, 865 m ü. M., 30.5.2023. – Vila Real, Serra do Alvão, Bilhó, Bobal, 41°23'54"N, 7°49'42"W, 941 m ü. M., Hügelkuppe, 31.5.2023. – Braga, Serra do Barroso, 11 km NE Cabeceiras de Basto, 41°35'45"N, 7°56'26"W, 1000 m ü. M., kleiner Eichen-Restwald, 1.6.2023. – Braga, Serra do Gerês, 4.5 km NE Gerês, 41°46'02"N, 8°08'33"W, 1010 m ü. M., *Quercus*, *Erica*, *Arbutus*, 4.6.2023.

Die Zucht der Larven wurde in Plastik-Schraubdosen durchgeführt, Details dazu finden sich in Germann (2021b). Fundorte von Sammlungstieren werden in Anführungszeichen zitiert, und wurden wörtlich den Etiketten entnommen, eigene Ergänzungen stehen in eckigen Klammern. Die Lebendaufnahmen wurden mit einer Olympus-Kamera des Modells T4 gemacht, die Aufnahmen der Präparate erfolgte mit dem Fotosystem VHX-6000 von Keyence am Naturhistorischen Museum Basel (NMB).

Resultate

Taxonomie

Capiomont (1876) beschrieb *Hypera proxima* auf der Grundlage eines Männchens « La description qui précède est faite sur un individu mâle, le seul que j'aie pu examiner. » [Die folgende Beschreibung basiert auf einem männlichen Individuum, das einzige, welches ich untersuchen konnte.] und verglich die neue Art mit *Donus montivagus* (Capiomont, 1868) beschrieben von demselben Autor aus der Sierra Nevada in Südspanien. Der Typenfundort von *Donus proximus* liegt in der Serra do Gerês in Nordportugal: «Appartient à M. L. von Heyden, de Francfort, qui l'a capturé à Gérez, au nord du Portugal. »[Gehört Herrn L. von Heyden aus Frankfurt, der es in Gerês gefangen hat, im Norden Portugals]. Der Holotypus befindet sich in Müncheberg (Senckenberg Deutsches Entomologisches Institut; SDEI) in der Sammlung Lucas von Heyden und konnte Dank Fotos überprüft werden (Fig. 1).

In der Sammlung Georg Frey am NMB befinden sich folgende weitere Vergleichstiere von *Donus proximus*: «2 ex. Cancas Ast. [Spanien, Asturien], leg. Paganetti, coll. J. Breit. – 1 ex.: Caboalles [Spanien, Leon] ditto. – 3 ex. Sabrosa, Lusitan. – 2 ex. S. Martinho, leg. G. de Barros. – 4 ex. S. Martinho, Portugal». Zudem konnten topotypische Tiere aus der Serra do Gerês, und diejenigen des Synonyms *Donus barrosi* (Guérin, 1894) von San Martinho (Sammlung G. Frey) untersucht werden. Dabei konnte zweifelsfrei festgestellt werden, dass *Donus proximus* nicht zu *Brachypera* Capiomont, 1868 gehört, wie dies von Skuhrovec (2008: 687) vorgeschlagen wurde, sondern in die Gattung *Donus* Jekel, 1865 gehört, was hiermit berichtigt wird: *Donus proximus* comb. nov. Die ovale Form der Elytren ohne Schulterbeule, die vergleichsweise kurzen und breiten Abdominalsegmente, das stark gerundete Pronotum und der lange und stielrunde Rüssel gehören allesamt zu den charakteristischen Merkmalen der Gattung *Donus*, adaptiert nach Jekel (1865) (Figs 1–3). Die Anzahl der Zähne auf den Mandibeln der Larven wurde nicht überprüft, nach Skuhrovec (2008) müssten bei *Donus* drei dieser Zähne zu sehen sein (vier bei *Brachypera* und nur zwei bei *Hypera* Germar, 1817). Dieses Merkmal – erst bei sechs der über 40 Arten der Gattung *Brachypera* überhaupt untersucht – sollte zukünftig noch geprüft werden.

Figure 1. Habitus Holotypus *Hypera proxima* Capiomont, 1876 und Etiketten (Fotos: Kevin Weißing).

Biologie

Während einer Exkursion in den Norden Portugals wurden Anfang Juni 2023 die Gebirgszüge Serra do Marão, Serra do Alvão, Serra do Barroso und die Serra do Gerês besucht (Details dazu in Material & Methoden). In wenigen Restwäldern – der Grossteil der heutigen Waldfläche besteht leider aus aufgeforsteten *Pinus halepensis* Mill.-, *Eucalyptus* sp.-, *Thuja* sp.- oder *Acacia*-Forsten – des ursprünglichen Eichenwaldes, bestehend aus *Quercus pyrenaica* Willd., *Q. cerris* L., *Erica* spp. und verschiedenen Ginsterarten, wurden Larven (Figs 4–6, 11) und Imagines (Fig. 10) von *Donus proximus* gefunden. Eine gezielte Nachsuche ergab *Erica umbellata* L. als Wirtspflanze (Figs 8, 9). Die Standorte lagen alle auf Lichtungen oder an Rändern naturnaher Waldflächen, meist in der Nähe von Felsformationen oder Wegrändern (Figs 8, 9).

Die weitere Zucht der Larven an *Erica umbellata* verlief unproblematisch; innert einer Woche sponnen die ersten Larven einen Gitterkokon (Fig. 7) und verpuppten sich innerhalb von 3–4 Tagen. Am 19. Juni, also 14 bis 18 Tage nach der Verpuppung, waren alle Imagines geschlüpft.

Figures 2, 3. 2. Männchen von *Donus proximus*, rechts unten das Genital (ventrale Sicht). **3.** Weibchen, beide aus Vila Real, Bobal (Fotos: C. Germann).

Figures 4–7. 4. Mehrere Larven wurden an *Erica umbellata* gefunden und gezüchtet. **5, 6.** Die Larven sind durch ihre kontrastreiche Zeichnung, bestehend aus fünf hellen Längsstreifen auf grüner Körperfarbe, hervorragend in den Ästen der Wirtspflanze getarnt. **7.** Bereits nach einer Woche begannen die ersten Larven einen rötlichbraunen Seiden-Netzkokon zu spinnen (Fotos: C. Germann).

Figures 8–11. 8, 9. Typische Habitate auf Lichtungen in naturnahen Eichenwäldern auf der Serra do Alvão und Serra do Barroso in Nordportugal. **10.** Imago bei Frassaktivität auf der Wirtspflanze *Erica umbellata*. **11.** Letztes Larvalstadium kurz vor der Verpuppung (Fotos: C. Germann).

Diskussion

Mit diesem Beitrag und der problemlosen Überprüfung des Holotypus im SDEI konnte die Art- und Gattungszugehörigkeit von *Donus proximus* einwandfrei geklärt werden. Da bisher eine Revision aller *Donus*-Arten noch immer fehlt, und die neusten zusammenfassenden Arbeiten lange zurückliegen (Capiomont 1868a, 1868b; Petri 1901) und neuere Revisionen nur punktuell vorliegen (Skuhrovec and Borovec 2007; Skuhrovec 2008), sind solche Anpassungen nicht weiter überraschend. Durch die Zucht der gefundenen Larven derselben Art in den nördlichen Gebirgen Portugals konnte erstmals eine Ericaceae als Wirtspflanze belegt werden, dass Ericaceae von Hyperinae als Wirtspflanzen genutzt werden, war bisher gänzlich unbekannt; Skuhrovec (2005) trug 15 verschiedene Pflanzenfamilien zusammen, welche nachweislich zur Entwicklung genutzt werden.

Zudem konnte der Lebensraum von *Donus proximus* hier erstmals aufgezeigt werden. Es bleibt zu betonen, dass dieses natürliche Habitat der Eichenwälder im Norden Portugals leider bereits stark dezimiert wurde und durch Brandrodung, überdurchschnittlich häufige Waldbrände (Nunes and Duarte 2006), sowie Aufforstungen durch gebietsfremde Baumarten stark bedroht ist (Garcia et al. 2008; Queirós 2012), was dementsprechend auch für *Donus proximus* gilt. Ob frühere küstennahe Vorkommen von *D. proximus* (wie das Synonym *barrosi* von der küstennahen Lokalität San Martinho belegt) überhaupt noch bestehen, dürfte durch die stark degradierten Habitate (Garcia et al. 2008) beinahe ausgeschlossen sein. Somit sind die Restwälder in den nördlichen Sierras die letzten Rückzugsräume für diese Rüsselkäfer-Art in Portugal.

Danksagung

Ich danke Michael Balkenohl (Bonstetten), Carlo Braunert (Mensdorf), Ruedi Bryner (Biel) und Salome Steiner (Bern) für ihre Unterstützung während der Exkursion. Ganz herzlichen Dank an Kevin Weißing und Mandy Schröter (beide SDEI) für ihre Unterstützung bei der Suche nach und beim Vergleich mit dem Holotypus, sowie der Möglichkeit der Nutzungsrechte der Fotos aus der Sammlung Von Heyden. Den Reviewern sei für ihre hilfreichen Anmerkungen und Ergänzungen zum Manuskript gedankt.

Referenzen

Capiomont G (1868a) Révision de la tribu des hypérides, Lacordaire, et en particulier des genres *Hypera* Germ, *Limobius*, Schönh. et *Coniatus* (Germ.) Schönh. renfermant la description de plusieurs genres nouveaux et de 85 espèces nouvelles. [Cont.]. Annales de la Société Entomologique de France (4) 7(4): 457–560.

Capiomont G (1868b) Révision de la tribu des Hypérides, Lacordaire, et en particulier des genres *Hypera* Germ, *Limobius*, Schönh. et *Coniatus* (Germ.) Schönh. renfermant la description de plusieurs genres nouveaux et de 85 espèces nouvelles. Suite. Annales de la Société Entomologique de France (4) 8(1): 73–160. [pls. 1–2]

Capiomont G (1876) Description d'une espèce nouvelle d'*Hypera*. Annales de la Société Entomologique de France 5(4)[1875]: 467–468.

Curculio Team East (2010) Digital-Weevil-Determination for Curculionoidea of West Palaearctic. Transalpina: Brachypera/Donus (Hyperinae: Hyperini). Snudebiller 11: 102–108.

Dieckmann L (1989) Die Zucht mitteleuropäischer Hyperini-Arten. Entomologische Nachrichten und Berichte 33(3): 97–10.

Garcia C, Sérgio C, Jansen J (2008) The bryophyte flora of the natural park of Serra da Estrela (Portugal): Conservation and Biogeographical approaches. Cryptogamie Bryologie 29(1):49–73.

Germann C (2011a) Observations on the biology of Hyperini (Curculionidae, Hyperinae) in France. Results from an excursion to the department of Var in April 2011. Weevil News 71: 5 pp.

Germann C (2011b) Beobachtungen zu Rüsselkäfern in der Schweiz (Coleoptera, Curculionoidea). Entomo Helvetica 4: 65–75.

Germann C (2016) Beobachtungen zur Biologie von *Donus longicollis* (Coleoptera, Curculionidae). Entomologische Nachrichten und Berichte 60(1): 15–18.

Germann C (2021a) *Hypera temperei* Hoffmann, 1958 – first discovery of the western alpine element in the Swiss Alps with biological details, and new morphological insights (Coleoptera, Curculionidae). Alpine Entomology 5: 5–13. https://doi.org/10.3897/alpento.5.61597

Germann C (2021b) Beitrag zur Praxis in der Entomologie: Zucht von phytophagen Käferlarven in Mehrzweckdosen (Coleoptera). Entomo Helvetica: 14: 105–108.

Jekel H (1865) Recherches sur la classification naturelle des curculionides. Annales de la Société Entomologique de France (4) 4(3)[1864]: 537–566.

Nunes A, Duarte J (2006) In: Viegas DX (Ed.) V International Conference on Forest Fire Research. Assessment of forest fire risk in the Serra da Estrela Natural Park (Portugal): methodological application and validation, 1–10.

Petri K (1901) Monographie der Coleopteren – Tribus Hyperini. Berlin: R. Friedländer, Sohn, 210 pp.

Queirós M (2012) Natural Parks in Portugal: A Way to Become More Ecologically Responsible? Special Places and Protected Spaces: Historical and Global Perspectives on Non-National Parks in Canada and Abroad 18(4): 585–611. https://doi.org/10.3197/096734012X13466893037189

Skuhrovec J (2005) Živné rostliny nosatců rodu *Hypera* (Coleoptera: Curculionidae) vyskytujících se na území České republiky (Host plants of weevils of the genus *Hypera* (Coleoptera: Curculionidae) occurring in the Czech Republic). Klapalekiana 41: 215–255. [In Czech and English]

Skuhrovec J (2008) Taxonomic changes within the tribe Hyperini (Coleoptera: Curculionidae). Acta Entomologica Musei Nationalis Pragae 48(2): 677–690.

Skuhrovec J, Borovec R (2007) Revision of *Donus caucasicus* group (Coleoptera: Curculionidae: Hyperini). Snudebiller 8: 175 pp.

Alpine Entomology 7 2023, 219–267 | DOI 10.3897/alpento.7.112514

Annotated checklist of the Swiss bees (Hymenoptera, Apoidea, Anthophila): hotspots of diversity in the xeric inner Alpine valleys

Christophe Praz[1,2], Andreas Müller[3], Dimitri Bénon[4], Mike Herrmann[5], Rainer Neumeyer[6]

1 *info fauna – Swiss Zoological Records Center, Avenue de Bellevaux 51, 2000 Neuchâtel, Switzerland*
2 *University of Neuchâtel, Institute of Biology, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland*
3 *ETH Zurich, Institute of Agricultural Sciences, Biocommunication and Entomology, Schmelzbergstrasse 9/LFO, 8092 Zurich, Switzerland*
4 *Rue des Prés 80e, 2503 Bienne, Switzerland*
5 *Sonnentauweg 47, 78467 Konstanz, Germany*
6 *Probsteistrasse 89, 8051 Zürich, Switzerland*

https://zoobank.org/AEBF05FF-AC3C-451D-8B7C-E73C21E1F422

Corresponding author: Christophe Praz (christophe.praz@unine.ch)

Academic editor: Jessica Litman ◆ **Received** 11 September 2023 ◆ **Accepted** 19 October 2023 ◆ **Published** 10 November 2023

Abstract

We present a checklist of the Swiss bees and provide information on the distribution of every bee species in all 26 Swiss cantons. 632 species are reported, including the European honeybee *Apis mellifera* Linnaeus, 1758 and the exotic species *Megachile sculpturalis* Smith, 1853. Species richness in each canton was correlated with the canton area, with the four largest cantons hosting the highest number of species. Bee diversity hotspots were located in some Alpine inner valleys characterized by a dry and warm climate due to the rain shadow effects of surrounding mountains. These hotspots are mostly located in the steppe-like habitats of the Valais and Graubünden cantons. They host diverse wild bee communities which include a unique assemblage of submediterranean faunal elements and subalpine species. In addition, these habitats host rare species with strongly disjunct distributions in Europe, further stressing the conservation priority of these habitats for wild bee conservation. Intensive faunistic surveys performed in the last 20 years have revealed that about 20 bee species, either previously unknown for Switzerland or which had disappeared from the country for several decades, have colonised areas close to the borders of France and Italy. Most of these new or reappeared species were observed in the warmest area of the country and presumably colonized or recolonized the country from neighbouring regions following global warming. Lastly, DNA barcodes are presented for 394 specimens, including for many species so far not represented in the BOLD database. The taxonomic status of numerous unclear taxa is briefly discussed based on combined genetic and morphological analyses.

Key Words

Bees, pollinators, conservation, DNA barcoding, biodiversity, biogeography

Introduction

Despite its small size, Switzerland has received much attention from entomologists for more than a century. This is particularly true for the Alps which cover nearly 60% of the country, and which have attracted botanists and entomologists for a long time, resulting in numerous studies documenting the Swiss flora and fauna (see for example Morawitz (1867) for an early work on Swiss Alpine bees).

The first author who extensively studied the Swiss bee fauna was Emil Frey-Gessner (1826–1917; Carl and Steck 1918). After being employed as a teacher near Aarau, Frey-Gessner was for some time the curator of the Hymenoptera collection of the Natural History Museum in Geneva. He collected in different places in Switzerland, mostly around Geneva, but also in the Valais, in Ticino, and in some localities in the Alps. He also identified bees from other Swiss entomologists, mostly Baptiste Jacob

(1830–1918; region of Neuchatel), Henri Tournier (1834–1904; region of Geneva), Moritz Paul (1835–1898; region of Sierre, Valais), Walter Schmid (1843–1904; region of Basel), Emile Favre (1843–1905; region of Martigny and Sierre), and Theodor Steck (1857–1937; regions of Bern and Basel). Frey-Gessner compiled the first monograph of the Swiss bees, published as supplements to the Mitteilungen der Schweizerischen Entomologischen Gesellschaft (Frey-Gessner 1899–1912). In this first treaty of the bees of Switzerland, 454 "species" and 52 "varieties" were recognized; translating these numbers into a precise count of species is difficult since these varieties include both colour morphs (e.g., *Bombus mucidus* var. *mollis* Pérez, 1879, the slightly lighter form of *B. mucidus* Gerstäcker, 1869) or valid species (e.g., *B. pomorum* var. *elegans* Seidl, 1837, the valid species now referred to as *B. mesomelas* Gerstäcker, 1869). The main part of his collection is preserved as a separate collection in the Natural History Museum of Bern; it is very well-preserved and still organized as Frey-Gessner originally arranged it, so that the records published in his monograph can be backed up with the precise specimens studied (see for example Blüthgen 1921). Frey-Gessner wrote locality information by hand on small labels (Suppl. material 1: fig. S1A); the date is only indicated as day and month; most specimens also bear a printed number, probably referring to a species catalogue; for some common localities, the locality is printed, the date (without year) being added by hand (Suppl. material 1: fig. S1A, B). His collection is remarkably well-maintained, with most specimens bearing locality labels; no apparently mislabeled specimens has been detected (but see comments under *Epeolus alpinus* Friese, 1893 for an obvious exception).

Jacques de Beaumont (1901–1985; see Besuchet 1986), a renowned sphecid wasp specialist, was the next important author who studied the Swiss bees, although his contributions on the bees were mostly a "by-product" of his intensive work on other groups of aculeate Hymenoptera, mostly the sphecid and pompilid wasps. De Beaumont, curator at the Museum of Zoology in Lausanne, collected bees in several regions of Switzerland, mostly western Switzerland, the Valais, Ticino, and the National Park region (Graubünden). He published three main accounts on the bees of Switzerland, two accounts on the bees of western Switzerland (de Beaumont 1955, 1960) and one account on the bees of the National Park region in the Graubünden (de Beaumont 1958). His well-preserved collection is mostly deposited at the Zoology Museum in Lausanne.

While de Beaumont and Frey-Gessner largely documented the wild bee fauna of western Switzerland, and to a very limited extent that of Ticino and of the National Park region in the Graubünden, large parts of Switzerland remained virtually uninvestigated until about 1960, especially the north-eastern corner, as well as Graubünden with the vast valleys of the upper Rhine river system. Even the eastern part of the Valais, corresponding to the German-speaking part of the Valais, perhaps the most remarkable entomological "hotspot" in Switzerland due to its dry and continental climate, also remained largely unexplored until well after 1950. As noted by Amiet (1991), *Andrena probata* Warncke, 1973 and *A. ranunculorum* Morawitz, 1877 (Fig. 1), two remarkable and for the former, conspicuous and locally abundant species (at least historically), were only recorded in Switzerland after 1975, probably because they occur in the less accessible eastern part of the Valais, a region that Frey-Gessner and de Beaumont hardly visited.

The intensive work of Erwin Steinmann (1923–2020; see Müller 2021) has partly contributed to fill these gaps in the knowledge of the Swiss bee fauna, at least for the eastern part of the country (Graubünden). As a passionate mountain hiker, Erwin Steinmann investigated the Swiss Alpine bee fauna like no one else. He published an account on the bee fauna of the dry inner Alpine valleys (Steinmann 2002). His collection is preserved in the Natural History Museum of Chur, Graubünden.

The Swiss bee fauna is and will forever be associated with the name of Felix Amiet, who has dedicated much of his life to the study of the Swiss bees. Felix Amiet started his work on the bees in the 1960s. After that and until now, he has explored every corner of Switzerland to study its bees. He has assembled the most comprehensive collection to date, with well-preserved specimens from all biogeographic regions of the country. His collection is preserved in the Natural History Museum of Bern. Felix Amiet published the first checklist of the Swiss bees (Amiet 1991), where 575 species are mentioned; he then coordinated the publication of the six volumes of the atlases on the Swiss bees, which include distribution maps and identification keys for all species, and which were published in the series Fauna Helvetica (Amiet et al. 1999–2017). A first volume on the genus *Bombus* was published in the series Insecta Helvetica (Amiet 1996). The publication of these well-known identification keys has been the opportunity for him and his coauthors to entirely revise the museum specimens preserved in Swiss institutions, initiating the creation of the important database that underlies the present work. The activities of F. Amiet and E. Steinmann paved the way for numerous surveys of the native bee fauna, which were carried out from the 1980s onwards, predominantly as part of student theses and expert reports in different regions of Switzerland.

Goal of the present checklist

The present checklist builds upon the previous work coordinated by Felix Amiet. Since 2012, much faunistic work has been conducted on the Swiss bees in a project aiming at updating the Red List of the Swiss bees; during this project, numerous inventories have been undertaken, partly in poorly investigated regions of Switzerland. Several new species for Switzerland have been found, and our knowledge of the distribution of the bees has substantially improved. In parallel, bee systematic studies have seen a

Figure 1. *Andrena probata* (left) and *Andrena ranunculorum* (right), two rare and emblematic species of the dry, inner Alpine Valleys of Switzerland. Pictures by Dimitri Bénon (www.swisswildbees.ch).

renewed impetus, in part due to the increased use of genetic markers to delineate species, leading to numerous taxonomic changes in the central European fauna. Before the publication of the Swiss red list (Müller and Praz, in press), we wish to summarize all these changes in the present work. We thus present a revised checklist of all Swiss bee species, giving for each species its distribution in all cantons of Switzerland. We also comment on each species: i. if it is new for Switzerland; ii. if it is a recently described species, or a recently recognized taxon previously treated as a synonym; iii. if its current distribution is different from that previously published (Amiet et al. 2001–2017), for example due to identification errors, to the finding of new populations, or to marked range expansions; iv. if the taxon is referred to differently in recently published bee checklists in Europe (Ghisbain et al. 2023; Scheuchl et al. 2023; Reverté et al. in press) and v. if there are open taxonomic questions that require additional work.

Methods

Critical examination of ancient records

As in other central or northern European countries, the bee fauna of Switzerland has seen massive declines, which gradually began after the main rivers had been channeled and the lowland areas subjected to urbanization and agricultural intensification. The few scientific collections that predate these important changes are thus irreplaceable testimonies of historical bee diversity. Unfortunately, these collections are small and their geographic coverage very fragmentary; moreover, the standards for curating specimens, especially with respect to the locality information on the labels, were not those of today. Consequently, some of these collections are somehow problematic, and some records dubious, for example because the supposed locality information refers to the place of residence of the author, or simply because of labelling mistakes. We followed here the guidelines of Monnerat et al. (2015) to accept or reject records from such ancient collections. Briefly, a record is accepted if it originates from a “reliable” collection (see below), if a more or less accurate locality is indicated on the label, if this label is original (i.e., written by the collector and not recopied or added posteriorly; see Suppl. material 1: fig. S1), if the record is ecologically plausible (e.g., in term of phenology, habitat or, for cuckoo bees, the presence of the host), and if the record lies within the known potential or former distribution of the species in Europe.

Given the difficulties inherent in the identification of bees, we only validated records that are based on a preserved specimen; some old records based only on literature mentions are not validated (see for example the case of *Andrena hystrix* Schmiedeknecht, 1883, below). As indicated above, one criterion to validate or reject isolated records is whether the record lies within the overall distribution of the species in Europe (Monnerat et al. 2015), especially for species whose presence in Switzerland is based on a single specimen or a single collecting event. This criterion can prove challenging to evaluate given that the distribution of numerous bee species has drastically changed since the 19th century and given the poor knowledge of the historical distribution of numerous bee taxa in Europe (Tischendorf 2020). For example, *Andrena incisa* Eversmann, 1852, with numerous independent and reliable records in Switzerland between 1884 and 1939, is very rare in Europe, with ancient (<1970) records from Spain and Ukraine (as well as possibly Poland), and current records only from Turkey and Central Asia (T. Wood, pers. communication). To state that the records in Switzerland lie within the distribution of this bee in Europe would be a stretch, yet there are absolutely no doubts concerning these Swiss records. Similarly, numerous species with reliable historical records near Geneva and no other record in central Europe, are entirely unknown in nearby parts of France, with confirmed records only in southern France, more than 200 km from the Swiss records (e.g., *Andrena mucida* Kriechbaumer, 1873, with confident records in the Geneva region; see below). Accepting or rejecting a historical record, especially if based on a single specimen, is thus to some extent an arbitrary process. As stressed above, the historical record of bees in Switzerland (and generally in central Europe) is extremely incomplete; compared to other groups (e.g., Coleoptera or Lepidoptera), bees are underrepresented in historical collections; in addition, bee communities are highly dynamic, and some rare species such as cuckoo bees, are difficult to detect. It is thus not surprising that the repeated sampling of bees in particularly rich habitats will continue to uncover regionally new species even after decades of sampling, and that such repeated sampling produces lists of species characterized by a high number of singletons.

In some insect groups, occurrences based on isolated individuals are sometimes considered to represent erratic individuals (vagrants) outside their reproductive range. Examples include historical records of butterflies in southern Switzerland, for example *Gonepteryx cleopatra* (Linnaeus, 1767) in Ticino or *Coenonympha dorus* (Esper, 1782) in the Geneva region; both species are not considered to be native in Switzerland and were not evaluated in the red list of the Swiss butterflies (Wermeille et al. 2014). We did not adopt this approach for the Swiss bees, for the following reasons. First, there is no indication that bees have a migratory behavior, unlike numerous species of butterflies. Second, as indicated above, singletons are a common feature of all bee surveys, simply because some species are particularly hard to detect. For these reasons, we consider each species observed at least once within Swiss territory as native and potentially reproducing, with the exception of the exotic species *Megachile sculpturalis* Smith, 1853 and one recent, isolated record of *Osmia latreillei* (Spinola, 1806) (see below).

Unlike in some other insect groups, notably the Coleoptera (Monnerat et al. 2015), most Swiss collections of Hymenoptera can be considered as reliable. Two problematic collections with respect to the bees are those of Henri Tournier (1834–1904; Suppl. material 1: fig. S1G) and Walter Schmid (1843–1904; Suppl. material 1: fig. S1F). Tournier collected numerous specimens near his home in Peney (Satigny, Geneva), a small village located 250 m from the shore of the Rhone River. At that time, the Rhone River was not channeled, and Tournier was probably able to collect in vast sandy habitats near his house. He also exchanged material with other entomologists. Several records of Tournier supposedly from Peney have been suggested to be erroneous (e.g., de Beaumont 1946; Neumeyer 2008; Neumeyer and Merz 2012; Neumeyer 2014). Based on the examination of his entire bee collection, the majority of us conclude that the bee collection is overall reliable and that most specimens labeled with "Peney" (usually only indicated by "P." and the date; Suppl. material 1: fig. S1G) were probably indeed collected near Peney. Another abbreviated locality is "R." for "Reculet", the highest peak of the Jura mountains, where Tournier collected an interesting series of bees, among other numerous specimens of *Bombus mendax* Gerstäcker, 1869, a species now extinct in the Jura. At Tournier's time, many species were not yet described, especially in difficult species groups (e.g., *Andrena*, *Lasioglossum*, *Nomada*), and the knowledge of the bees in central Europe was very fragmentary, since the major catalogues and identification works (e.g., Dalla Torre 1896; Friese 1895–1901; Schmiedeknecht 1907) were not yet published. Despite this, the bees preserved in the Tournier collection, and labeled as being from Peney, do in fact belong to central European species, with only a few exceptions that are possibly based on mislabeled specimens (see below). As an illustration, we identified the numerous specimens of the subgenus *Micrandrena* of the Tournier collection, superficially very similar species that no one could identify at Tournier's time. All *Micrandrena* specimens belong to species currently present near Geneva, or to species also collected by Frey-Gessner near Geneva at the same time as Tournier (*Andrena distinguenda* Schenck, 1871, *A. floricola* Eversmann, 1852, *A. niveata* Friese, 1887, *A. pauxilla* Stöckhert, 1935, and *A. pusilla* Pérez, 1903). The same is true for the species of the taxonomically challenging subgenus *Taeniandrena*. Nevertheless, some records represented by singletons in Tournier's collection belong to species whose known distribution area does not encompass Switzerland. These records are possibly based on mislabeled specimens, and the records for three species are not accepted here (*Andrena ventricosa* Dours, 1873, *Lasioglossum sphecodimorphum* (Vachal, 1892) and *Colletes nasutus* Smith, 1853), following Monnerat et al. (2015). These cases are briefly discussed below.

The collection of Walter Schmid is slightly more problematic because the specimens were not labeled with original locality data by Schmid himself. All specimens in his collection bear a printed label that simply mentions "Basel, W. Schmid" (Suppl. material 1: fig. S1F), and it is probable that these labels were added after W. Schmid's death. Consequently, some of Schmid's records supposedly from Basel are probably erroneous (see for example *Nomada gribodoi* Schmiedeknecht, 1882, below); moreover, some records may originate from the much larger Basel region (including nearby France or Germany) and not from the Swiss Basel region. However, Frey-Gessner corresponded with W. Schmid and confirmed in his book some unique records for Switzerland, such as *Andrena sericata* Imhoff, 1868, *Colletes collaris* Dours, 1872 and *Systropha planidens* Giraud, 1861, all three of which occur north of Basel in the Rhine Valley, and which W. Schmid collected near Basel according to Frey-Gessner. We consider the historical presence of these species highly likely in the Basel region. Consequently, to simply discard all of W. Schmid records would be erroneous, and for this problematic collection we accepted occurrences that are plausible from a biogeographic point of view and that are backed up with a specific reference in Frey-Gessner's book.

The Swiss bee dataset

All Swiss bee records, including those based on museum material, faunistic inventories or citizen-science based observations, are assembled into a database centralized at info fauna, Neuchatel (www.infofauna.ch). The main task of info fauna is to maintain faunistic databases, to publish them as open resource at a low resolution (5 × 5 km) nationally and internationally, and to diffuse precise occurrence data to actors active in conservation, such as nature reserve managers and conservation agencies. The entire bee dataset can be accessed freely on GBIF (Praz et al. 2022), although in this open-access dataset the coordinates are rounded to a grid of 5 × 5 km; the underlying reason is that numerous occurrences are private, and for these private occurrences, the observer maintains exclusive ownership of the precise data. Distribution maps with a precision of 5 × 5 km can be accessed freely at https://lepus.infofauna.ch and the biology of the Swiss species is summarized in a dedicated website (https://species.infofauna.ch/groupe/1).

Subspecies

Subspecies are not recognized in this dataset. In some cases, the initial database assembled for the publication of the identification keys by Amiet et al. (1999–2017) included subspecies. Overall, the recognition of subspecies is a controversial matter in systematics; it may make sense in some cases, for example to highlight incipient speciation, or for pragmatic, conservation purposes for geographically isolated units that may eventually be treated as a distinct taxon. However, the subspecies rank has also been used in the past for distinct colour morphs co-occurring in sympatry with regular-looking forms (e.g., the numerous forms within *Bombus humilis* Illiger, 1806, or *Bombus confusus* Schenck, 1859 and *Bombus confusus “paradoxus”* Dalla Torre, 1882), an approach that makes little sense since such forms do not represent significant evolutionary or conservation units. Overall, subspecies are not recognized in legal documents or by local conservation practitioners in Switzerland, and for such a small country, we see little need to recognize subspecies for bees. In some species, the Swiss populations belong to a recognized subspecies that is distinct form the nominal subspecies. An example in *Lasioglossum limbellum* (Morawitz, 1876): the nominal subspecies *L. limbellum limbellum* occurs eastwards from the Pannonian region of Austria, while the subspecies *L. limbellum ventrale* (Pérez, 1903) occurs westwards, including in Switzerland (Ebmer 1988). For practical reasons, we do not mention the subspecies in such cases (the subspecies are mentioned in Amiet et al. 2001–2017). We discuss below how we treat previously recognized subspecies (see for example under *Halictus confusus* Smith, 1853, *Nomada panzeri* Lepeletier, 1841, *Panurginus montanus* Giraud, 1861 and *P. sericatus* (Warncke, 1972)).

Species aggregates

In bees, there are numerous groups of species where a confident identification is only possible in fresh specimens or when some specific characters are visible, for example the male genitalia. In addition, only one sex can be identified with confidence in several groups. For example, the females of the *Halictus simplex* group (*Halictus simplex* Blüthgen, 1923, *H. langobardicus* Blüthgen, 1944 and *H. eurygnathus* Blüthgen, 1931) are nearly impossible to separate (Ebmer 1969; Amiet et al. 2001; Pauly 2015; pers. obs.). In such cases, all females were lumped in a species aggregate and the distribution data is inferred based on male specimens only. The different aggregates recognized in the Swiss database are listed in Table 1. For some difficult groups (e.g., the *Bombus terrestris*-group or the *Hylaeus gibbus*-group), an identification at the species level was only performed in typical specimens where a set of different morphological characters was in agreement. If one important morphological character was equivocal, the specimen was identified at the aggregate level.

Generic classification

We adopt here the classification of Michener (2007) with a few exceptions, which are detailed here. Compared to previous work on the Swiss bees (Amiet et al. 2001–2017) this new classification leads to the break-up of the genus *Anthophora* into *Anthophora* and *Amegilla*, of the non-parasitic Anthidiini into the six genera *Anthidiellum*, *Anthidium*, *Icteranthidium*, *Pseudoanthidium*, *Rhodanthidium* and *Trachusa*, of the genus *Osmia* into *Osmia*, *Hoplitis* and *Protosmia*, of the genus *Dioxys* into the genera *Allodioxys* and *Dioxys*, and of the genus *Epeolus* into the genera *Epeolus* and *Triepeolus*. In contrast to Michener (2007), the genus *Nomiapis* is recognized for the species *Nomiapis diversipes* (Latreille, 1806) (formerly *Nomia diversipes* or *Pseudapis diversipes*), following Pauly (1990), Baker (2002), Astafurova and Pesenko (2006), Bossert et al. 2021 and Wood and Le Divelec (2022). Then, the genera *Coelioxys* and *Dioxys* are considered to be masculine (Rasmont et al. 2017). In the tribe Eucerini, several changes have recently been proposed (Dorchin et al. 2018; Freitas et al. 2023; Dorchin 2023), which result in the recognition of only two genera for the central European fauna, *Eucera* and *Tetralonia*, in contrast with the classification of Michener (2007) which recognized the genus *Tetraloniella* in addition to *Tetralonia*. The genus *Eucera* includes all two-celled species plus the three-celled subgenus *Synhalonia*, while the genus *Tetralonia* includes all other three-celled species, including species formally included in the genus *Tetraloniella*. Consequently, the three-celled species *Eucera* (*Synhalonia*) *hungarica* Friese, 1896 is treated here as a member of *Eucera*, not of *Tetralonia* as in Amiet et al. (2007). Lastly, we treat *Seladonia* as a subgenus of *Halictus* and not as a distinct genus, following Ebmer (1988), Michener (2007), Gibbs et al. (2012), Scheuchl and Willner (2016), and Scheuchl et al. (2023).

Table 1. The species aggregates recognized in the Swiss bee database.

Species aggregate	Included species	Remark
Lasioglossum alpigenum/bavaricum aggr.	*Lasioglossum alpigenum, L. bavaricum*	All females of these two species are included in this species aggregate, unless a DNA-based identification was performed.
Lasioglossum fratellum/subfulvicorne aggr.	*Lasioglossum fratellum, L. subfulvicorne*	All females of these two species are included in this species aggregate.
Hylaeus gibbus aggr.	*Hylaeus confusus, H. gibbus, H. incongruus*	Most specimens were identified using morphology; specimens that could not be re-rexamined recently, as well as morphologically unclear specimens, were included in this aggregate.
Panurginus montanus aggr.	*Panurginus montanus, P. sericatus*	Most females of these two species were included in this aggregate.
Andrena proxima aggr.	*Andrena alutacea, A. ampla, A. proxima*	Morphologically unclear specimens (mostly males, but also worn females) were included in this aggregate. All specimens from the Valais upstream from Martigny were assigned to *A. ampla* (McLaughlin et al. 2023).
Halictus simplex aggr.	*Halictus eurygnathus, H. langobardicus, H. simplex*	All females of these three species are included in this species aggregate, unless a DNA-based identification was performed.
Hylaeus taeniolatus/pictipes aggr.	*Hylaeus pictipes, H. taniolatus*	Females were systematically assigned to this aggregate until 2019; thereafter, most females were separated based on their morphology.
Bombus terrestris aggr.	*Bombus cryptarum, B. lucorum, B. magnus, B. terrestris*	All workers were included in this species aggregate, unless identified using DNA. Queens and males were mostly identified to the species level.

DNA barcoding

For the present work, numerous identifications have been verified using DNA barcoding, following lab protocols published elsewhere (e.g., Praz et al. 2019). Our general approach is to amplify the entire or part of the 658-bp "barcoding" fragment of the mitochondrial gene Cytochrome Oxidase I in two independent PCRs (Polymerase Chain Reactions) with the primers pairs LepF/LepR and UAE3/LepR (Suppl. material 2), producing fragments of 658 and 409 bp, respectively. These two PCRs can be done together with identical PCR conditions (see Praz et al. 2019, 2022). The PCR products were examined on an agarose gel; if both PCR worked, the 658-bp fragment was sequenced using the reverse primer LepR, and the 409-bp fragment with the forward primer UAE3; both sequences were assembled in Geneious Prime 2022.2.2, yielding the complete 658-bp fragment. For old specimens (> 10 years), often only the 409-bp fragment was successfully amplified, and this fragment was then sequenced bidirectionally with the primers UAE3 and LepR. The advantage of using two independent PCRs is that without increasing sequencing costs, the technique provides a way of checking for contamination or pipetting errors, as well as a way of minimizing the sequencing of nuclear pseudogenes (NUMTs). In addition, approximately 10% of the sequences produced with the primer pairs LepF/LepR in bees amplify *Wolbachia* DNA; this ratio was much lower with the primers UAE3/LepR. For some groups that failed to produce clear chromatograms with the primers LepF, LepR and UAE3, clade specific primers were developed; if neither the 658-bp nor the 409-bp fragments yielded clear chromatograms, these specific primers were used. A list of all primers used is given in Suppl. material 2.

We generated DNA barcodes with the following aims. First, in numerous cases, DNA-assisted identifications allowed to delineate the distribution of some species and generated confidently identified material to evaluate morphological criteria (see for example the case of the *Hylaeus gibbus*-group, below). Second, we generated DNA barcodes to evaluate the taxonomic status of some "forms" with unclear taxonomy. Lastly, we generated DNA barcodes for Swiss species not yet represented in DNA barcode libraries (www.bold.org, hereafter BOLD). All generated DNA barcodes have been submitted to BOLD; a full list of specimens for which DNA barcodes were generated, including locality information as well as BOLD accession numbers, is given in Suppl. material 3. In all figures, new sequences are indicated in red; all other sequences have been downloaded from the BOLD website.

Results

The Swiss bee checklist

The database includes 473653 occurrences between 1817 and 2021 (inclusive), distributed in 7027 1 × 1-km grid cells; all records, even the historical records, are attributed to one 1 × 1-km grid cell, corresponding to the kilometer grid of the national topographic maps (www.map.geo.admin.ch); one occurrence may include several specimens when more than one specimen was collected at the exact same locality on the same day. The evolution of the database in time is shown in Fig. 2.

To date, 632 bee species have been recorded for Switzerland, including one exotic species, *Megachile sculpturalis* and the European honeybee, *Apis mellifera* Linnaeus, 1758. The distribution of these species in all Swiss cantons is given in Table 2 and Suppl. material 4.

A distance-based tree was build using the unweighted pair group method with arithmetic mean (UPGMA) with all newly produced sequences (Suppl. material 5). In this tree, only sequences above 300 bp were included; previously published DNA barcodes from Swiss studies were also included (Praz et al. 2019, 2022; Gueuning et al. 2020; McLaughlin et al. 2023).

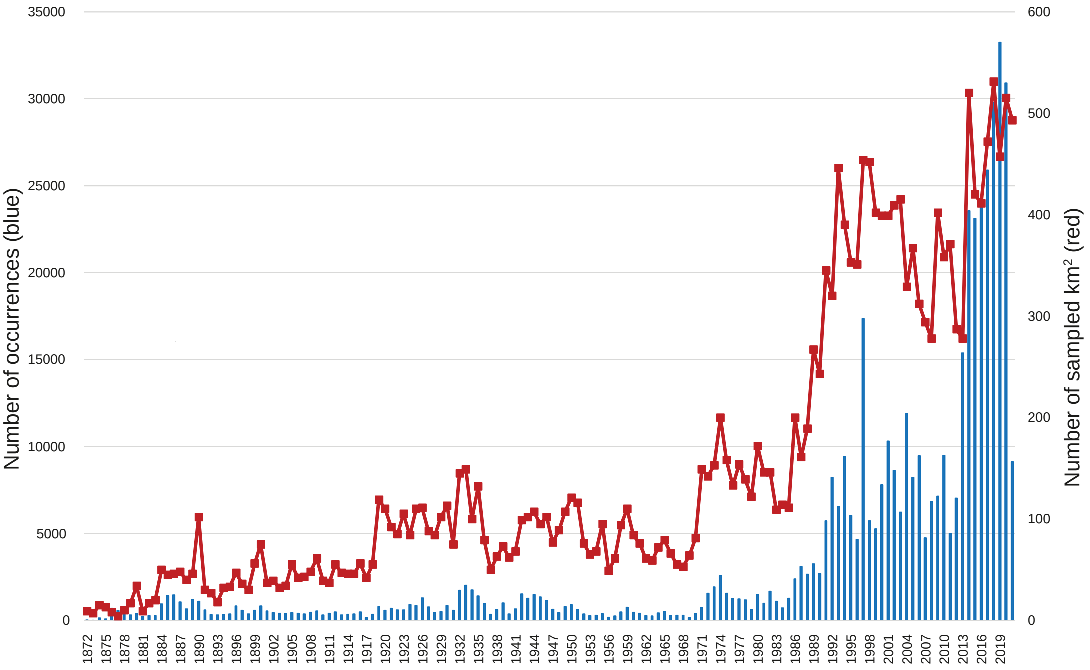


Figure 2. Evolution of the Swiss bee database over time, showing the number of occurrences (blue) and the number of sampled 1 × 1 km-quadrates (number of quadrates with at least one bee observation).

Comments on selected species

Amegilla salviae **(Morawitz, 1876)**

This species is known from a single specimen collected in Sierre by Frey-Gessner. Sierre is a famous entomological locality; it lies in the Rhone Valley in the Valais and the region between Sierre and Leuk (the alluvial site of Finges) was until the beginning of the 20th century the last place in the Valais where the Rhone River was not channeled. Since Frey-Gessner's collection is reliable, this record is accepted, even if it represents an isolated record at the European scale. That such a conspicuous species was collected only once is surprising, but illustrates how even the Valais fauna was poorly sampled until well into the 20th century (see also comments under *Nomada confinis* Schmiedeknecht, 1882 and *Tetralonia pollinosa* (Lepeletier, 1841)). Frey-Gessner was one of the last entomologists who could visit the alluvial site of Finges before the construction of the Susten water dam in 1910. The construction of this dam for electricity production likely led to the loss of the natural river dynamic and to important habitat degradation at this site.

Andrena afzeliella **(Kirby, 1802)**

This species has recently been separated from *A. ovatula* (Kirby, 1802), a taxon which has so far not been reported from Switzerland (Praz et al. 2022). The closest record of *A. ovatula sensu stricto* known to us is a male collected near Freiburg in Breisgau (Flughafen, Mull, 22.4.1992, leg. & coll. C. Schmid-Egger, *A. ovatula* s. str. det. F. Burger 2001, confirmed C. Praz 2022), only 50–60 km north of Basel, rendering the presence of *A. ovatula* in Switzerland possible, at least in the past, for example in the region of Basel. A morphological separation of *A. afzeliella* and *A. ovatula* is mostly possible, at least in the female sex (see identification key in Praz et al. 2022).

Andrena alfkenella **Perkins, 1914**

Males of this taxon have so far often been misidentified in Switzerland, mainly with *A. floricola* and *A. minutula* (Kirby, 1802). All three species exhibit distinct DNA barcodes (Suppl. material 5) and can readily be identified in the female sex. We barcoded several male specimens initially identified as *A. alfkenella* or *A. floricola*, which highlighted the fact that the males of *A. alfkenella* have mostly been misidentified as *A. floricola*, and the males so far identified as *A. alfkenella* mostly belong to *A. minutula*. Unlike the indication in Amiet et al. (2010), the male of *A. alfkenella* has the terga shiny and the stigma at least partly yellow-brown, as in *A. floricola*, from which it differs by the more sparsely punctate terga (comparison with reference material is needed and some specimens are difficult to identify) (see also Schmid-Egger and Scheuchl 1997 and Wood 2023a). See additional comments under *A. floricola*.

Andrena allosa **Warncke, 1975**

The status of this species and its distribution in Europe were presented by Praz et al. (2019). This western Alpine species reaches its eastern limit in the Bernese Alps near Kandersteg. Although it has never been found in the Swiss Jura, an observation on the Salève south of Geneva (France) renders its occurrence in the Western Jura possible. *Andrena allosa* is included in the identification key given in Praz et al. (2019).

Table 2. Checklist of the Swiss bees, showing the presence of each species in each canton. Open circles indicate records before 2000, closed circles after 1999. Abbreviations: AG: Aargau; AI: Appenzell Innerrhoden; AR: Appenzell Ausserrhoden; BE: Bern; BL: Basel-Landschaft; BS: Basel-Stadt; FR: Fribourg; GE: Geneva; GL: Glarus; GR: Graubünden; JU: Jura; LU: Luzern; NE: Neuchâtel; NW: Nidwalden; OW: Obwalden; SG: St. Gallen; SH: Schaffhausen; SO: Solothurn; SZ: Schwyz; TG: Thurgau; TI: Ticino; UR: Uri; VD: Vaud; VS: Valais; ZG: Zug. This table is also available as a supplemental table (Suppl. material 4).

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Aglaoapis tridentata					●			●		●	●												○	●			6	5
Amegilla albigena										○														●			2	1
Amegilla garrula								○		●											●			○			4	2
Amegilla quadrifasciata						○				○														○			3	0
Amegilla salviae																								○			1	0
Ammobates punctatus																								●			1	1
Andrena aeneiventris								●		○											●		○	●			5	3
Andrena afrensis																								●			1	1
Andrena afzeliella	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Andrena agilissima				●	●	○	○	●		●			●				●	○		●			●	○		●	13	9
Andrena alfkenella	●			●		○	●	●		●	●	●	○			●	●			●	●		●	●		●	16	14
Andrena allosa				●			●									●		●					●	●			6	6
Andrena alutacea							○			●			●			○		●			●					●	7	5
Andrena amieti				●			●		●	●				●	●	●					●	●	●	●			11	11
Andrena ampla										●											●			●			3	3
Andrena apicata	○		●	●			●			●			●	●		●	●	●	●	●	●	○	●	●		○	17	14
Andrena argentata				○				○		○											●		○	○			6	1
Andrena assimilis				○																				○			2	0
Andrena barbareae										●						●					●	○		●			5	4
Andrena barbilabris	●			●	●	○	●	○		●		●	●	●	●	●	●	●		●	●	●	●	●	●	●	21	19
Andrena bicolor	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Andrena bimaculata				○				○		●											●		●	●			6	4
Andrena bucephala	●		●	●	●	●	●	●			●	●	●	●		●	●	●		●			●	●		●	18	18
Andrena chrysopus																					●			●			2	2
Andrena chrysosceles	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Andrena cineraria	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Andrena clarkella				●		○	●			●	●	●	●	●		●		●	●		●	○	●	●		●	16	14
Andrena coitana				○		○	●	○	●	●			○			●					●		●	●			11	7
Andrena combinata	●			●	●		○	○		●		●	●	●		○	●	●	●	●	●	●	●	●		●	19	16
Andrena confinis				○			○	●		●			○				○	○			●		○			○	10	3
Andrena congruens				○				○		●			○			○		○			●		●	●			9	4
Andrena curvungula	●		●	●			●	●		●	●		●				●	●			●	●	●	●		●	15	15
Andrena decipiens								○															○			○	3	0
Andrena denticulata					●			○	●	●			○								●			●			7	5
Andrena distinguenda	●					○		○									●										4	2
Andrena dorsata	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	23
Andrena falsifica	●	●	●	●	●		○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	24	23
Andrena ferox				○				○		●			○								○		○	●			7	2

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Andrena flavilabris								○																			1	0
Andrena flavipes	●			●	●	●	●	●	○	●	●	●	●	●		●	●	●		●	●	●	●	●	●	●	22	21
Andrena florea	●			●	●	●	●	●					●				●	●			●		●	●		●	13	13
Andrena floricola						○		○		○			○				○			○			○	●			8	1
Andrena florivaga											●																1	1
Andrena freygessneri										●											○	○		●			4	2
Andrena fucata	●	●	●	●		●		○	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●		●	23	21
Andrena fulva	●			●	●	●	●	●		●	●	●	●	●		●	○	●	●	●	●		●	●		●	20	19
Andrena fulvago	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Andrena fulvata	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Andrena fulvicornis	●				●						●						●										4	4
Andrena fulvida				●			○			●						●					●						5	4
Andrena fuscipes								○		●											●			●			4	3
Andrena fuscosa																								○			1	0
Andrena gelriae				○			○	●										○					●	●		●	7	4
Andrena gravida	●		●	●	●	●	●	●		●	●	●	●		●	●	●	●	●	●		●	●	●	●	●	22	22
Andrena haemorrhoa	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Andrena hattorfiana	●		●	●	●	○	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	25	23
Andrena helvola	●		●	●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●	○	●	●	●	●	23	22
Andrena hesperia				●	●													○									3	2
Andrena humilis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Andrena hypopolia								○																○			2	0
Andrena incisa								○																○			2	0
Andrena intermedia		●	●	●		○	●	○	●	●		●		●	●	●	○	●	●		●	●	●	●		●	20	17
Andrena labialis				●	●	●		●		●	●		●			●	●	●			●		●	●			13	13
Andrena labiata	●	●	●	●	●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	24
Andrena lagopus	●			●	●	●	●	●			●	●	●			○	●	●		●			●	●	●	●	17	16
Andrena lapponica				●			○		●	●	●	●	●	●		●			●		●	●	●	●		●	15	14
Andrena lathyri	●			●	●	●	○	●		●	●	●	●			●	●	●		●	●	●	●	●	●	●	20	19
Andrena lepida								○																			1	0
Andrena limata	○			○		○		○		●											●		○				7	2
Andrena livens																					○						1	0
Andrena marginata	●			●				○		●						●				○	●		○	●	●		10	7
Andrena minutula	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Andrena minutuloides	●			●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	23
Andrena mitis	●			●		●	●	●		●	●	●	●			●	●	●		●			●	●	●	●	17	17
Andrena montana				●					●	●												●		●			5	5
Andrena mucida								○															○				2	0
Andrena nana	●			○	○	○	●	●		●		○	●			●	●	●		●	○		●	●		●	17	12
Andrena nanula										●											●						2	2
Andrena nigroaenea	●			●		●	●	●		●	●	●	●	●	○	●	●	●	○	○	●	●	●	●		○	21	17
Andrena nigroolivacea	●			●	●	●					●		●					●					●			●	9	9
Andrena nigrospina						○		○															○				3	0

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Andrena nitida	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Andrena nitidiuscula	●			○	●	●	●	●		●	●		●			○	●	●		●	●		●	●		●	17	15
Andrena niveata							○	○										○			●			●			5	2
Andrena nuptialis								○																●			2	1
Andrena nycthemera	○			○		○							○											○		○	6	0
Andrena ovata								○													●						2	1
Andrena pallitarsis						○		○		○											●		○				5	1
Andrena pandellei	●			●	●	●	●	●		●	●	●				●	●	●		●	●		●		●	●	17	17
Andrena parviceps							○	●															○	●			4	2
Andrena pauxilla								○																			1	0
Andrena pellucens																					●						1	1
Andrena pilipes				○		○		○		○										○	○		○	●			8	1
Andrena polita				○						●						●		●					●	●		●	7	6
Andrena potentillae				○		○		○					●										●	●			6	3
Andrena praecox	●			●	●	○	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22	21
Andrena probata										○														●			2	1
Andrena propinqua				○		○	●	●		○			●								○		●	●		○	10	5
Andrena proxima	●			●	●	●	●	●		●	●	●	●	●	●	●	●	●	○	●	●	●	●	●		●	22	21
Andrena pusilla						○		●													○		○				4	1
Andrena ranunculorum																								●			1	1
Andrena rhenana					●	●		●																			3	3
Andrena rogenhoferi				●	●		●		●	●			●	●		●		●			●	●		●			12	12
Andrena rosae	●			●	●	●	○	●		○	●	●	●			○	●	●	●	●	●		●	○	●	●	20	16
Andrena ruficrus	●			●			●			●			●	●	●	●		●			●	●	●	●		●	14	14
Andrena rufizona				○				○		●						○					●		●	●		○	8	4
Andrena rufula				●							●		●					●					●			●	6	6
Andrena rugulosa				○								●	●				○	●								●	6	4
Andrena russula				○			○	○		●			●			●	●			○	●		●	●		●	12	8
Andrena saxonica										●																	1	1
Andrena schencki	●			●	●	○		●		○	●	●	●				○	●		○	●		●	●			15	11
Andrena scotica	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	25	25
Andrena semilaevis				●		○	○	●		●	●	○	●			●		●	●		●	●	●	●		●	16	13
Andrena sericata						○																		○			2	0
Andrena simillima										●											○			●			3	2
Andrena simontornyella								●													●						2	2
Andrena strohmella	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	24
Andrena subopaca	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Andrena suerinensis								●																○			2	1
Andrena symphyti																					●		○				2	1
Andrena synadelpha				○			●	○					○										○	●		●	7	3
Andrena taraxaci										●											●						2	2
Andrena tarsata				●		○			●	●			●			●			●		○		●	●			10	8
Andrena tenuistriata								●																			1	1

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Andrena thoracica						○				●											●			●			4	3
Andrena tibialis	●			●	●	●	●	●		●	●	●	●			●	●	●		●	●		●	●	●	●	19	19
Andrena tridentata										○																	1	0
Andrena trimmerana	●			●		○	○	●		●	●		●			●	●	○			●		●	●		●	15	12
Andrena tscheki																					○						1	0
Andrena vaga	●			●	●	●	●	●		●	●	●	●			●	●	●	●	●	●	●	●	●	●	●	21	21
Andrena varians	○			○		○		○		○			○					○		○	○		○	●		●	12	2
Andrena ventralis	●			●		●	●	●		●	●	●	●	○		●	●	●	●	●	●	●	●	●	●	●	21	20
Andrena viridescens	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Andrena vulpecula										●											●						2	2
Andrena wilkella	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	24	24
Anthidiellum strigatum	●		●	●	●	○	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	23
Anthidium cingulatum				○		○		●		○			○											○			6	1
Anthidium florentinum										●											●						2	2
Anthidium loti								○													●						2	1
Anthidium manicatum	●			●	●	●	●	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	22
Anthidium montanum		●	●	●			●		●	●		●	●	●		●		○	●		●	●	●	●			16	15
Anthidium oblongatum	●			●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	23
Anthidium punctatum	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●		●	●		●	●	●	●	21	21
Anthidium septemspinosum						●				●											●						3	3
Anthophora aestivalis	●			●	●	○	●	●		●	●	●	●	●	●		●	●		●	●	●	●	●	●	●	21	20
Anthophora balneorum										○													○	●			3	1
Anthophora bimaculata								○		●											●			●			4	3
Anthophora canescens								○																			1	0
Anthophora crassipes										○														●			2	1
Anthophora crinipes				●			●	●		●		○	●						●		●		●	●			10	9
Anthophora dispar																					●						1	1
Anthophora fulvitarsis								○																○			2	0
Anthophora furcata	●			●	●	○	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	22
Anthophora mucida																					○			●			2	1
Anthophora plagiata				●		○		○		●			○									●		●			7	4
Anthophora plumipes	●		○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	24
Anthophora pubescens								○		●						○					●			●			5	3
Anthophora quadrimaculata	●			●	●	●	●	●	●	●	○		●	●	●	●	●	●	●	●	●	●	●	●		●	22	21
Anthophora retusa										●										●	●					●	4	4
Apis mellifera	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Biastes emarginatus								○															●	●			3	2
Biastes truncatus										●														○			2	1
Bombus alpinus				●						●						○					●	●	●	●			7	6
Bombus argillaceus										●											●			●			3	3
Bombus barbutellus	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus bohemicus	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Bombus campestris	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	23

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Bombus confusus				○			○	○		●			○	○	○					○		○	○	○		○	12	1
Bombus cryptarum				●					○	●	○		●		○	●			●		●	●	●	●			12	9
Bombus distinguendus				○				○					○										●				4	1
Bombus flavidus				●						●				●	●	○					●	○	●	●			9	7
Bombus gerstaeckeri		●		●			●		●	●		●		●	●	●			●		●	●	●	●			14	14
Bombus hortorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus humilis	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Bombus hypnorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus inexspectatus										●											●			●			3	3
Bombus jonellus		●		●					●	●		●	●	●	●	●		○	●		●	●	●	●		●	16	15
Bombus lapidarius	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus lucorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus magnus													○														1	0
Bombus mendax		●		●			●		●	●		●	○	●	●	●			●		●	●	●	●			15	14
Bombus mesomelas			○	●			●	○	●	●			●	●	○	●		○	●		●	●	●	●			16	12
Bombus monticola		●		●			●	○	●	●		●		●	●	●			●		●	●	●	●			15	14
Bombus mucidus		●		●			●	○	●	●		●	○	●	●	●			●		●	●	●	●			16	14
Bombus muscorum	●			○		○	●	○				●		○		●	○		●	●	○		●	○	●	●	16	9
Bombus norvegicus			●	●	●		●	●	●	●	●	●	●		○	●	●	●	●	●	●	●	●	●	●	●	22	21
Bombus pascuorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus pomorum	○			○	○	○	○	○		○	○	○	○					○		○		○	○	○		○	16	0
Bombus pratorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus pyrenaeus		●		●			●		●	●		●		●	○	●			●		●	●	●	●			14	13
Bombus quadricolor		●		●			●	○	●	●	○	○	○	○	○	●			○		●	●	●	●		○	18	10
Bombus ruderarius	●	●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●		●	24	22
Bombus ruderatus	●			●		○	●	●		●	●	●	●			●	●	●	●	●			●	●	●	●	18	17
Bombus rupestris	●	●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	24
Bombus sichelii		○	○	●			●		●	●		●	○	●	●	●		○	●		●	●	●	●			17	13
Bombus soroeensis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus subterraneus	●	●		●	●		○	○		●	●	●	●			○	●	●	●	●			●	●	●	●	19	16
Bombus sylvarum	●	●		●	●	●	●	●		●	●	●	●	○		●	●	●	●	●	○	●	●	●	●	●	23	21
Bombus sylvestris	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Bombus terrestris	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	24
Bombus vestalis	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	22	22
Bombus veteranus	●	●	○	●			○	○			●	●	●	○	○	●	○	●	●	○			●			●	18	11
Bombus wurflenii	●	●	●	●	●		●	○	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●		●	24	22
Ceratina chalcites																					●						1	1
Ceratina chalybea	●			●	●	○	●	●		●	●		○					●			●		●	●			13	11
Ceratina cucurbitina	●			●	●	●	●	●		●	●		●				●	●			●		●	●		●	15	15
Ceratina cyanea	●		○	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	23
Ceratina gravidula										●											●			○			3	2
Ceratina nigrolabiata																					●						1	1
Chelostoma campanularum	●		●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Chelostoma distinctum	●			●	●		●	●		●	●	●	●		●	●	●	●		●	●	●	●	●	●	●	20	20
Chelostoma emarginatum								○													●		○				3	1
Chelostoma florisomne	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Chelostoma foveolatum										●											○		●	●			4	3
Chelostoma grande				●						○					○	○						●	●	●			7	4
Chelostoma rapunculi	●		●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	25	24
Coelioxys afer	●			●	●	●	●	●			●		●	●			●			●	●		●	●		●	15	15
Coelioxys alatus										○							●			○		●	●				5	3
Coelioxys aurolimbatus	●			●		○	●	●		●	●	●	●	●		●	●	●	●	●			●	●	●	●	19	18
Coelioxys conicus	●			●	●		●	●	●	●		●	●	○		●	●			●	●	●	●	●		●	18	17
Coelioxys conoideus				●		○	○	●		○	●		●				○			○	○		●	●		○	13	6
Coelioxys echinatus	●				●			●		●							●				●						6	6
Coelioxys elongatus	●			●		●	●	●	●	●	●		●	●		●	●	●	●		●	●	●	●		●	19	19
Coelioxys emarginatus								○																			1	0
Coelioxys inermis	●			●	●	●	●	●	●	●				○		●	●				●	●	●	●		●	16	15
Coelioxys lanceolatus				●					●	●				○		●						●	○	●			8	6
Coelioxys mandibularis	●	●		●			●		○	●				○		●	●				●		○	●		●	13	10
Coelioxys rufescens	●			●	●		●	○	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22	21
Colletes collaris						○																					1	0
Colletes cunicularius	●			●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22	22
Colletes daviesanus	●			●	●	●	●	●		●	●	●	●				●	●		●	●		●	●	●	●	18	18
Colletes floralis										●											●			●			3	3
Colletes fodiens						○		○		○											●			●			5	2
Colletes gallicus								○															○				2	0
Colletes hederae	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●		●	●	●	●	●	●	●	22	22
Colletes impunctatus				●					●	●											●	●		●			6	6
Colletes marginatus								○		○											●			●			4	2
Colletes mlokossewiczi								○																●			2	1
Colletes nigricans								○																●			2	1
Colletes sierrensis																					○			●			2	1
Colletes similis	●			●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	21	21
Colletes succinctus								○		●											●			●			4	3
Dasypoda argentata										○														●			2	1
Dasypoda hirtipes				●			●	●		●							●	●		○	●		○	●		○	11	8
Dioxys cinctus				●				○		●			○							○	○		○	●		○	9	3
Dufourea alpina				●					●	●				●		●					●	●	○	●			9	8
Dufourea dentiventris				●				○	●	●						●	○	○	○		●	●	●	●		●	13	9
Dufourea halictula																								●			1	1
Dufourea inermis				○						●											○	●		●			5	3
Dufourea minuta				○						●			○			●								●			5	3
Dufourea paradoxa				●						●						○					●	●		●			6	5
Epeoloides coecutiens	●			●			●	●		●	●	●				●	○	○	●	●		●	●	●	●	●	17	15
Epeolus alpinus				●				○		●					○							○		●			6	3

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Epeolus cruciger	●			●		○	●	●		●							●	●		●	●		●	●		●	13	12
Epeolus fallax					●																						1	1
Epeolus productulus																								●			1	1
Epeolus variegatus	●			●	●	●	●	●		●	●	●	●			●	●	●			●		●	●	●	●	18	18
Eucera hungarica																								○			1	0
Eucera interrupta								○								●					●			●			4	3
Eucera longicornis	●			●	●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	22
Eucera nigrescens	●	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	24
Eucera nigrifacies								●													●						2	2
Eucera pollinosa										●											●			○			3	2
Halictus carinthiacus				●			●						●										●	●			5	5
Halictus confusus	●			●	●	○	●	●		●		●	●	●		●	●		●		●		●	●		●	17	16
Halictus eurygnathus	●			●	●			●		●	●		●				●				●		●	●	○		12	11
Halictus fulvipes																					○						1	0
Halictus kessleri								○																○			2	0
Halictus langobardicus	●			●	●	●	●	●			●	●	●				○	●			●		●	●		●	15	14
Halictus leucaheneus					●					●													●	●		○	5	4
Halictus maculatus	●			●	●	●	●	●		●	●	●	●			●	●	○		●	●	●	●	●	●	●	20	19
Halictus quadricinctus	●			●	●			●		●			●			●					●		○	●			10	9
Halictus rubicundus	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Halictus scabiosae	●	●		●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	24
Halictus seladonius								○													●			●			3	2
Halictus sexcinctus	○			●			●	○		●		○	●				●	○		●	●		●	●		●	14	10
Halictus simplex	●			●	●	○	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22	21
Halictus subauratus	●			●	●	●	●	●		●	●	●	●	●		●	●	●		●	●	●	●	●	●	●	21	21
Halictus submediterraneus					●	●				○														●		●	5	4
Halictus tectus																								○			1	0
Halictus tumulorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Heriades crenulata	●			○	●			●		○		●									●		○	●		●	10	7
Heriades rubicola						●															●			○			3	2
Heriades truncorum	●		●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	25	24
Hoplitis acuticornis								○																●			2	1
Hoplitis adunca	●			●	●	●	●	●	●	●	●	●	●	●	○	●	●	●		●	●	●	●	●	●	●	23	22
Hoplitis anthocopoides				○			○	○		○			○				○						●	●		○	9	2
Hoplitis claviventris	●	●	●	●	●		●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	25	24
Hoplitis dalmatica										●											●			●			3	3
Hoplitis lepeletieri				●			●	○		●					○	○					●	●	●	●			10	7
Hoplitis leucomelana	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Hoplitis loti		●		●			●		●	●		●	○	●		●			●		●	●	●	●			14	13
Hoplitis mitis		●		●			○	○		●		●	○	●		●		○			●	○	●	●		●	15	10
Hoplitis papaveris								○															○				2	0
Hoplitis praestans																								●			1	1
Hoplitis ravouxi	●			●	●		●	●		○	●		●				○	●					●	●	●	○	14	11

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Hoplitis robusta										●						●								●			3	3
Hoplitis stecki										○																	1	0
Hoplitis tridentata	●			●	●	●	●	●		●	●	●					●	○			●		●	●	●	●	16	15
Hoplitis tuberculata		●	○	●			○		●	●		●		○	○	●		○	○		●	●	●	●			16	10
Hoplitis villosa		●		●			●	○	●	●		●	●	●	●	●		●	●		●	●	●	●			17	16
Hylaeus alpinus		●		●			●		●	●		●				●					●	●	○	●		○	12	10
Hylaeus angustatus				●			●	●	●	●			●			●	●	○		○	●	○	○	●		○	15	10
Hylaeus annulatus				●					●	●				●		●					●	●	○	●			9	8
Hylaeus bifasciatus								○													○		○				3	0
Hylaeus brevicornis	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	23
Hylaeus cardioscapus										●																	1	1
Hylaeus clypearis	●			●	●	○	●	●		●	●		●				●	●		●	●		●	●	●	●	17	16
Hylaeus communis	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	25	25
Hylaeus confusus	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	23
Hylaeus cornutus	●			●	●	●	●	●		●			●				●	●		●			●	●	●	●	15	15
Hylaeus crassanus										○											○			●			3	1
Hylaeus difformis	●			●	●		●	○	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	22	21
Hylaeus dilatatus	●			●	●	●	●	●	●	●	●		●			●	●	●	●	●	●		●	●		●	19	19
Hylaeus duckei	●			○		○	●	●										○					○	●			8	4
Hylaeus euryscapus								○																			1	0
Hylaeus gibbus	●			●	●	●	●	●	●	●		●	●			○				●	●		●	●		●	16	15
Hylaeus glacialis										●														●			2	2
Hylaeus gredleri	●			●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22	22
Hylaeus hyalinatus	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Hylaeus incongruus	●			●			●	●	●	●		●	○			●			●	●	●		●	●	●	●	16	15
Hylaeus intermedius								●		●											●						3	3
Hylaeus kahri	●			●	●	●	○	○	●	●			●	●		●	●			●	●		●	●		●	17	15
Hylaeus leptocephalus	●				●	●	○	●		○		●				●	●	○		●	○			●	●	●	15	11
Hylaeus moricei																○							●			●	3	2
Hylaeus nigritus	●			●	●	●	●	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	22
Hylaeus nivalis				●					●	●		●				●					●	●		●			8	8
Hylaeus paulus	●			●			○			●		●				●	○	●		●			○			●	11	8
Hylaeus pectoralis				●			●										○						●	○		●	6	4
Hylaeus pfankuchi	●						●					●				●	●		●	○	●	●	●	●	●	●	13	12
Hylaeus pictipes	●				●			●		○		●	○										○	●		●	9	6
Hylaeus pilosulus							●																				1	1
Hylaeus punctatus	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	23
Hylaeus punctulatissimus	●			●		○	○	○		○		●	○			○	●			●	●		●	●		●	15	9
Hylaeus rinki	●			●					●	●		●		●		●	●	○	●	○	●	●	●	○	●	●	17	14
Hylaeus signatus	●			●	●	●	●	●	○	●	●	●	●			●	●	●		●	●	●	●	●	●	●	21	20
Hylaeus sinuatus	●			●	●	●	●	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	22
Hylaeus styriacus	●			●	●	●	●	●		●	●	●	○	●		●	●	●	●	●	●		●	●	●	●	21	20
Hylaeus taeniolatus	●			●	●					●		●		●		●	●	○	●	●	●	●	●	○	●	●	17	15

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Hylaeus tyrolensis	●			●	●		●	●		●		●				●		●	●				○	●		○	13	11
Hylaeus variegatus	●			○		○		●		●	●		○								○		○	●		●	11	6
Icteranthidium laterale										○													○	●			3	1
Lasioglossum aeratum	●			●			○	○		●			○								●		●	●			9	6
Lasioglossum albipes	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Lasioglossum albocinctum								●													○			●			3	2
Lasioglossum alpigenum				●			●		●	●		●		●	●	○					○	●		●			11	9
Lasioglossum angusticeps	●							●																			2	2
Lasioglossum bavaricum				●			●		●	●						●					○	●	●	●			9	8
Lasioglossum bluethgeni	●				●			●					●				●				●		●			●	8	8
Lasioglossum brevicorne								○		●											●	○		●			5	3
Lasioglossum breviventre				○														○						●			3	1
Lasioglossum buccale								○													●			●			3	2
Lasioglossum calceatum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Lasioglossum clypeare							○	●					○								○			●			5	2
Lasioglossum convexiusculum				○		○		○		●			○								●			●			7	3
Lasioglossum costulatum	●			●	●	○	●	○		●	●	●					●	●		●	●			●		●	15	13
Lasioglossum cupromicans		●		●			●		●	●		●	●	●	●	●		●	●		●	●	●	●			16	16
Lasioglossum discum										●											●			○			3	2
Lasioglossum elegans								○																●			2	1
Lasioglossum euboeense								○															○	●			3	1
Lasioglossum fratellum				●			●		●	●	●	●	●	●		●		●	●		●	●	●	●			15	15
Lasioglossum fulvicorne	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Lasioglossum glabriusculum	●			●	●	○	●	●		●	●	●	●				●	●	●	●	●		●	●	●	●	19	18
Lasioglossum griseolum								●															●	●			3	3
Lasioglossum intermedium	●			●	○		●	●		●		●		●		●	●	●		●	●	●	●	●	●	●	18	17
Lasioglossum interruptum	●			●	●	●	●	●		●	○	●	●			●	●	●	○	●	●		●	●		●	19	17
Lasioglossum laeve				○		○		○					○										○	●			6	1
Lasioglossum laevidorsum							●			●											●			○			4	3
Lasioglossum laevigatum	●		●	●	●	○	●	●	●	●	●	●	○	●	●	●	○	●	●	○	●	●	●	●	●	●	25	21
Lasioglossum laterale																					●						1	1
Lasioglossum laticeps	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Lasioglossum lativentre	●			●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	21	21
Lasioglossum leucopus	●	●	●	●	●		●	○	●	●	●	●	●	●	●	●	○	●	●	○	●	●	●	●		●	24	21
Lasioglossum leucozonium	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Lasioglossum limbellum	●			●		●	●	●	●	●		●	●			●	○	●		●	○		●	●	●	●	18	16
Lasioglossum lineare	●			●	●	○	●	●		●	●	●	●			●		●		●			●	●		●	16	15
Lasioglossum lissonotum				○				○		●			○								○			●			6	2
Lasioglossum lucidulum	●			●			●	●		●		●	●			●	●	●		●	●		●	●	●	●	16	16
Lasioglossum majus	●			●			●	●		●						●				●	○		●	●		●	11	10
Lasioglossum malachurum	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Lasioglossum marginatum	●			○	●	●		●					●				●	●		●	●		●	●		●	13	12
Lasioglossum marginellum								●															○	●			3	2

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Lasioglossum medinai				●																			●				2	2
Lasioglossum minutissimum	●			●	●	●	●	●				●	●				●	○		●	●		●	●		●	15	14
Lasioglossum minutulum				●	●			○		●			●			○	●	●			●		●	●			11	9
Lasioglossum monstrificum	●			●	●	●	●			●		●				●	○		●	●	●		●	●		●	15	14
Lasioglossum morio	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Lasioglossum nigripes	●			●	●	○	●	●	●	●	●	●	●			●	●	●	●	●	●		●	●	●	●	21	20
Lasioglossum nitidiusculum	●			●	○	○	●	●		●	●	●	●	●		●	●	●		●	●		●	●	●	●	20	18
Lasioglossum nitidulum	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	24	23
Lasioglossum pallens	●			●	●	●	●	●		●			●			●	●	●		●	●		●	●		●	16	16
Lasioglossum parvulum	●			●	●	●	●	●		●	●	●	●	●	●	●	●	●		●	●	●	●	●		●	21	21
Lasioglossum pauperatum	○							○													○			○			4	0
Lasioglossum pauxillum	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Lasioglossum peregrinum																					○						1	0
Lasioglossum pleurospeculum																○			●			●			●	●	5	4
Lasioglossum podolicum										●						●								●			3	3
Lasioglossum politum	●	●		●	●	●	●	●		●	●	●	●			●	●	●		●	●		●	●	●	●	20	20
Lasioglossum punctatissimum	●			●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	23
Lasioglossum puncticolle	●			●	●			●			●					●	●	●					●	○		●	11	10
Lasioglossum pygmaeum				○		○	●	●		●	●		●			●		●			●		●	●			12	10
Lasioglossum quadrinotatulum								○		●											●			●		●	5	4
Lasioglossum quadrinotatum					○			○																○			3	0
Lasioglossum quadrisignatum						○		○									○				○			●			5	1
Lasioglossum rufitarse	●	●	●	●	●		●		●	●	●	●	●		●	●	○	●	●	●	●	●	●	●	○	●	23	21
Lasioglossum semilucens	●			●	●	●	●	●		●	●	●	●			●	●	●		●	●	●	●	●	●	●	20	20
Lasioglossum setulosum										●											●						2	2
Lasioglossum sexmaculatum										○																	1	0
Lasioglossum sexnotatum	○			●	●	○	○	○		●	●		○				○	●		○	●		○	●		○	16	7
Lasioglossum sexstrigatum	●			●			●	●		●		●	●			●	●	●		●	●	●	●	●	●	●	17	17
Lasioglossum subfasciatum				○		○		○		○			○			○		○			○	○	●	●		○	12	2
Lasioglossum subfulvicorne				●						●			●			●					●			●			6	6
Lasioglossum subhirtum								●															●				2	2
Lasioglossum tarsatum							○			●											●			●			4	3
Lasioglossum transitorium																					●						1	1
Lasioglossum tricinctum	●			●	●	●	●	●			●		●					●			●		●	●			12	12
Lasioglossum villosulum	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Lasioglossum xanthopus	●			●	●	○	○	○		●			●			●	●	●		●	●		●	●		●	16	13
Lasioglossum zonulum	●			●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	23
Lithurgus chrysurus								●		○											●						3	2
Macropis europaea	●			●	●	●	●	●		●	●	●	●			●	●	●	●	●	●	●	●	●	●	●	21	21
Macropis fulvipes	●			●	●		●	●		●		●		●		●	●	●	●	●	●	●	●	●	●	●	19	19
Megachile alpicola	●		●	●	●		○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	22
Megachile analis				●						●								○			●	●		●			6	5
Megachile apicalis					●	●		○		○											○			○			6	2

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Megachile argentata	●			●	●	●	●	●		○	●	●	●	●		●	●	●		●	●		●	●	●	●	20	19
Megachile centuncularis	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	23
Megachile circumcincta	●		●	●	●	●	●	●	●	●		●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	23
Megachile ericetorum	●	●	○	●	●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	23
Megachile flabellipes										○											●						2	1
Megachile genalis										●																	1	1
Megachile lagopoda				○		○		○		●			○								●		●	●		○	9	4
Megachile lapponica									●	●						●								●		○	5	4
Megachile leachella								○		●											●			●			4	3
Megachile ligniseca	●			●	●	○	●	●	●	●	●	●				●	●	●	●	●	●	●	●	●	●	●	21	20
Megachile maritima	●			●		○	○	●		○	●		●				●			○	●		●	●		○	14	9
Megachile melanopyga										●											●			●			3	3
Megachile nigriventris	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	25	24
Megachile parietina	●		○	○	○	○	○	●		●			○			●	●		○	●	●		○	●		●	17	9
Megachile pilicrus										●											●			○			3	2
Megachile pyrenaea				●		○				●			●			○		○			●	●	●	●			10	7
Megachile pyrenaica				●		○	●	○		●		●	○	●	●						●		●	●			12	9
Megachile rotundata	●				●	●		●		●							●	●		●	●		●	●		●	12	12
Megachile sculpturalis	●			●				●		●		●					●				●	●	●	●		●	11	11
Megachile versicolor	●			●	●		●	●	●	●	●	●	●	●		○	●	●	●	●	●	○	●	●	●	●	22	20
Megachile willughbiella	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Melecta albifrons	●			●	●	●	●	●		●	●	●	●	●		●	●	●		●	●	●	●	●	●	●	21	21
Melecta festiva																								●			1	1
Melecta luctuosa				○		○	○	○		●		○	●			○	●				●		●	●			12	6
Melitta dimidiata										●														●			2	2
Melitta haemorrhoidalis	●			●	●	○	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	23	22
Melitta leporina	●			●	●	●	●	●		●	●	●	●			●	●	●		●	●		●	●		●	18	18
Melitta nigricans	●			●	●	●	●	●		●	●	●	●			●	●	●	●	●		○	●	●	●	●	20	19
Melitta tricincta				●			○			●						●	●		●				●	●			8	7
Melitturga clavicornis																								●			1	1
Nomada alboguttata	●			●		○	●	○		●	●	●	●			●	●	●		●	●	●	●	●	●	●	19	17
Nomada argentata								○		●											●		○	○	●		6	3
Nomada armata	●			●	●	○	●	○		●		●	●			●		○		●	●	●	●	●		●	17	14
Nomada atroscutellaris	●			●	●		●	●		●	●	●	○	●		●	●	●		●	●		●	●		●	18	17
Nomada baccata								○		○														○			3	0
Nomada bifasciata	●		○	●	●	●	●	●		●	●	●	●			●	●	●	○	●		●	●	●	●	●	21	19
Nomada bispinosa																	○			○							2	0
Nomada blepharipes								○																●			2	1
Nomada bluethgeni								○																			1	0
Nomada braunsiana				○		○		○		●											○		○	●		●	8	3
Nomada carnifex																					○						1	0
Nomada castellana	●			○		●	○	○	●	●		○	○			●	●	●		○	●		●	●			16	10
Nomada confinis																								○			1	0

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Nomada conjungens	●			●	●	○	○	●		●	○	○	●			●	●	●		●	○		●	●		○	18	12
Nomada connectens																								○			1	0
Nomada discrepans								○																			1	0
Nomada distinguenda	●			○	●	●	○	●		○							●	●		●	○		○	○		●	14	8
Nomada emarginata				○				○		●										●	○	●	●	●			8	5
Nomada errans				○		○	●	●		●								○					○	○			8	3
Nomada fabriciana	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Nomada facilis	●			●		○	●	○		●	●	●	●	●		●		●	●	○	●	●	●	●		●	19	16
Nomada femoralis				○				○		●			○			●				○	●		○	●		○	10	4
Nomada ferruginata				●	●	○	●	●		●	●		○							○			●	●		○	12	8
Nomada flava	●		●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Nomada flavilabris																								○			1	0
Nomada flavoguttata	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Nomada flavopicta	●			●		○	●	●		●		●	●			●	●	●		●	●	●	●	●	●	●	18	17
Nomada fucata	●			●	●	○	●	●		●	●		●			●	●	●		●		●	●	●	●	●	18	17
Nomada fulvicornis	●			●	○	○	●	●		●	●	●	●	●		●	●	●		●	●		●	●		●	19	17
Nomada furva								○															○	●			3	1
Nomada fuscicornis				○						●								●						●		○	5	3
Nomada goodeniana	●			●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	23
Nomada gransassoi				●						○													○	●			4	2
Nomada guttulata	○			●	●		○	○		●	●	●	●			●	●	●			●		●	●		●	16	13
Nomada hirtipes	●		●	●	●		○	●			●	●	●	●		●	●	●		●			●		●	●	17	16
Nomada integra	●		●	●	●	○	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	24	22
Nomada italica																								○			1	0
Nomada kohli	●				●			●									●										4	4
Nomada lathburiana	●		○	●	●	●	●	●		●	●	●	●			●	●	●		●	○		●	●	●	●	20	18
Nomada leucophthalma				●		○	●	○		●		●	○	●		●		○	●		○	○	●	●		●	16	10
Nomada linsenmaieri																								●			1	1
Nomada marshamella	●		●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	25	23
Nomada mauritanica																					○			○			2	0
Nomada melathoracica				○			○	○			○		○					○			○		○	●		○	10	1
Nomada minuscula								○													○						2	0
Nomada moeschleri				●						●	●	●	●	●	●	●		●	●			●	●	●			13	13
Nomada mutabilis								○																●			2	1
Nomada mutica				○				○		●			○								●		●	●			7	4
Nomada nobilis																								●			1	1
Nomada obscura				●										●				●					○	●		●	6	5
Nomada obtusifrons									●	●									○					●			4	3
Nomada opaca				○		○														○			○	○			5	0
Nomada panurgina								○															○				2	0
Nomada panzeri	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	24
Nomada piccioliana				○						●							○	●			●			○		○	7	3
Nomada pleurosticta										●														●			2	2

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Nomada posthuma	●									●									●	○	●			●		●	7	6
Nomada rhenana				○		○		●												○			○	○			6	1
Nomada roberjeotiana						○		○																		○	3	0
Nomada ruficornis	●		●	●	●	○	●	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	22
Nomada rufipes				○				○	●	●											●			●			6	4
Nomada sexfasciata	●			●	●	○	●	●		●	●	●	●	●		●	●	●		●	●	●	●	●		●	20	19
Nomada sheppardana	●			○	●		●	●		●	●	●				●	●	○		●	●		●	○		●	16	13
Nomada signata	●			●	●	●	●	●		●	○	○	●			●	●	●		●	●	●	●	●		●	19	17
Nomada similis				○						●											●	○		●			5	3
Nomada stigma				○		○		○		●	●		○			○							○	○		○	10	2
Nomada striata	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	24	24
Nomada succincta	●			○		○	●	●		●		●	●	●		●	○			○	●		●	●		●	16	12
Nomada tormentillae									●	●											○			○			4	2
Nomada tridentirostris								○																			1	0
Nomada villosa	●			○			○	○		●	●		○			●	○	○	●	●			●	●		○	15	8
Nomada zonata	●				●			●		●	●	○	○								●		●	●		●	11	9
Nomiapis diversipes								○													●			●			3	2
Osmia alticola										●											●			●			3	3
Osmia anceyi																								●			1	1
Osmia andrenoides				●			○	○		●			●			○		●			○		●	●			10	6
Osmia aurulenta	●	●	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	24
Osmia bicolor	●	●		●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	24	23
Osmia bicornis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Osmia brevicornis	●			●	●	○	●	●		●		●				●	○	●		●	●		●	●		●	16	14
Osmia caerulescens	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Osmia cornuta	●			●	●	●	●	●		●	●	●	●			●	●	●		●	●	●	●	●	●	●	20	20
Osmia gallarum	●			●	●		○	●		●	●		●				●	●		●	●		●	●		●	15	14
Osmia inermis		●		●			●		●	●				●	●	○	○				●	●	○	●			13	10
Osmia labialis		●		●			●	○		●	●	●	●	●	●	○		○			●	●	●	●		●	17	14
Osmia latreillei								○																		●	2	1
Osmia leaiana	●			●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	23
Osmia ligurica								○																			1	0
Osmia mustelina		●		●			○	○	●	●			○	●	●	●		○	●		●	●	○	●			16	11
Osmia nigriventris				●						●						●			○		●	○	●	●			8	6
Osmia niveata	●			○	○	○	○	●	●	●	●	●	●	○			●	●		○	●	●	●	●	●	●	21	15
Osmia parietina	●	●	●	●	●		●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●		●	23	22
Osmia pilicornis	●			○			○	○				●	○				●	●		○			●			●	11	6
Osmia rufohirta	●			●	●	○	●	●		●	●		●			○	●	●			●		●	●		●	16	14
Osmia scutellaris										●											●			●			3	3
Osmia spinulosa				●	○	●	●	●		●			●			●	●				●		●	●		●	13	12
Osmia steinmanni		●		●						○					●									●			5	4
Osmia submicans				●	●	○	○	●		●	●	○	●			●	○	●		○	●		●	●	●	○	18	12
Osmia tergestensis																					○			●			2	1

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Osmia uncinata	●		●	●	●		●		●	●	○	●	●	○		●	●	●	○	●			○	●		●	19	15
Osmia viridana				●			○	○					●				○						●				6	3
Osmia xanthomelana	●	●	●	●	●	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	25	23
Panurginus herzi				●			○		●	●		●		●	●	●			●			●	○	●			12	10
Panurginus montanus									●	●																	2	2
Panurginus sericatus				●						●											●	●		●			5	5
Panurgus banksianus			●	●		○	○	○	●	●		●				●					●	●		●	●		13	10
Panurgus calcaratus	○			●		○	○	●		●			○			●	○	○		○	●	●		●		●	15	8
Panurgus dentipes				○	○	○		●					●					●					●	●			8	5
Pasites maculatus																					●			●			2	2
Protosmia minutula																								●			1	1
Pseudoanthidium nanum					●	●		●		●							○				●		●	●			8	7
Rhodanthidium caturigense																								●			1	1
Rhodanthidium septemdentatum				○				○		●											●		●	●			6	4
Rhophitoides canus						○				●																	2	1
Rophites algirus				○				●		●											○		●	●			6	4
Rophites quinquespinosus				●	●	○		○		●	●							●		○	○		●	●		○	12	7
Sphecodes albilabris	●			●	●	●	●	●		●	●	●	●			●	●	●		●	●		●	●	●	●	19	19
Sphecodes alternatus								○		○											●						3	1
Sphecodes crassanus																								○			1	0
Sphecodes crassus	●		●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Sphecodes cristatus						●																		○			2	1
Sphecodes croaticus	●				●			●			●		○				●			●	●		●	●		●	11	10
Sphecodes dusmeti																								●			1	1
Sphecodes ephippius	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Sphecodes ferruginatus	●			●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	23
Sphecodes geoffrellus	●		●	●	●	○	●	○	●	●	●	●	○	●		●	●	●	●	●	●	●	●	●		●	23	20
Sphecodes gibbus	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	24
Sphecodes hyalinatus	●		●	●	●		●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	23
Sphecodes longulus	●			●	●	●	●	●		●	○	●	●			●	●	●		●	●		●	●	●	●	19	18
Sphecodes majalis	●				●			●			●		●				●	●		●			●			●	10	10
Sphecodes marginatus				○				○																			2	0
Sphecodes miniatus	●			●	○	○	●	●		●		●	●	○		●	●	●			●	○	●	●		●	18	14
Sphecodes monilicornis	●			●	●	●	●	●		●	●	●	●	●		●	●	●		●	●		●	●	●	●	20	20
Sphecodes niger	●			●	●	○	●	●		●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	21	20
Sphecodes pellucidus	○			●			●	●		●						●		○		●	●		●	●		●	12	10
Sphecodes pseudofasciatus	●						●	●		○	●		●					●			●		●	●		○	11	9
Sphecodes puncticeps	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24	24
Sphecodes reticulatus	●			●	●	●	●	●		●	●	●	●			●	●	●	●	●	●		●	●	●	●	20	20
Sphecodes rubicundus				●				●		●			●			●		●			●		●	●		○	10	9
Sphecodes ruficrus	●			●	●	○	●	●			○	●	●			○	●	●		●	●		●	○		●	17	13
Sphecodes rufiventris	●			○			●	●		●	●		○			●	●	○		●	●		●	●		●	15	12
Sphecodes scabricollis	●	●		●	●		●	●		●	●	●	○		●	●		●	●	●	●	●	●	●	●	●	21	20

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Sphecodes schenckii	●			●	●			●		●		●				●	●	●	●	●	●		○	○		●	15	13
Sphecodes spinulosus								○		●										●				●			4	3
Sphecodes zangherii																					●			●			2	2
Stelis annulata																								○			1	0
Stelis breviuscula	●			●		○	●	○	●	●	●	●	●	●		●	●	●		○	●	●	●	●	●	●	21	18
Stelis franconica				●						●						●					○	●		●			6	5
Stelis minima				○						●								○			○		●	●		●	7	4
Stelis minuta	●			○	●			○		●						●	○	●			○	●		●		●	12	8
Stelis nasuta	○							○		●										○			○	●		○	7	2
Stelis odontopyga				●																				●			2	2
Stelis ornatula	●			●			●	●	●	●	●	●		●			●	●	●	●	●	●	●	●		●	18	18
Stelis phaeoptera				●		○	●	○		●		●				●	○	○		○	●	●	●	●		○	15	9
Stelis punctulatissima	●			●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22	22
Stelis signata	●	●		●			○	●	●	●		●	●			○	●	●	●	●		○	●	●		●	18	15
Stelis simillima																					●						1	1
Systropha curvicornis								○		○											○			●			4	1
Systropha planidens					○	○																					2	0
Tetralonia alticincta								●													○						2	1
Tetralonia dentata										○											●			●			3	2
Tetralonia fulvescens								●													○			●			3	2
Tetralonia inulae																					●						1	1
Tetralonia malvae								●		○											○		○				4	1
Tetralonia pollinosa																								○			1	0
Tetralonia salicariae	●			●				●		●						●					●			●			7	7
Thyreus hirtus																								●			1	1
Thyreus histrionicus										○											●						2	1
Thyreus orbatus	●			●			●			●								○					●	●		●	8	7
Thyreus ramosus																							○	●			2	1
Thyreus truncatus																								●			1	1
Trachusa byssina	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Trachusa interrupta								○		○														●			3	1
Triepeolus tristis																					●			○			2	1
Xylocopa iris							●	●		●	●										●		○	●			7	6
Xylocopa valga	●			●	●	●	●	●		●			●				●				●		●	●		●	13	13
Xylocopa violacea	●			●	●	●	●	●		●	●	●	●			●	●	●		●	●	●	●	●	●	●	20	20
Total number	295	76	94	410	259	271	331	436	171	464	243	266	324	202	127	320	290	306	198	272	445	239	416	532	185	334	632	575
Total number (after 1999)	283	72	80	341	247	158	276	281	161	413	232	254	265	188	109	289	255	262	185	232	387	219	348	475	182	295		

Andrena alutacea Stöckhert, 1942

The distinctiveness of *A. alutacea* from *A. proxima* (Kirby, 1802) has been confirmed recently (Schmid-Egger 2005; Schmidt et al. 2015; McLaughlin et al. 2023). In Switzerland, *A. alutacea* occurs in the Plateau, in the Rhine Valley north of Chur, in the Engadin, in the Val Müstair, and south of the Alps in Ticino as well as in the Mesolcina and Poschiavo Valleys. In addition, there are ancient records from the Reculet, France (three females, Natural History Museum, Geneva) and one possible record from the Salève (three male specimens, leg. Frey-Gessner, tentatively identified as *A. alutacea*, Natural History Museum, Geneva; identification in males is particularly challenging in this group). In Switzerland, *A. alutacea* is nearly always found in sympatry with *A. proxima*, except in the Lower Engadin, where only *A. alutacea* has been recorded. See also comments under *A. ampla* Warncke, 1967. An identification key for the three species of the *A. proxima*-group can be found in Schmid-Egger (2005).

Andrena amieti Praz, Müller & Genoud, 2019

This widely distributed, alpine species has been described recently (Praz et al. 2019); an identification key with all central European species of this species group is included in the cited article.

Andrena ampla Warncke, 1967

The distinctiveness of *A. ampla* from *A. proxima* has been confirmed recently (Schmid-Egger 2005; McLaughlin et al. 2023). *Andrena ampla* has a mosaic-like distribution in the Swiss Alps (Valais, some valleys in Ticino, some valleys in Graubünden) and forms several narrow contact zones with *A. proxima*; both taxa have so far not been found in sympatry (McLaughlin et al. 2023). The contact zone between Martigny and St-Maurice (Valais) is only a few kilometers wide, and no hybrid specimen has been found (McLaughlin et al. 2023). Another contact zone is found in the Chur Region (Graubünden). *Andrena alutacea* and *A. ampla* have also never been found in sympatry. An identification key for the three species of the *A. proxima*-group present in Europe can be found in Schmid-Egger (2005).

Andrena assimilis Radoszkowski, 1876

Following Wood and Monfared (2022), *A. gallica* Schmiedeknecht, 1883 is treated as a synonym of *A. assimilis*.

Andrena barbareae Panzer, 1805 and *A. cineraria* (Linnaeus, 1758)

Andrena barbareae and *A. cineraria* have mostly been treated as distinct species (Gusenleitner and Schwarz 2002; Amiet et al. 2010), although Warncke (1986) treated *A. barbareae* and *A. cineraria* as synonyms. The distinctiveness of these two species was recently shown using multi-locus genetic data (Gueuning et al. 2020), even if both taxa share DNA barcodes in central Europe (Schmidt et al. 2015; Gueuning et al. 2020). In Switzerland, a morphological separation of some Alpine populations is ambiguous. It is possible that some of these populations present some degree of introgression between both species. Also, whether both species are present in sympatry remains to be established. In particular, *A. cineraria*, although widely distributed at low elevation in northern Switzerland, has not been reported from mid-elevation sites in the Valais where *A. barbareae* occurs. This pattern suggests that these two taxa may be in an early phase of the speciation process, and that some reproductive interference may still prevent their presence in sympatry.

Andrena bicolor Fabricius, 1775

The distinctiveness of *A. bicolor* from *A. allosa* and *A. amieti* is discussed under these two species (see above). According to previous genetic analyses (Schmidt et al. 2015; Praz et al. 2019; Gueuning et al. 2020), what has so far been considered as "*Andrena bicolor*" may represent two distinct cryptic taxa, both of which are widely distributed across Europe. These two taxa have distinct DNA barcodes and are mostly distinct based on nuclear genetic sequences (Gueuning et al. 2020). Based on available DNA barcodes, the most widely distributed form or taxon is distributed throughout Europe (Barcode Index Number, hereafter "BIN" BOLD:AAD0134) and is present in all biogeographic regions in Switzerland (Suppl. material 5, upper clade in *A. bicolor*). The second form (BIN BOLD:AAD0135; lower clade in Suppl. material 5) has been recorded, among other countries, in the UK, in Portugal, Spain, Germany, France and Greece; in Switzerland, it has so far only been reported from the Valais in spite of extensive barcoding in other regions, suggesting different climatic preferences in these two cryptic taxa. Since these nearly cryptic forms are currently not associated with names, and since there are still uncertainties on their taxonomic status, they are so far not treated as distinct species in the Swiss database. Numerous names have been proposed from the UK by Kirby (e.g., *Andrena gwynana* (Kirby, 1802)), where both cryptic taxa supposedly occur; future work is needed to further delineate species in this group, to determine the geographic distribution of each taxon, and to associate each taxon with a name, possibly through the designation of barcoded neotypes.

Andrena bimaculata (Kirby, 1802)

Amiet et al. (2010) mention that this species occurs in three forms in Switzerland: form 1 with terga 2 and 3 (partly) red, legs dark; form 2 with terga dark and legs red; and form 3 with terga and legs dark. The names given to these forms by Amiet et al. (2010) are incorrect (Schmid-Egger 2012). Form 1 is restricted to the valleys south of the Alps, where it occurs in sympatry with form 3, whereas intermediate specimens between both forms are unknown. DNA barcodes from forms 1 and 3 in sympatry from several sites in Ticino did not reveal divergences between both (Suppl. material 5), suggesting that they simply represent color forms within the same biological species, in agreement with the general gradient in color observed elsewhere (Falk and Lewington 2015). We have not been able to examine specimens of Amiet's form 2 and believe these specimens to be misidentified specimens of *A. tibialis* (Kirby, 1802).

***Andrena confinis* Stöckhert, 1930, *A. congruens* Schmiedeknecht, 1884 and *A. dallatorrei* Clément, 1922**

These three species have so far been treated as conspecific in Switzerland (Amiet et al. 2010). Schmid-Egger (2012) mentions that the presence of *A. confinis* in Switzerland requires confirmation. The analysis of DNA barcodes by Schmidt et al. (2015) suggests that both taxa are distinct, although their published sequences of *A. confinis* and of *A. congruens* originated from populations in widely different geographic regions, possibly confounding species boundaries with isolation by distance. No sequence is available for the unclear taxon known as *A. dallatorrei*, known only from the Alps in Switzerland and Austria (see below).

Based on morphological criteria, we consider *A. confinis* and *A. congruens* to represent distinct species; these differences were confirmed by DNA barcodes from Ticino and the Geneva region (*confinis*) and the Alps (*congruens*) (Fig. 3). The Swiss material of these two taxa was entirely revised by one of us (MH) and suggests the following pattern: *A. confinis* was historically widely distributed in northern Switzerland, with numerous records on the Plateau between Lake Geneva and Schaffhausen, as well as in the Rhine Valley around Chur and northwards. The last record of *A. confinis* in northern Switzerland is of 1945. There is no historical record south of the Alps. Recently, *A. confinis* was found twice in the Geneva region; these records are confirmed by DNA barcodes. It is not clear whether the species has maintained undetected populations in that region, or whether it has recolonized this area from France, as other taxa in the Geneva region (e.g., *Tetralonia malvae* (Rossi, 1790)). In addition, *A. confinis* was recently found twice south of the Alps (Ticino and Bregaglia Valley, Graubünden); the record from Ticino was confirmed using DNA barcodes. In Switzerland, *A. confinis* has only been found at low elevations (below 1000m).

Andrena congruens is widely distributed in the western Alps and is present locally in Graubünden; there are isolated records in Ticino, mostly at intermediate elevations. Currently, *A. confinis* and *A. congruens* do not appear to occur in sympatry, although both taxa occur in Ticino. Historically however, there are records of *A. congruens* along the Jura between the Neuchatel region and Solothurn (last record in the Jura in 1978), in a region with records of *A. confinis*. These historical specimens would represent the first sympatric occurrence of *A. confinis* and *A. congruens* in Europe.

The status of the third taxon remains unclear. *A. dallatorrei* is characterized by conspicuous differences in vestiture (mostly the nearly entirely dark vestiture on the female clypeus), but also consistent sculptural differences (in particular, the margin of tergum 2, which is nearly impunctate in *A. dallatorrei*, and strongly and distinctly punctate in *A. congruens*). *Andrena dallatorrei* is also appreciably larger (body length 12 mm, compared to 10–11 mm in *A. congruens* and *A. confinis*). These differences correspond to interspecific differences in *Andrena*. *Andrena dallatorrei* is known from very few localities and nearly entirely from old (<1950) specimens, but numerous specimens exhibiting constant morphology are available from some of these localities. All localities are in the dry valleys of the Alps (Rhone Valley near Sierre, as well as some alpine localities in the Valais; Val Müstair; Rhine Valley near Chur; Engadin). The last Swiss record of this taxon is from 2003 in the Valais. In the absence of genetic data, we do not treat *A. dallatorrei* as a valid species, and correspondingly do not include this taxon in the checklist. Future work is urgently needed to settle the status of this restricted and possibly endangered Alpine bee taxon.

***Andrena decipiens* Schenck, 1861 and *A. flavilabris* Schenck, 1874**

Andrena flavilabris has long been treated as the first generation of *A. decipiens*. It was recently elevated to species rank based on congruent mitochondrial genetic divergences, and phenological and biological differences (Mandery et al. 2008). Both species occurred historically in Switzerland and appear to have gone extinct approximately in the same period in the early 1900s.

***Andrena dorsata* (Kirby, 1802) and *A. propinqua* Schenck, 1853**

The status of these two taxa has remained controversial (Gusenleitner and Schwarz 2002; Schmidt et al. 2015). A morphological separation of both taxa is mostly straightforward in Switzerland (Amiet et al. 2010), and the distinctiveness of these two taxa has recently been confirmed by an analysis of multi-locus genetic data (Gueuning et al. 2020). The lack of mitochondrial divergences highlighted by Schmidt et al. (2015) possibly relies on identification errors.

***Andrena floricola* Eversmann, 1852**

As indicated under *A. alfkenella*, the males of *A. floricola* and *A. alfkenella* have so far been misidentified in Switzerland. Most records of *A. floricola* from northern Switzerland indicated by Amiet et al. (2010) in fact belong to *A. alfkenella*. The distribution of *A. floricola* in Switzerland is currently restricted to the Valais, where the species is very rare. There are confirmed historical occurrences elsewhere in Switzerland (Geneva and Lausanne

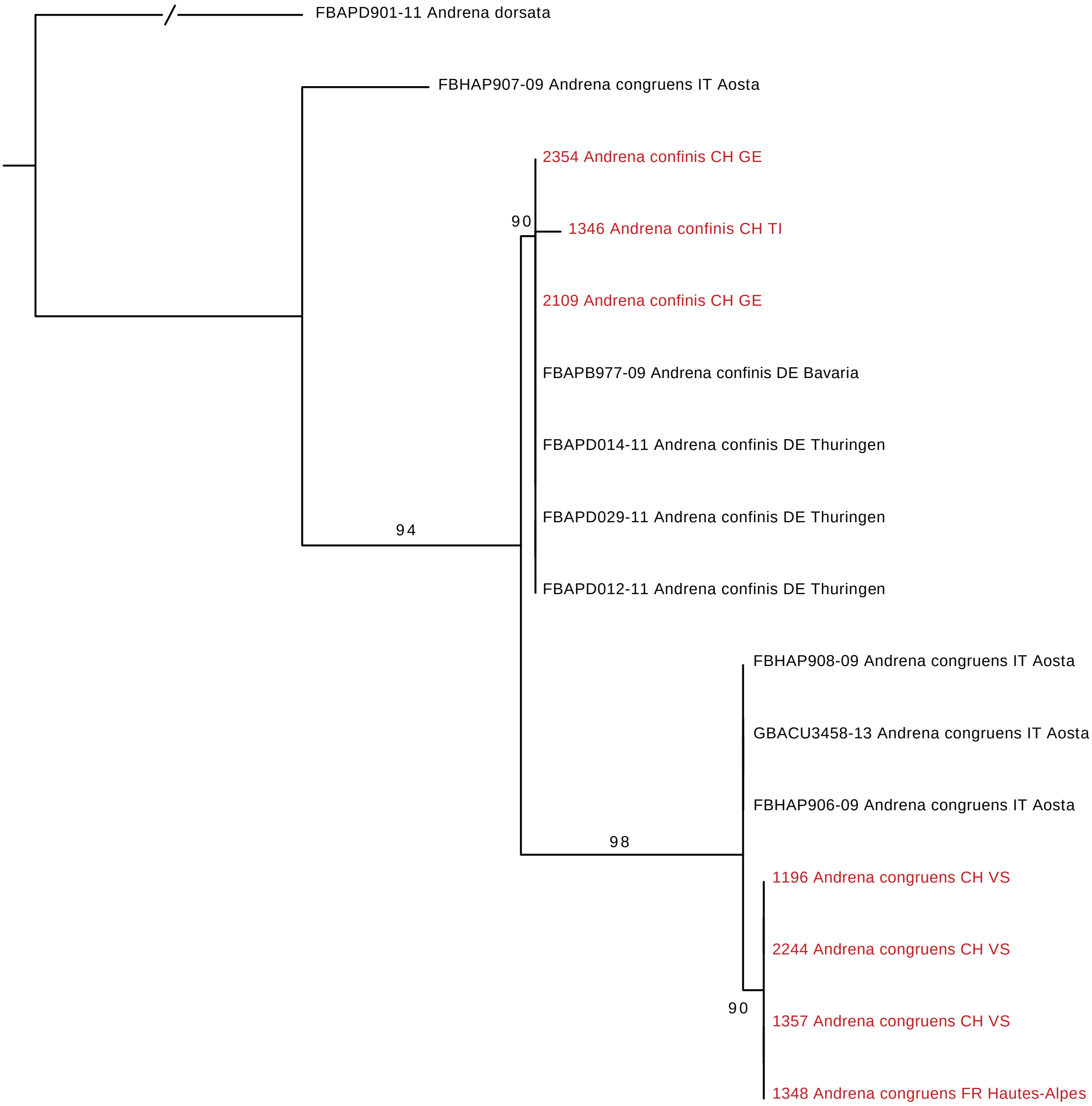


Figure 3. Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Andrena confinis* and *A. congruens*. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Andrena dorsata*; this branch was shortened for better graphic representation. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2).

Region, Jura near Neuchâtel, Basel, Schaffhausen, Rhine Valley near Chur). For the separation of *A. alfkenella* and *A. floricola* see under *A. alfkenella* as well as Schmid-Egger and Scheuchl (1997) and Wood (2023a).

Andrena florivaga Eversmann, 1852

This species was first observed in Switzerland in 2015 (Bénon and Praz 2016), likely mirroring the range expansion of this species in Europe (e.g., Mandery 1999). *Andrena florivaga* is included in the key of Schmid-Egger and Scheuchl (1997); see also Bénon and Praz (2016).

Andrena fulvicornis Schenck, 1853

This taxon was treated as a synonym of *A. nitidiuscula* Schenck, 1853 by Amiet et al. (2010). It has recently been reported from northern Switzerland (Bénon and Praz 2016), where it has been observed a few times from 2015 onwards. We obtained DNA barcodes for three specimens identified as *A. fulvicornis* based on morphology; these three DNA barcodes were identical to available sequences of *A. fulvicornis*, and distinct from *A. nitidiuscula*, confirming the specific status of these two taxa (Suppl. material 5). De Beaumont (1960) mentions that both *A. fulvicornis* and *A. nitidiuscula* occur in western Switzerland; we have revised the entire museum material identified as *A. nitidiuscula* (including the specimens in the de Beaumont collection) and did not find specimens of *A. fulvicornis* collected before 2015. It must be stressed however that the identification of old specimens with lightened (light brown/brown orange) integument color is challenging. The presence of *A. fulvicornis* in Switzerland is thus possibly the result of a recent range expansion. For the separation of *A. fulvicornis* and *A. nitidiuscula* see Schmid-Egger and Scheuchl (1997) and Schwenninger (2013). A third species of this groups occurs in central Europe, *A. curvana* Warncke, 1965. This species was found in a restricted region in Baden-Württemberg (Schwenninger 2013), but so far not in Switzerland.

Andrena gelriae **van der Vecht, 1927**

Revision of the material deposited in the Swiss museums revealed that many of the occurrences published by Amiet et al. (2010) were based on misidentified females (Praz et al. 2022). Confirmed occurrences of this species are restricted to pre-1970 records in the Swiss Plateau, and recent occurrences in the north of Switzerland, in the region of Geneva, in Vaud and in the Valais. The identification of females is difficult and requires comparative material (see identification key in Praz et al. 2022).

Andrena hesperia **Smith, 1853**

Amiet et al. (2010) report one record from the Valais. We have not been able to find a specimen associated with this record, which is considered doubtful and has been deleted from the database. In Switzerland, this species has only been found in a few northwestern localities after 1986. This population appears to be widely separated from the nearest populations in southern France.

Andrena limata **Smith, 1853 and** ***A. nitida*** **(Müller, 1776)**

The status of these two species remains controversial. The mostly central to northern European species *A. nitida* is univoltine, while the mostly southern European species *A. limata* is bivoltine (Schmid-Egger and Scheuchl 1997; Amiet et al. 2010). In Switzerland, we are confident that two distinct species occur, the univoltine *A. nitida*, which is widely distributed, and a bivoltine taxon that has so far been referred to as *A. limata*. This bivoltine taxon is morphologically slightly distinct from *A. nitida* (Amiet et al. 2010), in both sexes and in both generations, although the differences are more pronounced in the second generation (there are only few confidently identified specimens of the first generation in collections). Morphological differences are mostly restricted to vestiture length (unclear in first generation) and colour: female: vestiture on face and mesonotum (especially posteriorly) shorter in *A. limata*; vestiture on sides of mesosoma yellowish-brown in *A. limata*, greyish-white in *A. nitida*; male: hairs on face and on sterna predominantly greyish-white in *A. nitida*, dark in *A. limata*. Long series of this bivoltine taxon are available in historical collections from the Geneva area, from the southern Alps (Ticino, Mesolcina), as well as isolated records in the Swiss Plateau. Isolated specimens have been collected recently in the southern Alps (Ticino, Graubünden) and in the Engadin (Graubünden).

Two taxonomic issues persist in this group. First, the Swiss specimens attributed to *A. limata* are morphologically divergent from southern European specimens of *A. limata*; in the latter, the hairs on the thorax are even shorter, and there are additional subtle differences in the sculpture between Swiss and southern European *limata*. In some respects, the Swiss *limata* are intermediate between typical *nitida* and southern European *limata*, possibly leading Warncke (1986) to treat *limata* and *nitida* as two subspecies. Second, DNA barcodes also present ambiguous results with respect to the status of Swiss specimens of *limata*: we present DNA barcodes for three specimens of *A. limata*, one from southern Ticino, one from the Bregaglia Valley (Graubünden) and one from the Engadin, as well as one barcode of *A. nitida* from southern Ticino (Fig. 4), within the known range of *A. limata*. In agreement with morphology, DNA barcoding suggests minimal, but constant differences between *nitida* and *limata* in Switzerland, and divergences between the Swiss *limata* and the southern European *limata* (Fig. 4). We therefore recognize *A. limata* and *A. nitida* as distinct taxa but highlight that more research is needed to further delineate species at the European level in this group (see also Wood 2023a). In addition, we stress that the identification of some Alpine specimens is unclear; barcodes could not be obtained from these unclear specimens.

Andrena montana **Warncke, 1973**

The status of this species was confirmed by Praz et al. (2019), who provide data on its biology and distribution, and include *A. montana* in an identification key.

Andrena mucida **Kriechbaumer, 1873**

This Mediterranean species was so far only known from three specimens collected by H. Tournier and F. Chevrier, both in the Geneva region, rendering the isolated occurrence of this species near Geneva somehow doubtful, as this species in known in France only from the southern part of the country (Warncke et al. 1974). Six specimens collected on several occasions by Frey-Gessner in the Salève Region in France, just 10–20 km south of Geneva confirm the presence of this species in the Geneva region. Moreover, the species was collected by F. Amiet in St-Pierre, near Aosta in northern Italy, indicating that the Swiss records are not unique in central Europe.

Andrena nanula **Nylander, 1848**

Two records from the Bernese Alps and Geneva regions (Amiet et al. 2010) were based on a misidentified specimen and on a misinterpreted locality. This species is present in Switzerland only south of the Alps and in Graubünden.

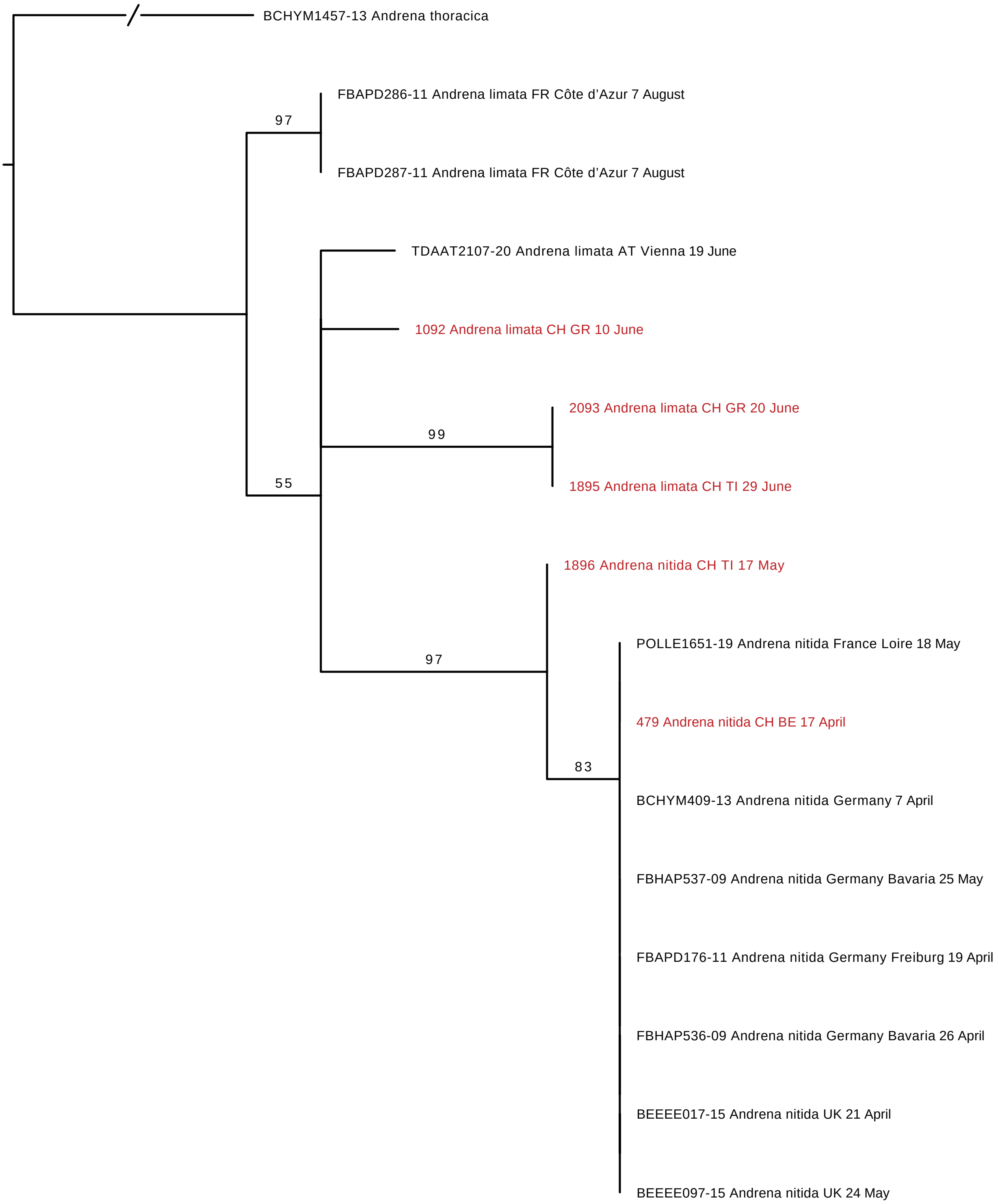


Figure 4. Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Andrena limata* and *A. nitida*. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *A. thoracica*; this branch was shortened for better graphic representation. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2); the collection day and month are also indicated.

Andrena nigroolivacea (Kirby, 1802)

This species, first observed in Switzerland in 1991, has progressively expanded its distribution in northern Switzerland, where it now occurs between Yverdon and Lake Constance.

Andrena nigrospina Thomson, 1872 and *A. pilipes* Fabricius, 1781

The status of both taxa has long remained controversial (Schmid-Egger and Patiny 1997; Gusenleitner and Schwarz 2002). Recent studies suggest that both taxa differ in their genital morphology, vestiture colour, phenology and DNA barcodes in northern Europe (Falk and Lewington 2015; Else and Edwards 2018; Wood 2023b). In Switzerland, the bivoltine taxon (*A. pilipes*) occurs in the Valais; based on the only two known occurrences in Ticino, both of which are from the month of July, the bivoltine taxon likely also occurred historically in Ticino. Four specimens from Vaud, Geneva, and the region of Basel however, are from May and June, thus unlikely to be the bivoltine taxon. Morphologically, these specimens perfectly agree with *A. nigrospina* (Falk and Lewington 2015), in particular the narrow valve and the length of the antennal segments in males, and the color of the vestiture in both sexes. Accordingly, these specimens are attributed to *A. nigrospina*, which is newly added to the Swiss fauna. The last record of *A. nigrospina* in Switzerland is from 1958. Both taxa can be identified using the keys of Falk and Lewington (2015), Else and Edwards (2018), and Wood (2023b).

Andrena nuptialis Pérez, 1902

Some doubts remain on the taxonomic status of both generations of this species (Westrich 2018). In Switzerland, this taxon is clearly bivoltine; DNA barcodes from the two generations suggest that both generations belong to the same biological species (Suppl. material 5).

Andrena ovata Schenck, 1853

This taxon was resurrected from synonymy by Praz et al (2022), who mentioned a single Swiss specimen from Ticino. Since then, seven additional specimens have been found in collections, all collected in region of Geneva around 1900. This species is included in the identification key given in Praz et al. (2022).

Andrena pauxilla Stöckhert, 1935 and *A. pusilla* Pérez, 1903

The taxonomy of the species of the subgenus *Micrandrena* is challenging, especially in the *pusilla-spreta* group of species. Recently Wood (2023a) placed *A. curtula* Pérez, 1895 in synonymy with *A. spreta* Pérez, 1895, confirmed that *A. pusilla* and *A. spreta* represent distinct taxa, and resurrected *A. pauxilla* from synonymy with *A. curtula* (or *A. spreta*) (see also Scheuchl and Schwenninger 2015). In Switzerland, *A. pusilla* is known from historical records from Ticino and the Lake Geneva region, as well as from a single recent specimen collected in Geneva (verified using a DNA barcode; Suppl. material 5), possibly representing a recent range expansion from France after local extinction. *Andrena spreta* has not been reported in Switzerland so far (the closest occurrences are in southern France in the Ardèche Departement; see Suppl. material 5).

Schmid-Egger and Scheuchl (1997) mention the presence of *A. pauxilla* in the Valais, but we were not able to examine specimens from that canton. However we found two females of *A. pauxilla* from the Geneva region (one in the collection Tournier from Peney and one in the Frey-Gessner collection from Genthod). This species is newly added to the Swiss fauna and represents another example of a species with isolated records in the Geneva region; there are confirmed records of this species in Germany, in southern France and in Spain (Wood 2023a). *Andrena pauxilla* is included in the identification key of Wood (2023a).

Andrena pellucens Pérez, 1895

This species was recently found in Ticino, probably following a range expansion from northern Italy (Bénon and Giollo 2022). One record from Geneva from the Tournier collection is considered dubious and is not accepted here, since the collection date (2.7.1876) is improbable for this autumnal species. Criteria for separating *A. pellucens* from *A. marginata* Fabricius, 1776 are indicated in Wood (2023a).

Andrena rosae Panzer, 1801

Based on the multi-locus genetic analyses of Gueuning et al. (2020), spring (*stragulata* Illiger, 1806) and summer (*rosae*) generations are treated as belonging to the same biological species.

Andrena rufula Schmiedeknecht, 1883

The two only records mentioned by Amiet et al. (2010) for Switzerland were based on misidentified specimens. This species was thus reported in Switzerland for the first time by Artmann-Graf (2017). Since then, this species has rapidly expanded its range and is now found between Vaud and the Zurich region. *Andrena rufula* is included in the identification key in Praz et al. (2019).

Andrena russula Lepeletier, 1841

Following Praz et al. (2022), *A. similis* Smith, 1847 is treated as a junior synonym of *A. russula*.

Andrena scotica Perkins, 1916

Following Wood et al. (2022), the univoltine taxon so far referred to as *A. carantonica* Pérez, 1902 is referred to as *A. scotica*; *Andrena carantonica* is treated as a nomen dubium. By contrast, Scheuchl et al. (2023) advocated for the continued use of *A. carantonica* for this taxon. In agreement with Wood et al. (2022), we consider that a morphological identification of the female lectotype of *A. carantonica* is not possible, and especially that both the original description (“fin juin et juillet sur les fusains (…) et surtout sur le tilleul argenté” [end of June and July on the European spindle, *Euonymus europaeus* L. and above all on the silver linden, *Tilia tomentosa* Moench]) and the manuscript catalogue to Pérez's collection (available at https://science.mnhn.fr/catalogue/ey-bib-perez1/) ("la femelle très commune dans la première quinzaine de juillet 1900, sur le *Tilia argentea*, (…) sur les fusains (…). Recueille le pollen de la ronce" [female very common during the first half of July 1900, on *Tilia argentea*, (…) on European spindels (…). Collect pollen from *Rubus*] refer with high likelihood to the summer brood of the taxon known as *Andrena trimmerana*.

Andrena taraxaci Giraud, 1861

With the possible exception of *A. stabiana* Morice, 1899 (see below), only one species of the *taraxaci*-group occurs in southern Switzerland. We do not know whether *A. pastellensis* Schwenninger, 2007 and *A. taraxaci* represent distinct species, and pending further investigation we continue to refer to this taxon as *A. taraxaci*. Following Schwenninger (2007), we consider the record from the Luzern region (see Amiet et al. 2010) as being based on mislabeled specimens.

Andrena tenuistriata Pérez, 1895

Two males were recently found in the Geneva region (one male has been barcoded; Suppl. material 5), probably following range expansion from France. This species is included in the key in Wood (2023a).

Andrena tscheki Morawitz, 1872

This species is known in Switzerland from a single male collected in Ticino by Frey-Gessner. Since Frey-Gessner's collection is reliable and given that the species is known from northern Italy (Gusentleitner and Schwarz 2002), this record is accepted.

Andrena trimmerana (Kirby, 1802)

Based on the multi-locus genetic analyses of Gueuning et al. (2020), spring (*spinigera* (Kirby, 1802)) and summer (*trimmerana*) generations are treated as belonging to the same species. This taxon is currently undergoing expansion in western and northern Switzerland, where it is now regularly found along the Jura and in the Plateau.

Anthidium florentinum (Fabricius, 1775)

This species was first reported in the Lugano region in Ticino in 2006 (Kouakou et al. 2008). Since then, the species has expanded its range in Ticino and the Mesolcina valley.

Anthidium loti Perris, 1852

This species was considered extinct by Amiet (1994). It was recently reported from southern Ticino, presumably following range expansion from northern Italy.

Anthophora canescens Brullé, 1832

This species is known from a single female collected in Genthod by Frey-Gessner. This record is specifically mentioned in Frey-Gessner's book. Since Frey-Gessner's collection is reliable, this record is accepted, even if this occurrence represents the only record of this species in central Europe.

Apis mellifera Linnaeus, 1758

Although this species is treated as an indigenous species, info fauna does not keep a database for *Apis mellifera* because: i. its presence is nowadays nearly entirely dependent upon apicultural activities and ii. hypothetical free-living populations are almost certainly strongly impacted by and intermixed with populations from apiaries (Parejo et al. 2020; Kohl et al. 2022).

Bombus distinguendus Morawitz, 1869

After several decades without observation in Switzerland, the species was recently found in the western Jura mountain range (Bénon et al. 2020). Given that it has been observed in the French Jura (e.g., Prost et al. 1987; Gilles Mahé, pers. comm., 2020), it is possible that this species was constantly present in the region, although at very low densities, but has remained undetected in the Swiss Jura between 1958 and 2019.

Bombus inexspectatus (Tkalců, 1963)

This species, which was known in Switzerland from Ticino and Graubünden, was recently found in the Valais (Simplon region) in 2017.

Bombus jonellus (Kirby, 1802)

This species was recently found in three localities of the Swiss Jura; it is likely that the species has been overlooked in that region until now.

Bombus magnus Vogt, 1911

A single female of this species has been collected in Switzerland (Auvernier NE, 1933, leg. de Beaumont; see Amiet et al. 2017). De Beaumont's collection is reliable, and the identity of the specimen has been verified using a DNA barcode (Suppl. material 5). Given that populations of this species have been recorded not far from Switzerland in France and Germany, we see no reason to question the validity of this record. It is probable that the vast, Ericaceae-rich peatbogs that once covered entire valleys in the Jura hosted populations of this species.

Bombus pascuorum (Scopoli, 1763)

South of the Alps, the female pilosity of *B. pascuorum* is bright red-orange on the mesosoma and metasoma, while in other regions of Switzerland it is brown-orange intermixed with more or less black hairs on the mesosoma and on the terga. These geographic differences are rather striking, leading Amiet et al. (2017) to consider two subspecies to be present in Switzerland, *B. pascuorum pascuorum* south of the Alps and *B. pascuorum floralis* (Gmelin, 1790) in the rest of the country. For practical reasons, segregating two distinct subspecies is difficult, as transitional populations are known, e.g., in the Simplon region in the Valais. There is also substantial geographic variation north of the Alps; for example, some specimens of the Geneva region have no black hairs on the mesonotum, building a transition to the southern French populations. We see no advantage of recognizing subspecies for this species, and all specimens are lumped under a single taxon, *Bombus pascuorum*, in the Swiss database.

Bombus ruderatus **(Fabricius, 1775)**

This species has expanded its range in Switzerland after 2000. It is now widely distributed in the Swiss Plateau and was recorded for the first time in Graubünden in 2013. One worker (identification verified using DNA barcode; Suppl. material 5) was also collected in the Valais, suggesting that the species might currently be expanding its distribution in a region historically occupied only by *B. argillaceus* (Scopoli, 1763). Both taxa have however so far probably maintained non-overlapping distributions in Switzerland, since *B. argillaceus* has not been observed in the western parts of the Valais recently. The distance between the locality in the Valais where *B. ruderatus* has been observed, and the closest known population of *B. argillaceus* is only 20 km. Future research is needed to track the evolution of the distribution of both taxa in the Valais.

Ceratina nigrolabiata **Friese, 1896**

New record for Switzerland; two specimens were recently collected in Ticino, suggesting range expansion from Italy.

Chelostoma foveolatum **(Morawitz, 1868)**

Numerous recent records in the Valais (region of Martigny) and Vaud (region of Aigle) suggest a recent expansion or introduction. It is unlikely, though not impossible, that this species has so far remained undetected in this intensively sampled region.

Coelioxys conicus **(Linnaeus, 1758)**

This species is often referred to as *Coelioxys quadridentata* (Linnaeus, 1758) or *Coelioxys quadridentatus*. The case is similar to that of *Osmia bicornis* (Linnaeus, 1758) and *O. rufa* (Linnaeus, 1758), with both synonyms having been described in the same publication. For both cases, Kirby (1802), the first reviser, decided to use *Coelioxys conicus* and *Osmia bicornis*, respectively. By contrast, Dalla Torre (1896) selected the other name, presumably because of the so-called principle of page precedence, which is, however, not a valid argument (see Day 1979). As in the case of *Osmia bicornis*, we propose to maintain *Coelioxys conicus* as the valid name for this taxon (see also Scheuchl et al. 2023).

Coelioxys emarginatus **Förster, 1853**

This species is known in Switzerland from a single female collected in Genthod by Frey-Gessner. Since Frey-Gessner's collection is reliable, this record is accepted here, even if it represents the only record in central Europe.

Epeolus alpinus **Friese, 1893**

One female of this species supposedly collected in Genthod (a locality near Geneva) by Frey-Gessner is preserved in the Geneva Natural History Museum. Unlike most other records from Frey-Gessner, the locality label is not original but has been recopied (Suppl. material 1: fig. S1C), and there is no date. Given that the known hosts of *E. alpinus* have never been recorded from Genthod or the Geneva region, we exclude this record. In Switzerland, this species is restricted to the Alps.

Epeolus fallax **Morawitz, 1872**

New record for Switzerland; this cuckoo bee associated with *Colletes hederae* Schmidt & Westrich, 1993 was observed once in Switzerland in the canton Basel Landschaft (G. Artmann-Graf, pers. comm.).

Epeolus cruciger **(Panzer, 1799)**

Until 10 years ago, this species was very rare in Switzerland, where it was restricted to the southern parts of the country. Following the explosive spread of one of its hosts, *Colletes hederae*, it currently shows a fast range expansion towards northern Switzerland.

Eucera interrupta **Baer, 1850**

New isolated records in Ticino and in the Rhine Valley in eastern Switzerland suggest a possible recent range expansion of this species, as has recently been observed in southwestern Germany (Burger and Reder 2018).

Eucera nigrifacies **Lepeletier, 1841**

New record for Switzerland; this species was first recorded in Ticino in 2017 and one specimen was found in the Geneva region in 2021. These two records suggest a recent northwards expansion of this southern European species.

Eucera pollinosa **Smith, 1854**

This species, previously considered to be extinct in Switzerland (Amiet 1994), was found in several localities in Ticino and in the Mesolcina valley (Graubünden) in 2020 and 2021, suggesting recent range expansion, as has recently been observed in Austria (Pachinger et al. 2019).

***Halictus confusus* Smith, 1853**

Two subspecies are recognized in central Europe: *Halictus confusus alpinus* Smith, 1853 and *H. confusus perkinsi* Blüthgen, 1926. In Switzerland, the former is present in most of the country (Alps, southern Switzerland and Swiss Plateau), while the latter is likely restricted to the north of the country, along the Rhine River between Basel and Schaffhausen (Amiet et al. 2001). The two taxa are difficult to separate, especially in the female sex (Ebmer 1969, 1988); moreover, they display transitional populations (Ebmer 1988), rendering their recognition as distinct taxonomic units complicated at the scale of a region that includes the contact zone. While we acknowledge that it may make sense to continue to recognize these two subspecies at the European scale, for example to highlight incipient speciation or the presence of possible cryptic species, their recognition in the Swiss database would be problematic given that most records are not identified to subspecific rank. The subspecies could simply be delimited based on geography, but we see no benefit of such an approach for conservation, at least as long as these two taxa are treated as conspecific.

***Halictus eurygnathus* Blüthgen, 1931**

This species is sometimes referred to as *Halictus compressus* (Walckenaer, 1802) (Pesenko 1985, 2004; Ghisbain et al. 2023). This case is complicated and, in our opinion, not yet resolved in a satisfactory manner. The name *Halictus compressus* was originally proposed as a *nomen novum* for the preoccupied taxon *Apis flavipes* Panzer, 1798. Another replacement name for the same taxon is *Hylaeus tomentosus* Herrich-Schäffer, 1840, which is the type species of *Monilapis* Cockerell, 1931. To settle the identity of *Monilapis*, Pesenko (1985) designated a neotype for *Apis flavipes* Panzer, 1798, selecting a male of the taxon known as *H. eurygnathus*. Most subsequent authors have not followed Pesenko's neotype designation (e.g., Ebmer 1988; Schwarz et al. 1996), arguing that *Apis flavipes* Panzer, 1798 is a *nomen dubium*, a view advocated recently by Scheuchl et al. (2023). While we agree that similarly resurrected names for unclear taxa should not be accepted (e.g., *Apis sabulosa* Scopoli, 1763 for *Andrena scotica*; see Wood et al. 2022; or *Apis ocreata* Christ, 1791 for *Andrena russula*; see Praz et al. 2022), the situation of *Halictus compressus* is different given the need to settle the identity of the type species of *Monilapis* for taxonomic stability, just as was done by Michener (1997) for the type species of *Tetralonia* (see comments below under *Tetralonia malvae*). In these two cases, the designation of a neotype and the resurrection of an old name may exceptionnally be necessary for taxonomic stability. Awaiting further opinion on the matter, we continue to use the name *Halictus eurygnathus*.

Historically known only from the Alps, the region of Geneva and isolated records along the Jura and in the Swiss Plateau, *H. eurygnathus* has recently markedly expanded its range in northern Switzerland, where it is now regularly found along the Jura mountain range.

***Halictus fulvipes* (Klug, 1817)**

This southern European species has not been reported from Switzerland before (Amiet et al. 2001). A. Ebmer (pers. comm.) has examined a series of females collected in July 1954 in Brissago (Ticino), deposited in the Stockholm Natural History Museum. This occurrence is coherent with the distribution of this species in Europe (A. Ebmer, pers. comm.), and therefore this species is newly added to the Swiss fauna.

***Halictus seladonius* (Fabricius, 1794)**

This species so far known only in the Valais has recently been recorded from southern Ticino, probably following range expansion from northern Italy.

***Halictus submediterraneus* (Pauly, 2015)**

Pauly et al. (2015) investigated the *Halictus smaragdulus*-complex and concluded that several distinct species were present in Europe; only males can be identified with confidence using morphology. All the males that we examined from Switzerland belong to *H. submediterraneus*; as far as is known, other taxa of this group, such as *H. smaragdulus* Vachal, 1895, do not occur in Switzerland.

***Halictus tectus* Radoszkowski, 1875**

This species is sometimes treated as conspecific with *Halictus vestitus* Lepeletier, 1841 (Ghisbain et al. 2023; Reverté et al. in press; as *Seladonia vestita*). We follow Ebmer (1975, 1988) and treat *H. tectus* and *H. vestitus* as distinct taxa.

***Heriades rubicola* Pérez, 1890**

Historically only know from a single specimen from Sierre, this species was recently found in Ticino and in the Basel region, probably following range expansion, as reported elsewhere in Europe (Cross and Notton 2017; Saure and Wagner 2018). In both regions, the species was observed at several sites (Ticino) or during two different years (Basel), suggesting that populations are now established and reproducing.

***Hoplitis stecki* (Frey-Gessner, 1908)**

This species was resurrected from synonymy with *H. mucida* (Dours, 1873) by Müller et al. (2017).

***Hylaeus cardioscapus* Cockerell, 1924**

New record for Switzerland; this species was found in one site in Graubünden in 2020 and in 2021. Given that it is inconspicuous and belongs to a poorly sampled bee genus, it is difficult to know whether it has expanded its range recently, or whether it has always been present but remained undetected. *Hylaeus cardioscapus* is included in the identification key of Dathe et al. (2016).

Hylaeus confusus Nylander, 1852, *H. gibbus* Saunders, 1850 and *H. incongruus* Förster, 1871

These three taxa have only recently been separated based on morphology (Straka and Bogusch 2011; Dathe et al. 2016). They have distinct DNA barcodes in central Europe (Schmidt et al. 2015). When the Swiss database was assembled for the genus *Hylaeus* (Amiet et al. 1999, 2014), *Hylaeus incongruus* was not recognized as a distinct species. One of us (RN) thus revised the entire available material of this group in Swiss collections and recognized three species, using the morphological criteria of Straka and Bogush (2011); morphologically unclear specimens were recorded as the *Hylaeus gibbus*-aggregate. We sequenced 58 specimens and obtained 55 usable DNA barcodes for these three species (Suppl. material 5). Of these 55 specimens, two were identified as the *Hylaeus gibbus*-aggregate based on morphology (meaning that the morphological criteria were unclear or inconsistent) and turned out to belong to *H. confusus* based on their DNA barcodes. The remaining 53 specimens were identified as *H. confusus* (38 specimens), *H. gibbus* (11) and *H. incongruus* (4) based on morphology. Assuming that the DNA barcodes provide correct identification, all specimens of *H. confusus* and *H. incongruus* were correctly identified; three specimens identified as *H. gibbus* turned out to belong to *H. incongruus*. We conclude that a morphological separation of these three species is mostly possible based on morphology, although a separation of *H. gibbus* and *H. incongruus* is sometimes difficult; based on our limited dataset, we estimate the identification error rate between these two species to be approximately 20% (3 specimens out of 15). Based on all specimens identified using morphology (which may thus include identification errors) the following patterns can be observed in Switzerland: *Hylaeus confusus* is by far the most common species (2556 occurrences), followed by *H. gibbus* (572 occurrences) and *H. incongruus* (239 occurrences). The three species are present in all biogeographic regions of Switzerland, although *H. gibbus* appears restricted to low-elevations, warm areas and is absent or rare at high elevations and along the northern flank of the Alps, unlike the other two species.

Hylaeus euryscapus Förster, 1871

This species is known from five males collected in Peney between 1874 and 1885 (collection Tournier). Although this record is somehow isolated in central Europe, and although the species is not known in France near Geneva, the fact that the species was collected on five different occasions lead us to accept this record as valid. There are numerous other species with records near Geneva but no nearby record in France (see for example comments under *Andrena mucida*).

Hylaeus glacialis Morawitz, 1872

Amiet et al. (2014) mention the presence of two morphological forms in Switzerland; these two forms could not be analyzed using DNA barcodes due to the rarity of this species in Switzerland. Future work is urgently needed to examine the taxonomic status of these two forms, which may represent cryptic, endangered species.

Hylaeus intermedius Förster, 1871

Dathe et al. (2016) resurrected *H. intermedius* from synonymy with *H. gredleri* Förster, 1871. Based on their identification key and on pictures of the type specimens of *H. intermedius* and *H. imparilis*, the Swiss specimens hitherto referred to as *H. imparilis* Förster, 1871 (Amiet et al. 2014) appear to belong to *H. intermedius*. *Hylaeus imparilis* is probably a distinct species widely distributed in southern Europe but so far not found in Switzerland (R. Le Divelec, C. Praz, S. Schoder, in prep.). We have identified and sequenced specimens of *H. imparilis* from northern Italy (Aosta, St-Pierre) and from Ardèche, France (Suppl. material 5). *Hylaeus intermedius*, which was hitherto known only from south of the Alps in Switzerland, has recently been observed at several sites near Geneva, suggesting a recent range expansion.

Hylaeus kahri Förster, 1871

This species forms two BINs in Switzerland. One BIN (BOLD:AAN3379) is distributed in the northern parts of the country (Basel), in the Valais, as well as in the Aosta Valley in northern Italy. Outside of Switzerland, sequences are available from Belgium, France, Germany and Spain. The second BIN (BOLD:AAN3379) is distributed only in Ticino and Graubünden (Mesolcina), south of the Alps. Outside of Switzerland, sequences are available from Italy and Austria, as well as some slightly divergent sequences from Greece. Based on sequences available on BOLD (Schmidt et al. 2015; Schoder 2018), the two BINs are found in near sympatry in the Aosta Valley and in Austria. The average genetic distance between these two BINs in Switzerland is 4.38% (range 3.51–5.40). Morphologically, specimens from these two BINs are identical and treated as conspecific for now (R. Le Divelec, C. Praz, S. Schoder, in prep.).

Hylaeus moricei Friese, 1898

This species is sometimes referred to as *Hylaeus nigrifascies* (Bramson, 1879), a dubious name that was resurrected by Warncke (1972a, 1986). Dathe (1980) and Scheuchl et al. (2023) did not follow Warncke's view and maintained *Hylaeus moricei*. The matter is complicated by the fact that this taxon may actually be a complex of several closely related, cryptic species (Ghisbain et al. 2023), and if the taxon were to be split, the name that would eventually apply to central European populations is not yet clear (Ghisbain et al. 2023). For this reason, we prefer to continue to use the name *H. moricei* in the present checklist awaiting further taxonomic work on this group.

Hylaeus pictipes **Nylander, 1852 and *H. taeniolatus* Förster, 1871**

The females of these two taxa are difficult to identify, although the criteria of Doczkal and Schmid-Egger (1992) mostly allow for an unambiguous identification if comparative material is used (Müller 2023). In the database, the females have been treated as a species aggregate until recently.

Lasioglossum alpigenum **(Dalla Torre, 1877), *L. bavaricum* (Blüthgen, 1930) and *L. cupromicans* (Pérez, 1903)**

These three closely related species are treated as distinct following the clear morphological differences observed in the males (Ebmer 1988; Amiet et al. 2001), as well as the multi-locus genetic results of Gueuning et al. (2020). The females of *L. bavaricum* and *L. alpigenum* have not been separated in the database and are attributed to the *L. alpigenum/bavaricum*-aggregate. In some cases, the female of *L. cupromicans* are also difficult to separate from these two species. DNA barcodes can be used to discriminate *L. alpigenum* from the other two species (Suppl. material 5), which share DNA barcodes in Switzerland (Gueuning et al. 2020). Consequently, the combination of DNA barcodes and morphology mostly allows for a separation of the females of these three species.

Lasioglossum angusticeps **(Perkins, 1895)**

This species was considered to be extinct in Switzerland (Amiet 1994; Amiet et al. 2001), but has since then been observed in the Geneva and Aarau regions, probably following range expansions from France and Germany, respectively. Based on limited available material to us (Suppl. material 5), the females are difficult to separate from those of *L. punctatissimum* (Schenck, 1853) with certainty; since only the latter species is widely distributed in Switzerland, a species aggregate has not been defined for these two species. Some records of *L. punctatissimum* in the area where *L. angusticeps* occurs may refer to that species.

Lasioglossum fratellum **(Pérez, 1903) and *L. subfulvicorne* (Blüthgen, 1934)**

The females of these two species have not been separated in the Swiss dataset; they constitute the *L. fratellum-subfulvicorne*-aggregate. Males are however straightforward to tell apart. We barcoded 32 specimens of these two species (Suppl. material 5), of which two males of *L. subfulvicorne*. Although these two males appeared in one distinct clade, which could represent *L. subfulvicorne*, the rest of the specimens (presumably *L. fratellum*) formed a paraphyletic assemblage, and a clear separation of both taxa was not obvious. Future work is needed and additional males of these two species should be sequenced to examine whether DNA barcodes are diagnostic, as previously suggested based on a limited number of specimens (Schmidt et al. 2015).

Lasioglossum medinai **(Vachal, 1895)**

This species has only recently been separated from *L. villosulum* (Kirby, 1802) (Pauly et al. 2019), although the presence of a cryptic taxon in this group has long been suggested (Packer et al. 1999). We have examined three females perfectly corresponding to the morphological criteria listed by Pauly et al. (2019) for *L. medinai*; two of these females were barcoded and were genetically similar to sequenced individuals of *L. medinai* (Pauly et al. 2019; Suppl. material 5). These limited results bring support for the validity of *L. medinai* and confirm its presence in Switzerland. The wide geographic distance between both occurrences of *L. medinai* in Switzerland and the occurrence of this species in ordinary habitats in the agricultural area, suggest that the species is probably more widely distributed than hitherto known in Switzerland.

Lasioglossum monstrificum **(Morawitz, 1891)**

Following Scheuchl and Willner (2016), we treat *Lasioglossum sabulosum* Warncke, 1986 as a junior synonym of *L. monstrificum*.

Lasioglossum tarsatum **(Schenck, 1868)**

This species was newly found in the Valais near Sierre; the identification of the specimens underlying this record has been verified using DNA barcodes (Suppl. material 5).

Lithurgus chrysurus **Fonscolombe, 1834**

This species was recently observed in the Geneva region, probably following range expansion from nearby France. It was known before only from Ticino.

Megachile argentata **(Fabricius, 1793)**

Following Praz and Bénon (2023), *Megachile pilidens* Alfken, 1924 is treated as a junior synonym of *Megachile argentata*.

Megachile genalis **Morawitz, 1880**

Previously known from a single specimen from the Engadin, this species has recently been found in the Regional Nature Park Ela in Graubünden. The species is also known in the French Jura, where it has been observed close to the border with Switzerland near Les Rousses (D. Genoud, pers. comm.) or near Pontarlier (C. Praz, pers. observation).

Megachile sculpturalis Smith, 1853

This Asian species was first reported in Switzerland in 2010, and since then has colonized all biogeographic regions in Switzerland.

Nomada alboguttata Herrich-Schäffer, 1839

Nomada alboguttata has long been suggested to represent a complex of several species (Amiet et al. 2007; Sann et al. 2010). A recent study based on multiple nuclear markers confirms that two distinct species co-occur in Switzerland, one associated with *Andrena ventralis* Imhoff, 1832 and mostly flying in April (form A) and one associated with *A. barbilabris* (Kirby, 1802) and flying in May and June (form B) (Mignot 2020). The Swiss material has not been revised and is thus so far treated as a single species in the database. Taxonomic research is also needed to determine to which taxon the available species names can be applied.

Nomada bluethgeni Stöckhert, 1943

This species is known from a single female collected in Peney by Tournier. Since *Lasioglossum marginellum* Schenck, 1853, the only known host of this species has been collected repeatedly in the Geneva area, and based on the distribution of *N. bluethgeni* in Europe (southern France, Germany), the Swiss record is considered plausible and is accepted.

Nomada confinis Schmiedeknecht, 1882

A single male of this species has been collected near Sierre in 1951 by M. Schwarz. There are no doubts on the origin of this specimen and this record is considered to be valid.

Nomada discrepans Schmiedeknecht, 1882

Most records of this species indicated by Amiet et al. (2007) were based on misidentified specimens of *N. flavoguttata* (Kirby, 1802). Verified records of *N. discrepans* in Switzerland are restricted to a few correctly identified specimens from the Geneva region around 1900. *Nomada discrepans* is another example of a southern European species for which ancient records near Geneva represent the only central European records.

Nomada fulvicornis Fabricius, 1793 and *N. meridionalis* Schmiedeknecht, 1882

The status of these two forms remains controversial. Doczkal and Schmid-Egger (1992) mention that *N. meridionalis* occurs in sympatry with *N. fulvicornis* and list numerous morphological criteria to separate both taxa. However, as indicated by Falk and Lewington (2015), the two generations of *N. fulvicornis* in England show conspicuous morphological differences, corresponding to the differences mentioned by Doczkal and Schmid-Egger (1992) to separate *N. meridionalis* and *N. fulvicornis*. Since all records of "*N. meridionalis*" in Doczkal and Schmid-Egger (1992) are from the summer, it is unclear whether the differences that they mention point to specific differences or to intergenerational variation. The host of the bivoltine *N. fulvicornis* in England is *A. bimaculata*, while the mostly univoltine form found in northern and central Europe is associated with the closely related, univoltine *A. tibialis*. Doczkal and Schmid-Egger (1992) mention that "*N. meridionalis*" is associated with *A. carbonaria* auct. (probably *A. pilipes* given the collection dates indicated) in Germany; Falk and Lewington (2015) report subtle morphological differences between populations of *N. fulvicornis* parasitizing *A. bimaculata* and those associated with *A. pilipes*. Based on DNA barcoding results, Schmidt et al. (2015) indicated that several BINs were present in Germany and in central Europe, one of them (represented by one specimen from Slovakia) corresponding to *N. meridionalis*.

In northern Switzerland, nearly all records of *N. fulvicornis* are from the spring and are most probably associated with *A. tibialis*, given that neither *A. pilipes* nor *A. bimaculata* is currently present in this region. In Ticino, there are spring and summer records of *N. fulvicornis*; the summer specimens are morphologically strongly divergent from the spring specimens, in agreement with the characters mentioned by Falk and Lewington (2015). DNA barcodes from specimens from northern Switzerland and from Ticino suggest some divergences; both spring and summer specimens from Ticino were identical to one another, and also very similar to the specimen of "*N. meridionalis*" sequenced by Schmidt et al. (2015). The phylogenetic tree (Fig. 5) suggests a clade of specimens from Finland and Germany collected in late spring/early summer (possibly *N. subcornuta* (Kirby, 1802); see below), then a clade (or cluster) or specimens collected in the spring from Germany and Switzerland, then a clade of specimens collected in the summer as well as one specimen from Ticino collected in April. This last clade possibly refers to "*Nomada meridionalis*", even if it includes one specimen collected in the spring. Additional work is needed to determine: i. whether the differences in morphology mentioned by Doczkal and Schmid-Egger (1992) are due to intergenerational differences and ii. whether the univoltine (spring for one clade in *N. fulvicornis* and late spring/early summer for *N. subcornuta*) and bivoltine forms represent distinct species and whether they co-exist in sympatry; adding nuclear genetic data to the limited mitochondrial DNA barcode marker would be important.

One female from the Sierre region (Valais), collected in 20.07.1951 is morphologically identical to the summer form occurring in Ticino. This specimen was collected in a site where the bivoltine *A. pilipes* is present and was historically abundant (*A. bimaculata* is also present,

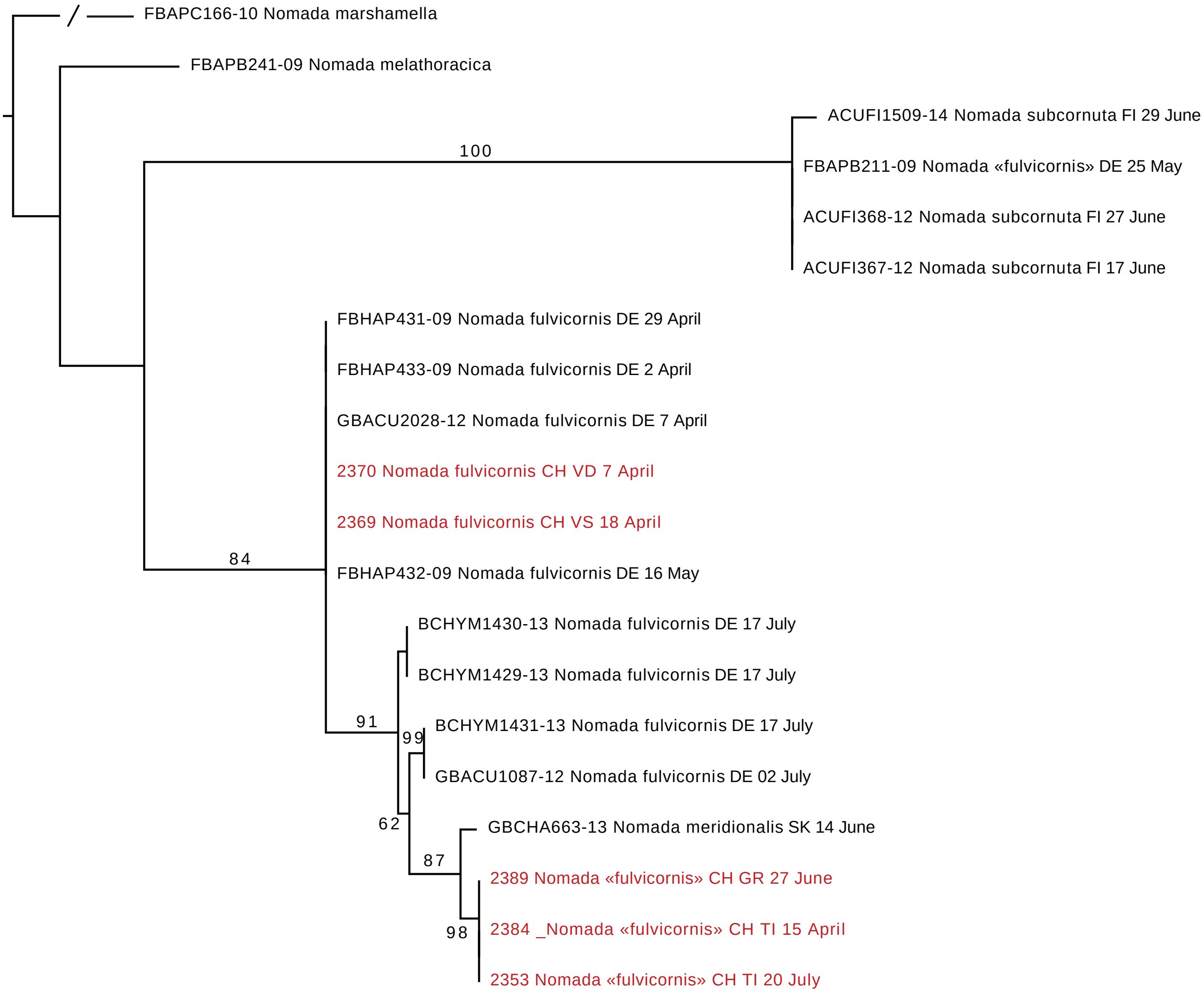


Figure 5. Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Nomada fulvicornis* and closely related species. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Nomada marshamella*; this branch was shortened for better graphic representation. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2); the collection day and month are also indicated.

although it is rare and has only been collected once in the Sierre region; *A. fuscosa* Erichson, 1835 was also present in this site until 1973). A DNA analysis has not been performed on this old specimen. The sampling location is very close to one sequenced specimen of *N. fulvicornis* collected in the spring (number 2369 on Fig. 5). This finding possibly points to the sympatric occurrence (at least historically) of these two forms, one associated with *A. tibialis* and the other potentially with *A. pilipes*. Whether the form associated with *A. pilipes* is bivoltine, remains unknown. Given the uncertainties in the taxonomic status of "*N. meridionalis*", this taxon is so far not recognized in Switzerland.

Nomada subcornuta, a form associated with the univoltine species *A. nigrospina* and *A. agilissima* (Scopoli, 1770), both of which are or were present in Switzerland, has recently been recognized as distinct (Falk and Lewington 2015). In Switzerland, there are some historical records (so far identified as "*N. fulvicornis*" in the database) from the month of June in sites where *A. nigrospina* was present near Lausanne; these records may well belong to *N. subcornuta* and should be further investigated. Awaiting additional results, *N. subcornuta* is not currently considered to be present in Switzerland.

Nomada goodeniana (Kirby, 1802) and *N. succincta* Panzer, 1798

These two taxa mostly differ in their color pattern, which is variable geographically. In addition, DNA barcodes cannot always unambiguously separate these two species in Europe (Schmidt et al. 2015; Creedy et al. 2020). However, recent genetic and morphology analyses demonstrate that these two taxa are distinct in Germany and Switzerland (Diestelhorst and Lunau 2008; Gueuning et al. 2020), in agreement with previous analyses based on the chemical composition of mandibular gland volatiles and phenology (Kuhlmann 1997).

Nomada kohli **Schmiedeknecht, 1882**

This species is in expansion in Switzerland; it has recently been observed in several localities in northern Switzerland and in the Geneva region.

Nomada linsenmaieri **Schwarz, 1974**

We present two DNA barcodes of this species, one from a female specimen from the Valais, and one from a female specimen from Spain. The specimen from the Valais had an identical DNA barcode with *N. similis* Morawitz, 1872, but not the specimen from Spain (Fig. 6). Since the morphological identification of the Swiss specimen is not in doubt, this result suggests DNA barcode sharing (possibly following mitochondrial introgression) between *N. linsenmaieri* and *N. similis* in Switzerland, but not in Spain (Fig. 6).

Nomada mauritanica **Lepeletier, 1841**

Nomada chrysopyga Morawitz, 1872 is treated as a junior synonym of *Nomada mauritanica* (Smit 2018).

Nomada minuscula **Noskiewicz, 1930 and** ***N. sheppardana*** **(Kirby, 1802)**

The status of these two taxa remains controversial. Based on the morphological criteria of Amiet et al. (2007) and Smit (2018), we consider these two taxa to be distinct and present in Switzerland. DNA barcodes from Germany also suggested that these two taxa were distinct (Schmidt et al. 2015). In Switzerland, *N. minuscula* was until recently only know from historical records from the Geneva region and from one specimen from Ticino (1995). We examined one recently collected specimen from the Geneva region, morphologically perfectly corresponding to *N. minuscula*; the DNA barcode from that specimen, however, was identical to DNA barcodes of both *N. minuscula* and *N. sheppardana* (Fig. 7). This result suggests that unlike in Germany (Schmidt et al. 2015), these two taxa share DNA barcodes in southern Europe and in the Geneva region (Fig. 7). Further work is needed to examine whether the specimens identified as *N. sheppardana* from Germany belong to a distinct species from the Swiss and southern European specimens of *N. sheppardana*. For now, we treat *N. minuscula* and *N. sheppardana* as distinct species due to the rather clear morphological differences.

Nomada mutabilis **Morawitz, 1871**

This species was recently newly recorded from the Müstair Valley (Graubünden).

Nomada panzeri **Lepeletier, 1841**

Several distinct species are likely mixed in the *Nomada panzeri* species complex, including *Nomada glabella* auct. nec Thomson, 1870 and another, unnamed species (Falk et al. 2022). Preliminary genetic work in Switzerland suggests the presence of four distinct species in this complex (Byrde 2022). Given the uncertainties surrounding the names applying to each of these species, and awaiting additional morphological and genetic evidence, only one species is recognized so far, *Nomada panzeri*, which includes the form so far referred to as *Nomada panzeri glabella* (Amiet et al. 2007; = *Nomada glabella* auct; see Falk et al. 2022). An identification key to these forms is given in Falk et al. (2022).

Nomada roberjeotiana **Panzer, 1799 and** ***Nomada tormentillae*** **Alfken, 1901**

These two closely related forms have often been referred to as a single species, *Nomada roberjeotiana*. In Switzerland, there are some scattered and ancient (all before 1900) records of *N. roberjeotiana* (sensu stricto) from the Swiss Plateau (regions of Geneva, Basel and Zurich), as well as some Alpine records of *Nomada tormentillae*. We generated DNA barcodes from one female of *N. tormentillae* from the Alps; this specimen originates from a site where numerous specimens of *Andrena tarsata* Nylander, 1848, the presumed host of *N. tormentillae*, were observed. This DNA barcode was highly similar to northern European DNA barcodes of *N. tormentillae* (average genetic distance 0.21%, range 0.16%-0.33%), and more divergent from sequences of northern European individuals of *N. roberjeotiana* (average distance 1.11%, range 1.09–1.20%). Although the divergence between *N. roberjeotiana* and *N. tormentillae* is weak and both species are included in the same BIN (Schmidt et al. 2015), this conserved differentiation at the continental scale strongly supports the recognition of these two taxa as different species. For the separation of *N. roberjeotiana* and *N. tormentillae* see Stöckhert *in* Schmiedeknecht (1930) and Scheuchl (2000) (in the latter work, *N. tormentillae* is referred to as *N. montana* (Mocsáry, 1894)).

Nomiapis diversipes **(Latreille, 1806)**

This species was recently recorded in Ticino, presumably following range expansion from northern Italy.

Osmia latreillei **(Spinola, 1806)**

A few specimens of this species were collected by Tournier near Peney. This locality is the only central European locality for this southern European species. Given that Tournier collected several specimens on different dates, we believe that these records are correct; it is also unlikely that these records are based on temporarily introduced populations, for example due to the transport of nest-containing wood. In addition, one female was collected in Zurich in 2015; this record likely represents an accidental and temporary introduction of this species in central Europe (see also Reder (2000) for a similar, unique record in Germany).

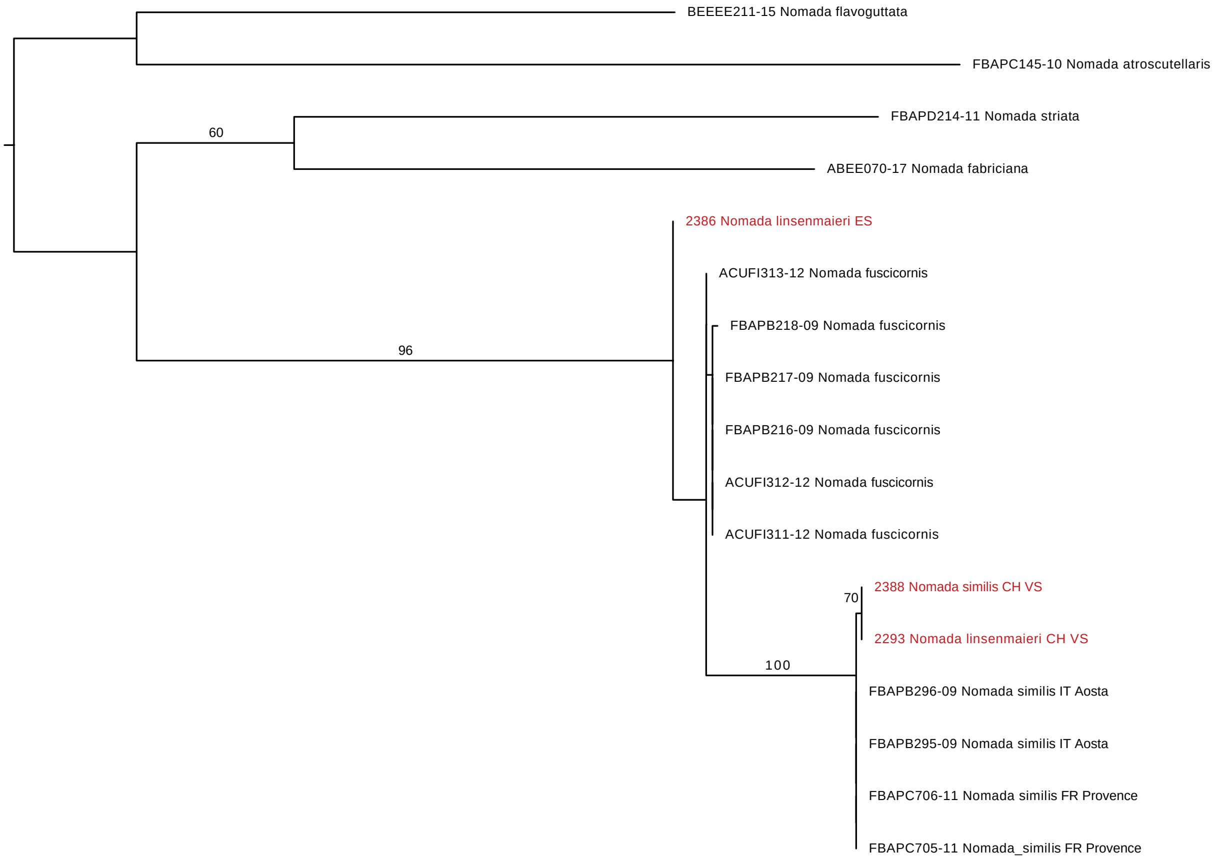


Figure 6. Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Nomada similis*, *N. linsenmaieri* and closely related species. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Nomada flavoguttata and N. atroscutellaris*. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2).

Osmia ligurica Morawitz, 1868

Osmia ligurica represents another species only collected by Tournier near Geneva. *Osmia ligurica* is present in central Europe near Aosta in northern Italy, rendering the Geneva record plausible.

Panurginus montanus Giraud, 1861 and *Panurginus sericatus* (Warncke, 1972)

The two Alpine taxa *Panurginus* (*montanus*) *sericatus* and *P.* (*montanus*) *montanus* have alternatively been recognized as subspecies or as distinct species (Warncke 1972b, Schwarz and Gusenleitner 1997; Ebmer 2001; Amiet et al. 2010). These two taxa differ in the shape of the gonostylus. In Switzerland, *P.* (*montanus*) *sericatus* is distributed in the entire Alpine bow except for its easternmost part and hardly overlaps in its distribution with *P. montanus s. str.*, which occurs in the easternmost part of Graubünden, mostly east from the Rhine River and from Chur. According to Amiet et al. (2010), the populations in the Bernina region are intermediate between both taxa, suggesting a recognition only as two subspecies of a broad *P. montanus*. However, a population of *P. montanus s. str.* was recently uncovered near Glarus, expanding the known distribution of this taxon in Switzerland. This finding leads us to treat both taxa as separate species. We interpret the deviating morphology of the populations in the Bernina region as morphological variability within *P. sericatus*, rather than a sign of transitional morphology between two subspecies. Future work is needed to examine species boundaries in this complex.

Pasites maculatus Jurine, 1807

This species was recently recorded in Ticino, presumably following range expansion from northern Italy along with its host *Nomiapis diversipes*.

Pseudoanthidium nanum (Mocsáry, 1880)

The central European taxon present in Switzerland is *Pseudoanthidium nanum*, whereas *P. scapulare* (Latreille, 1809) is a western Mediterranean species absent from Switzerland (Litman et al. 2021).

Sphecodes alternatus Smith, 1853

Two mentions from the Swiss Plateau and in Graubünden (Amiet et al. 2014) were based on misidentified specimens. In Switzerland, the species is known so far only from Ticino, as well as from historical records near Geneva.

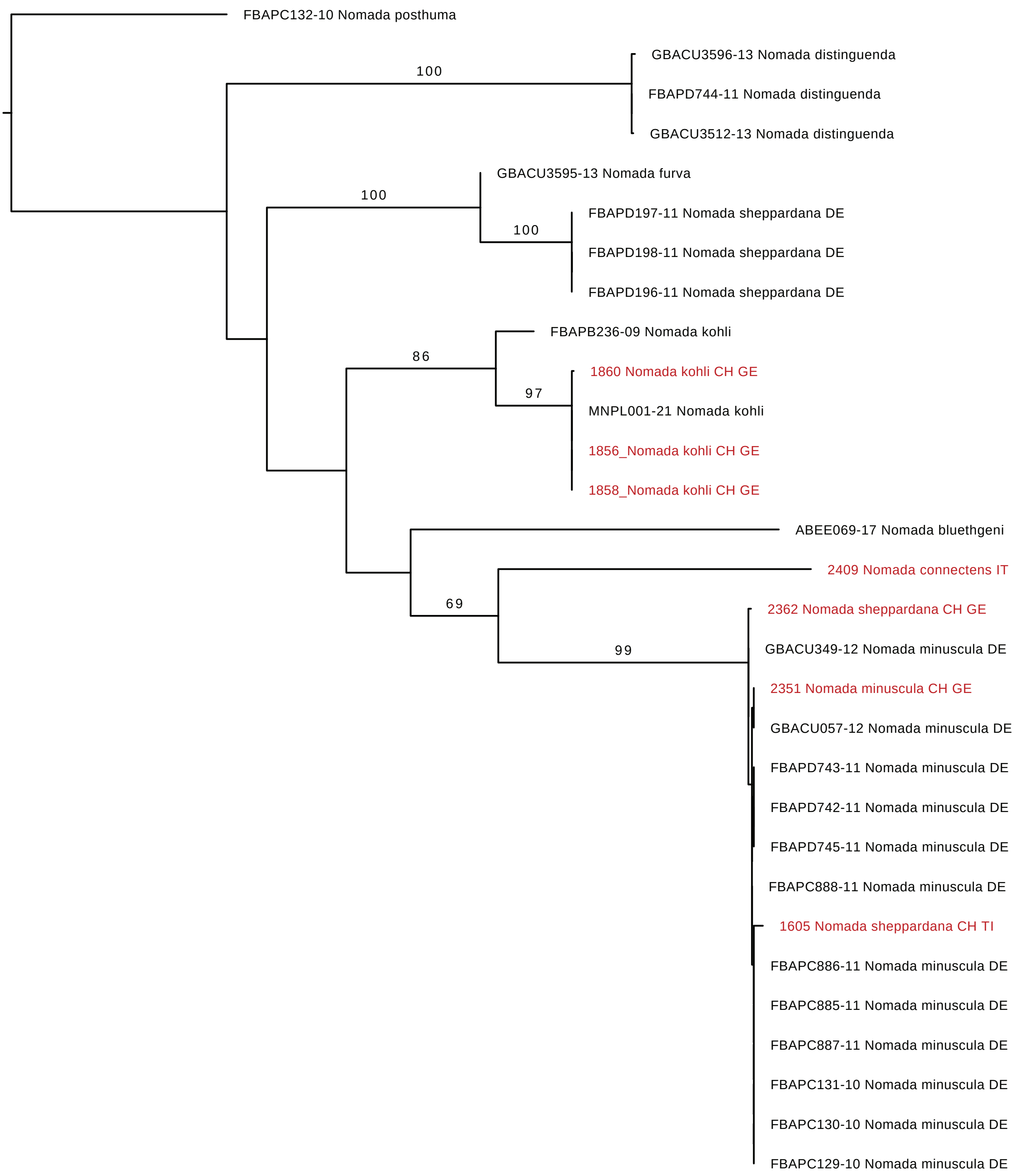


Figure 7. Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Nomada minuscula*, *N. sheppardana* and closely related species. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Nomada posthuma.* The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2).

Sphecodes crassanus Warncke, 1992

This species is known from two males from Switzerland, one collected in the Valais in 1928, another from Peney in 1884. The date of the record from Peney (5 May 1884) is dubious, but the record from the Valais originates from a reliable collection and is accepted here. The species occurs locally in northern Italy (Val d'Aosta, Val di Susa) in habitats highly similar to those found in the Valais, rendering the Swiss occurrence plausible.

Sphecodes cristatus **von Hagens, 1882**

Several mentions from the Swiss Plateau (Amiet et al. 2014) were based on misidentified specimens. In Switzerland, known occurrences of this species are restricted to historical records near Sierre (Valais) and recent records near Basel.

Sphecodes croaticus **Meyer, 1922**

This species has recently been found in the Valais, where it was probably present but undetected before (Amiet et al. 2014).

Sphecodes marginatus **von Hagens, 1882**

Most previous records (Amiet et al. 1999, 2014) were based on misidentified female specimens. Known records of this species in Switzerland are restricted to historical records (based on males) in the Geneva region.

Sphecodes zangherii **Noskiewicz, 1931**

The mention from the Geneva region (Amiet et al. 2014) was based on a misidentified specimen. The species occurs locally in the Valais and has recently been detected in Ticino.

Stelis minima **Schenck, 1861 and** ***Stelis minuta*** **Lepeletier & Audinet-Serville, 1825**

The status of these two taxa is controversial (Schmidt et al. 2015); our DNA barcoding data (Suppl. material 5) confirm that both taxa share DNA barcodes (Schmidt et al. 2015). For now, we continue to recognize them as separate species awaiting additional investigations.

Stelis simillima **Morawitz, 1876**

This species was first mentioned for Switzerland by Kouakou et al. (2008) in Ticino and has since then been reported from several sites in this canton.

Tetralonia malvae **(Rossi, 1790)**

Tetralonia macroglossa (Illiger, 1806) is treated as a synonym of *Tetralonia malvae*, following Michener (1997). By contrast, Scheuchl et al. (2023) state that the identity of *Apis malvae* Rossi, 1790 is unclear since the original description could apply to other eucerine species, for example *T. nana* (Morawitz, 1874). Regardless of the interpretation of this name, another name would have priority over *T. macroglossa* for this taxon: *Eucera antennata* Fabricius, 1793, for which a neotype was designated (Michener 1997). *Eucera antennata* is the type species of the genus *Tetralonia* and thus, in our opinion, can not simply be called a *nomen dubium* or a *nomen oblitum*, since such an approach would threaten taxonomic stability by rendering the identity of the genus *Tetralonia* unclear (see also comments under *Halictus eurygnathus*, above). The best approach to minimize nomenclatural changes would be to designate a neotype for *Apis malvae*, corresponding to the current concept of this species. Awaiting this, we keep the name *T. malvae* and treat *T. macroglossa* as a junior synonym.

This species, previously considered to be extinct in Switzerland (Amiet 1994), was observed in several sites near Geneva in 2019 and after, suggesting a recent range expansion from France after local extinction.

Tetralonia pollinosa **(Lepeletier, 1841)**

This species is known from a single specimen collected in Sierre by Frey-Gessner. Since Frey-Gessner's collection is reliable, this record is accepted (see also comments under *Amegilla salviae*).

Triepeolus tristis **(Smith, 1854)**

This species was recently observed in Ticino in association with *Tetralonia dentata* (Germar, 1839) (Bénon and Giollo 2022).

Species excluded from Switzerland

Andrena anthrisci **Blüthgen, 1925**

This species was previously treated as a native species in Switzerland (Amiet et al. 2010). Identification in this group is challenging, and the separation of *Andrena anthrisci* from *A. semilaevis* Pérez, 1903 particularly difficult (Schwenninger 2009; Wood 2023a). We present DNA barcodes for three specimens originating from Germany and identified as *A. anthrisci* by H. Schwenninger (Suppl. material 5). These specimens had identical barcodes with *A. minutuloides* Perkins, 1914. Given that the separation of these two species based on morphology is straight-forward due to the absence of a gradulus at the base of the terga in *A. anthrisci*, this result probably highlights a case of mitochondrial introgression between distinct species, *A. minutuloides* and *A. anthrisci*, in Europe. By contrast all barcoded specimens of *A. semilaevis* in Switzerland (Suppl. material 5) and Germany (Schmidt et al. 2015) had a distinct DNA barcode.

We barcoded several Alpine specimens initially identified as *A. anthrisci* using the key of Amiet et al. (2010). The female specimens had identical DNA barcodes with *A. semilaevis*; although their tergal margins were as shagreened as in *A. anthrisci*, the vestiture was longer than typically observed in that species, and we now consider these female specimens to be atypical, strongly shagreened specimens of *A. semilaevis*. The male specimens had identical DNA barcodes with *A. minutuloides*; while DNA barcodes do not allow for a separation of *A. minutuloides* and *A. anthrisci*, we consider these specimens to belong to *A. minutuloides* due to the presence of a gradulus at the base of the terga.

These identifications, as well as the identification of older specimens, which could not be analysed genetically, remain tentative. Most of us therefore prefer to exclude *A. anthrisci* from the Swiss fauna. One of us (MH) however considers *A. anthrisci* to occur in Switzerland based on specimens identified using morphology; these specimens could not be analysed genetically.

Andrena hystrix Schmiedeknecht, 1883

This species is mentioned in southern Switzerland by Stöckhert *in* Schmiedeknecht (1930). The presence of this species in Switzerland is highly possible given its wide historical distribution in France (Warncke et al. 1974). However, we exclude it from the Swiss checklist since we were not able to find specimens to back up this record.

Andrena nigriceps (Kirby, 1802)

This species was previously mentioned for Switzerland based on a single specimen collected in the Valais (Amiet et al. 2010). This specimen turned out to belong to *Andrena freygessneri* Alfken, 1904 after examination, and thus *A. nigriceps* is removed from the Swiss checklist.

Andrena stabiana Morice, 1899

Pérez (1903) described *A. emarginata* Pérez, 1903 from “Marseille, Suisse, Majorque, Sicile”; the lectotype is a male labelled “Suisse”, with no further indication on the locality. This taxon is treated as a synonym of *A. stabiana* (Gusenleitner and Schwarz 2002), a placement confirmed by Schwenninger (2007) based on the examination of the lectotype. The historical presence of *A. stabiana* in southern Switzerland is possible given the distribution of this species in northern Italy. However, given the vague locality information of the lectotytype of *A. emarginata*, this species is not included in the Swiss checklist.

Andrena ventricosa Dours, 1873

A single male of this species is preserved in the Tournier collection. It is labeled “P. [Peney], 12.07.1890”. Given that this record is based on a single male, that the date (for a fresh male specimen) is somehow unlikely (though not impossible), and that this species with a conspicuous morphology is not mentioned by Frey-Gessner (1899–1916), we exclude this species from the Swiss checklist. We stress that its historical presence in the Geneva region is, however, not impossible in the light of the European distribution of this species.

Camptopoeum friesei Mocsáry 1894

This species was mentioned as resident in Switzerland by Reverté et al. (in press), for unclear reasons.

Colletes nasutus Smith, 1853

There is only a single male of this species recorded for Switzerland (Peney, 4.6.1886, leg. & coll. Tournier). Since this record is far outside the known range of *Colletes nasutus* (closest record in Eastern Germany), this species is excluded from the Swiss fauna. We stress that its presence in Switzerland at the end of the 19th century in habitats that are now completely transformed is not impossible. However, following the general guidelines applied for this checklist, we do not include this species in the Swiss checklist.

Hylaeus lineolatus (Schenck, 1861)

This species was mentioned as resident in Switzerland by Scheuchl and Willner (2016) and by Reverté et al. (in press), for unclear reasons.

Lasioglossum sphecodimorphum (Vachal, 1892)

A single female of this species is known from Switzerland (Peney, 15.6.1884, leg. & coll. Tournier). Since this record is far outside the known range of *Lasioglossum sphecodimorphum*, this species is excluded from the Swiss checklist.

Nomada basalis Herrich-Schäffer, 1839

The only record of this species in Switzerland is based on a specimen deposited in the Tournier collection; the specimen is only labelled “Genève”, with no date, unlike most other bees collected by Tournier. Given that the collector is not specified and that only very few bees at that time were labelled with this vague locality (most bees from the Geneva region and from that time were labelled with more precise neighbourhoods or villages such as “Champel” or “Carouge”), this record is not accepted, and *Nomada basalis* is excluded from the Swiss fauna.

Nomada gribodoi Schmiedeknecht, 1882

A single record is available for this species in Switzerland, a specimen supposedly collected near Basel by W. Schmid, without further indication. Since *N. gribodoi* is unknown in Germany near Basel despite intensive collecting efforts, we consider this record as dubious and remove the species from the Swiss checklist.

Nomioides facilis Smith, 1853

This species was mentioned as resident in Switzerland by Reverté et al. (in press), for unclear reasons.

Nomioides minutissimus (Rossi, 1790)

This species was mentioned as resident in Switzerland by Scheuchl and Willner (2016), for unclear reasons.

Pseudoanthidium scapulare **(Latreille, 1809)**

This species was mentioned as resident in Switzerland by Reverté et al. (in press), probably based on confusions with *Pseudoanthidium nanum*; see under that species.

Discussion

About 2130 bee species occur in Europe (Ghisbain et al. 2023; Reverté et al. in press). Within Europe, the highest bee diversity is found in the Mediterranean countries, such as Greece, Spain and Italy hosting about 1190, 1170 and 1050 species, respectively (Reverté et al. in press). Based on the present checklist, 632 bee species (including the honeybee *Apis mellifera* and the exotic species *Megachile sculpturalis*) have been recorded for Switzerland to date, which accounts for 30% of the European bee diversity. However, almost 10% of these Swiss species are regionally extinct (Müller and Praz, in press), resulting in 575 species currently occurring in Switzerland and reducing the proportion of the Swiss bee fauna to 25% of the European fauna. The number of bee species found in Switzerland today is distinctly less than the 680 and 975 species assumed to be actually present in Austria and France, respectively, but almost identical to the 570 bee species currently occurring in Germany (Reverté et al. in press; see also Scheuchl 2023), a country that is almost nine times as large as Switzerland. Given the small size of the country, the Swiss bee fauna is remarkably rich compared to all the more northern countries of Europe including Germany.

Pattern of bee diversity in Switzerland

The remarkable richness in bee species in Switzerland can be explained by the habitat and climatic heterogeneity created by the two main mountain ranges that cross Switzerland, the Jura and especially the Alps. These two mountain ranges divide the country into several biogeographic regions (Gonseth and Sartori 2022), each characterized by strikingly different climatic conditions.

The southern flanks of the Alps are parts of the Po and Adige watersheds; these southern valleys are characterized by insubric climatic conditions with relatively mild winters and wet summers, and are densely covered with thermophilic deciduous forests such as oak (*Quercus sp.*), European hop-hornbeam (*Ostrya carpinifolia* Scop.) or chestnut (*Castanea sativa* Mill.). The southern flanks of the Alps host several remarkable bee species, such as *Tetralonia inulae* Tkalců, 1979 or *Andrena nanula,* both of which are rare in central Europe. In addition, numerous Mediterranean species reach their northern distribution limit in Ticino, for example *Andrena pellucens*, *Ceratina chalcites* Germar, 1839, *Triepeolus tristis*, *Andrena livens* Pérez, 1895 or *Nomada carnifex* Mocsáry, 1883 (the two latter are now considered extinct in Switzerland; Müller and Praz, in press).

By contrast, the northern flanks of the Alps, as well as the Jura, are characterized by high rainfall and cold winters and are mostly covered with coniferous forest that are dominated by European spruce (*Picea abies* (L.) H. Karst.) and European silver fir (*Abies alba* Mill.). These areas overall exhibit a lower species diversity, but host numerous boreo-alpine species, whose distribution becomes sparser from north to south in Europe; examples include *Osmia nigriventris* (Zetterstedt, 1838) (Müller et al. 2019), as well as *Andrena coitana* (Kirby, 1802) and its cuckoo *Nomada obtusifrons* Nylander, 1848 or *Andrena tarsata* and its cuckoo *Nomada tormentillae*. The Alps host only two strict Alpine endemics: *Osmia steinmanni* Müller, 2002 and potentially *Panurginus sericatus* (although see taxonomic notes above on the status of the latter taxon), a low proportion compared to other insect groups, such as butterflies or grasshoppers. Most alpine bee species present in the Swiss Alps also occur in other mountain ranges, e.g., in Western Europe (Pyrenees or Iberian Peninsula, e.g. *Andrena allosa*, *Bombus gerstaeckeri* Morawitz, 1881, *Bombus inexspectatus*, *Bombus mendax*, *Hylaeus glacialis*); in the Apennines or the Balkans (e.g. *Andrena amieti*, *Lasioglossum alpigenum*, *Andrena montana*); or they occur in Scandinavia (e.g. *Bombus alpinus* (Linnaeus, 1758)).

The highest peaks of the Jura mountains, mostly located in its western parts near Geneva, also host several alpine or boreo-alpine species, such as *Anthidium montanum* Morawitz, 1865, *Bombus mesomelas*, *B. mucidus*, *B. sichelii* Radoszkowski, 1859 and, historically, *B. mendax*, *B. monticola* Smith, 1849 and *B. pyrenaeus* Pérez, 1879. This part of the Jura hosts the southernmost population of *B. distinguendus* in Europe (Bénon et al. 2020), a species absent from the Alps.

The most distinctive and entomologically rich Alpine regions are the inner alpine valleys (Fig. 8), characterized by a much drier climate due to the rain shadow effect caused by the surrounding high mountains; see Steinmann (2002) for a summary of the bees associated with these inner alpine valleys, and Braun-Blanquet (1961), Delarzes et al. (2015), and Dengler et al. (2020) for a botanical description of the xeric grasslands and steppes that typically cover the south-facing slopes of these inner valleys. This rain shadow effect results in submediterranean, slightly continental climates with cold winters and dry and hot summers. Habitats in these inner alpine valleys offer isolated northern outposts in Central Europe for numerous Mediterranean species, for example *Amegilla albigena* (Lepeletier, 1841), *Anthophora mucida* Kriechbaumer, 1873, *Colletes sierrensis* Frey-Gessner, 1903, *Dasypoda argentata* Panzer, 1809, *Epeolus productulus* Bischoff, 1930, *Hoplitis praestans* (Morawitz, 1893), *Lasioglossum elegans* (Lepeletier, 1841), *Melecta festiva* Lieftinck, 1980, *Melitturga clavicornis* (Latreille, 1806), *Nomada mutabilis*, *Osmia anceyi* Pérez, 1879, *Pasites maculatus*, *Protosmia minutula* (Pérez, 1896),

Figure 8. Steppic grasslands characterizing the dry, inner Alpine valleys of Switzerland. These habitats represent important bee hot spots in Switzerland and in Central Europe. **A.** Mosaic of xeric grasslands, *Juniperus* steppe (in the background), and cultivated, extensive grassland (on the right) in Zeneggen, Valais; the yellow flower on the left is *Erysimum rhaethicum* (Hornem.) DC, the main or exclusive host plant of *Andrena probata* in Switzerland; in this 756-hectare municipality 307 species of bees have been recorded since 1943 (233 species in the last 20 years); **B.** Steppic grassland near Erschmatt, Valais; **C.** Flower-rich, extensive grassland near Scheidd, Graubünden; **D.** Steppic grassland near Ortenstein, Graubünden. Picture by Christophe Praz (**A**) and Albert Krebs (**B–D**).

Sphecodes dusmeti Blüthgen, 1924, or *Thyreus hirtus* (de Beaumont, 1940). Many of these species are also present in other alpine inner valleys in France or in Italy such as the Valle d'Aosta or the Val Venosta (Steinmann 2002), but are otherwise restricted to the Mediterranean parts of southern Europe. These inner-alpine, steppic habitats harbor 42 species which currently do not occur elsewhere in Switzerland, and host populations of species that are widely distributed, but overall rare and isolated in Europe, such as *Andrena simillima* Smith, 1851, *Lasioglossum laeve* (Kirby, 1802), *L. elegans*, and historically *Andrena assimilis*, *A. fuscosa*, *A. hypopolia* Schmiedeknecht, 1884, and *A. incisa*. Lastly, the most distinctive elements of these alpine inner valleys are some species with a strongly disjunct distribution in the Western Palearctic, i.e., *Andrena probata*, which is known only from the upper Valais, Italy, Albania, North Macedonia, Greece and Turkey, and *A. ranunculorum*, which occurs in a few isolated populations between the Pyrenees and the Caucasus including the upper Valais (Gusenleitner and Schwarz 2002). Numerous other insect species present in the upper Valais exhibit similar disjunct distributions, such as the rare butterfly *Kretania trappi* (Verity, 1927).

This increased diversity in regions harboring inner valleys with dry climates is also apparent when considering the diversity in the different cantons (Table 2 and Suppl. material 4; Fig. 9). In terms of number of species recorded after 1999, the cantons of Valais (n = 475 species) and

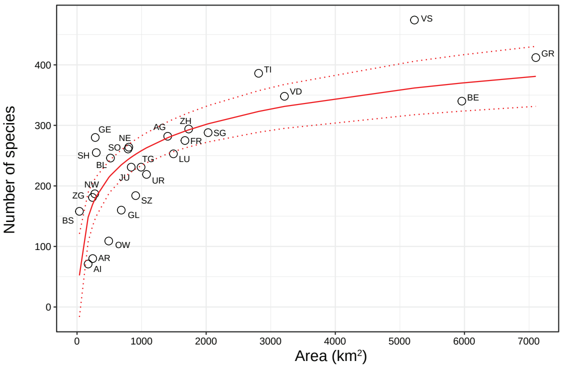


Figure 9. Relationship between the area of the 26 Swiss cantons (in km2) and the number of bee species recorded in each canton after 1999. The red line indicates a linear model between the area and the logarithm of the number of species (see text for details), the dotted lines represent the 95% confidence interval. See caption to Table 2 for the canton abbreviations.

Graubünden (413 species) rank first followed by Ticino (387 species), Vaud (348 species) and Berne (341 species) (Table 2 and Suppl. material 4). These five cantons are also the largest, suggesting that bee species diversity is largely determined by surface area. In fact, there is a significant positive relationship between the number of bee species and the area of the canton (linear model between the area and log (number of species), F=39.99, df = 24, p=<0.001, R^2=0.625; Fig. 9).

The two cantons with large dry, inner valleys (VS and GR) had substantially more species than the large canton of Bern, which is characterized by a more humid climate typical of the northern flank of the Alps (Fig. 9). Similarly, other cantons located along the northern flanks of the Alps (SZ, GL, OW, AI, AR) were also those with comparatively low species diversity (Fig. 9). Although also with a more humid climate, the Ticino canton is characterized by high species diversity; the numerous submediterranean species inhabiting the southern parts of the canton probably explain this high species richness.

The Valais and Graubünden also rank among the most bee species-rich cantons of Switzerland in terms of regional and local diversity. Nine of the ten most diverse 10×10 km^2 squares across Switzerland are located in these two cantons, comprising 237–357 species recorded after 1999, clearly indicating that these regions harbour nationwide hotspots of bee diversity (Fig. 10). These hotspots lie in the xeric inner valleys of the Valais (around Martigny and between Sion and Visp) and Graubünden (Domleschg to Chur) cantons as well as southwest of Geneva.

The inner alpine valleys of the Valais and Graubünden cantons are not only hotspots of bee diversity in Switzerland containing a large number of rare and exclusive species, but are also very rich in species on a larger geographical scale. The results of recent modelling of the taxonomic bee diversity across Europe revealed that the inner alpine valleys of Switzerland harbour particularly diverse bee communities on a continental scale (see fig. 1i in Leclercq et al. 2023), rendering them of European importance. In fact, probably the most species-rich bee fauna of central Europe was identified around Erschmatt in the Valais, where 247 bee species were recorded and 280 species statistically estimated on an area of just 2 km^2 (Oertli et al. 2005). Likewise, in the municipality of Zeneggen (Fig. 8A), with an area of just over 7 km^2, 307 species of bees have been recorded since 1943 (233 species in the last 20 years).

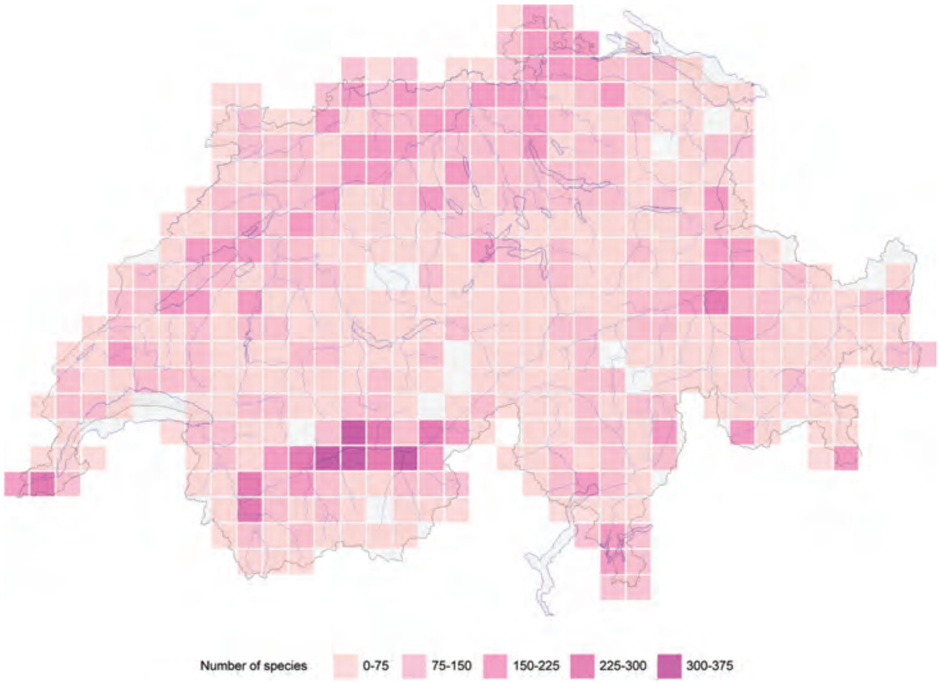


Figure 10. Map of Switzerland with a grid of 10 × 10 km; the colors reflect the number of bee species detected after 1999. The bee diversity hotspots of the Valais and Graubünden cantons are visible.

Conclusions

With 632 species ever recorded and 575 species assumed to currently occur, Switzerland hosts a remarkably rich bee fauna given the country's small size.

This high diversity is largely due to i. the pronounced topographic and climatic heterogeneity, which allows the occurrence of both highly thermophilous and strictly cold-adapted species within the country's borders, and ii. the geographic connection to Italy and France via the southern flanks of the Alps and Geneva, which act as immigration routes for species from more southern regions. The importance of these immigration routes is clearly evident from the fact that since 2000 about 20 bee species, either previously unknown for Switzerland or which had disappeared from the country for several decades, have colonized areas close to the borders of Italy and France, most likely due to climate warming (Müller and Praz, in press). Within Switzerland, the inner alpine valleys of the Valais and Graubünden cantons are hotspots of bee diversity due to the particularly diverse bee communities containing many rare and endangered species, the presence of numerous species not found elsewhere in Switzerland and the occurrence of isolated populations of species having widely disjunct distribution areas across the Western Palearctic. As the inner alpine valleys are not only of Swiss but even of European importance in terms of taxonomic bee diversity, appropriate measures must be taken to maintain and promote this exceptionally high diversity of bees.

Acknowledgements

We thank the curators of the Swiss Natural History Museums for facilitating access to their collections. Stefan Schmidt (Staatliche Naturwissenschaftliche Sammlungen Bayerns, München) kindly sent pictures of the types of *Hylaeus imparilis* and *H. intermedius*. Matthieu Aubert, Eric Dufrêne, P. Andreas Ebmer, Holger Dathe, David Genoud, Fritz Gusenleitner, Romain Le Divelec, Christian Schmid-Egger, Maximilian Schwarz, Stefan Tischendorf and Thomas Wood are thanked for providing material, for helping with the identification of some specimens and for numerous discussions on the status or distribution of some bee taxa. Laura Byrde, Laura Menoud, Maud Mignod and Cilia Schneider have helped in generating the DNA barcodes. Luna Sartori and Emmanuel Rey (info fauna, Neuchatel) are thanked for their help with Fig. 10 and Table 2, and Sofia Wyler for her help with the BOLD submission. Comments by Thomas Wood and Michael Kuhlmann substantially improved the manuscript. This study was financially supported by the Federal Office for Environment through the projects "Référentiel génétique des abeilles de Suisse", contract number 05.0039.PZ/576D0EEE8 and "Statut et conservation des abeilles sauvages de Suisse", contract number 05.0039.PZ/P071-1742; we thank Danielle Hofmann for accompanying these projects and for her support. We also warmly thank Yves Gonseth (info fauna, Neuchatel) for his continuous support.

References

Amiet F (1991) Verzeichnis der Bienen der Schweiz. Mitteilungen der naturforschenden Gesellschaft des Kantons Solothurn 35: 141–175.

Amiet F (1994) Rote Liste der gefährdeten Bienen der Schweiz. In: Duelli P (Ed.) Rote Listen der gefährdeten Tierarten in der Schweiz. Bundesamt für Umwelt, Wald und Landschaft, Bern, 38–44.

Amiet F (1996) Apidae, 1. Teil. Allgemeiner Teil, Gattungsschlüssel, die Gattungen *Apis*, *Bombus* und *Psithyrus*. Insecta Helvetica 12, SEG, Neuchâtel, 98 pp.

Amiet F, Müller A, Neumeyer R (1999) Apidae 2, *Colletes*, *Dufourea*, *Hylaeus*, *Nomia*, *Nomioides*, *Rhophitoides*, *Rophites*, *Sphecodes*, *Systropha*. Fauna Helvetica 4, CSCF & SEG, Neuchâtel, 219 pp.

Amiet F, Herrmann M, Müller A, Neumeyer R (2001) Apidae 3, *Halictus*, *Lasioglossum*. Fauna Helvetica 6, CSCF & SEG, Neuchâtel, 209 pp.

Amiet F, Herrmann M, Müller A, Neumeyer R (2004) Apidae 4, *Anthidium*, *Chelostoma*, *Coelioxys*, *Dioxys*, *Heriades*, *Lithurgus*, *Megachile*, *Osmia*, *Stelis*. Fauna Helvetica 9, CSCF & SEG, Neuchâtel, 273 pp.

Amiet F, Herrmann M, Müller A, Neumeyer R (2007) Apidae 5, *Ammobates*, *Ammobatoides*, *Anthophora*, *Biastes*, *Ceratina*, *Dasypoda*, *Epeoloides*, *Epeolus*, *Eucera*, *Macropis*, *Melecta*, *Melitta*, *Nomada*, *Pasites*, *Tetralonia*, *Thyreus*, *Xylocopa*. Fauna Helvetica 20, CSCF & SEG, Neuchâtel, 356 pp.

Amiet F, Herrmann M, Müller A, Neumeyer R (2010) Apidae 6, *Andrena*, *Melitturga*, *Panurginus*, *Panurgus*. Fauna Helvetica 26, CSCF & SEG, Neuchâtel, 316 pp.

Amiet F, Müller A, Neumeyer R (2014) Apidae 2, *Colletes*, *Dufourea*, *Hylaeus*, *Nomia*, *Nomioides*, *Rhophitoides*, *Rophites*, *Sphecodes*, *Systropha*. Deuxième édition revue et corrigée. Fauna Helvetica 4, CSCF & SEG, Neuchâtel, 239 pp.

Amiet F, Müller A, Praz C (2017) Apidae 1 – Allgemeiner Teil, Gattungen, *Apis*, *Bombus* / Partie générale, genres, *Apis*, *Bombus*. Fauna Helvetica 29, info fauna CSCF & SEG, Neuchâtel, 188 pp.

Artmann-Graf G (2017) Zwei Erstfunde von *Andrena rufula* Schmiedeknecht, 1883 in der Schweiz (Hymenoptera, Apoidea). Ampulex 9: 40–41.

Astafurova YA, Pesenko YA (2006) Bees of the subfamily Nominae (Hymenoptera: Halictidae) in Russia and adjacent countries: An annotated list. Entomological Review 86: 74–84. https://doi.org/10.1134/S0013873806010040

Baker D (2002) On palaearctic and oriental species of the genera *Pseudapis* W.F. Kirby, 1900, and *Nomiapis* Cockerell, 1919. Beiträge zur Entomologie 52: 1–83. https://doi.org/10.21248/contrib.entomol.52.1.1-83

Bénon B, Giollo L (2022) Nuove osservazioni sull'apifauna del Cantone Ticino e note sulla loro biologia (Hymenoptera: Anthophila). Entomo Helvetica 15: 29–46.

Bénon D, Giriens S, Genoud D, Praz C (2020) Redécouverte de *Bombus distinguendus* Morawitz, 1869 (Hymenoptera, Apidae) dans le Jura. Entomo Helvetica 13: 183–187.

Bénon D, Praz C (2016) Deux nouvelles espèces d'abeilles sauvages pour l'entomofaune suisse: observation d'*Andrena florivaga* Eversmann, 1852 et *Andrena fulvicornis* Schenck, 1853 dans les pâturages jurassiens. Entomo Helvetica 9: 69–78.

Besuchet C (1986) Jacques de Beaumont (1901–1985): notice biographique. Bulletin de la Société vaudoise des sciences naturelles 78: 81–85.

Blüthgen P (1921) Die schweizerischen *Halictus*-Arten der Frey-Gessner'schen Sammlung. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 13(3–4): 122–143.

Bossert S, Murray EA, Pauly A, Chernyshov K, Brady SG, Danforth BN (2021) Gene tree estimation error with ultraconserved elements: An empirical study on *Pseudapis* bees. Systematic Biology 70: 803–821. https://doi.org/10.1093/sysbio/syaa097

Braun-Blanquet J (1961) Die inneralpine Trockenvegetation. Von der Provence bis zur Steiermark. Geobotanica Selecta 1: 1–273.

Burger R, Reder G (2018) Erste Nachweise von *Nomada nobilis* Herrich-Schäffer, 1839 in Rheinland-Pfalz und Angaben zur Bestandsituation der Wirtsart *Eucera interrupta* Baer, 1850 in der Rheinebene (Hymenoptera: Anthophila). Ampulex 10: 50–53.

Byrde L (2022) Cryptic diversity in the *Nomada panzeri*-group offers insights into the diversification pattern of cuckoo bees (Hymenoptera, Apidae). Master Thesis, University of Neuchatel, Neuchatel, Switzerland, 68 pp.

Carl J, Steck T (1918) Dr. Emil Frey-Gessner 1826–1917. Verhandlungen der Schweizerischen Naturforschenden Gesellschaft 1918: 99–104.

Creedy TJ, Norman H, Tang CQ, Qing Chin K, Andujar C, Arribas P, O'Connor RS, Carvell C, Notton DG, Vogler AP (2020) A validated workflow for rapid taxonomic assignment and monitoring of a national fauna of bees (Apiformes) using high throughput DNA barcoding. Molecular Ecology Resources 20: 40–53. https://doi.org/10.1111/1755-0998.13056

Cross I, Notton DG (2017) Small-Headed Resin Bee, *Heriades rubicola*, new to Britain (Hymenoptera: Megachilidae). British Journal of Entomology & Natural History 30: 1–6.

Dalla Torre KW von (1896) Catalogus hymenopterorum hucusque descriptorum systematicus et synonymicus, Vol.10. Apidae (Anthophila). Engelmann, Leipzig, 643 pp.

Dathe HH (1980) Die Arten der Gattung *Hylaeus* F. in Europa (Hymenoptera: Apoidea: Colletidae). Mitteilungen aus dem Zoologischen Museum in Berlin 56: 207–294.

Dathe H, Scheuchl E, Ockermüller E (2016) Illustrierte Bestimmungstabelle für die Arten der Gattung *Hylaeus* F. (Maskenbienen) in Deutschland, Österreich und der Schweiz. Entomologica Austriaca – Supplement 1, 51 pp.

Day MC (1979) The species of Hymenoptera described by Linnaeus in the genera *Sphex*, *Chrysis*, *Vespa*, *Apis* and *Mutilla*. Biological Journal of the Linnean Society 12: 45–84. https://doi.org/10.1111/j.1095-8312.1979.tb00049.x

de Beaumont J (1946) Les Pompilides de la collection Tournier. Pompilinae de l'Europe centrale. Mitteilungen der Schweizerischen Entomologischen Gesellschaft - Bulletin de la Société entomologique suisse 20: 161–181.

de Beaumont J (1955) Hyménoptères des environs de Neuchâtel. Deuxième partie. Bulletin de la Société neuchâteloise des sciences naturelles 78: 17–30.

de Beaumont J (1958) Les Hyménoptères aculéates du Parc National suisse et ses régions limitrophes. Ergebnisse der wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks (N. F.) 6: 145–235.

de Beaumont J (1960) Apidés de Suisse romande (Hym.). Bulletin de la Société vaudoise des sciences naturelles 67(302): 349–356.

Delarze R, Gonseth Y, Eggenberg S, Vust M (2015) Guide des milieux naturels de Suisse. Ecologie, menaces, espèces caractéristiques. Rossolis, Bussigny, 440 pp.

Dengler J, Guarino R, Moysiyenko I, Vynokurov D, Boch S, Cykowska-Marzencka B, Babbi M, Catalano C, Eggenberg S, Gehler J, Monigatti M, Pachlatko J, Riedel S, Willner W, Dembicz I (2020) On the trails of Josias Braun-Blanquet II : first results from the 12th EDGG Field Workshop studying the dry grasslands of the inneralpine dry valleys of Switzerland. Palaearctic Grasslands 45: 59–88. https://doi.org/10.21570/EDGG.PG.45.59-88

Diestelhorst O, Lunau K (2008) Contribution to the clarification of the species status of *Nomada goodeniana* (Kirby, 1802) and *Nomada succincta* Panzer, 1798 (Apidae, Hymenoptera). Entomologie Heute 20: 165–171.

Doczkal D, Schmid-Egger C (1992) Ergänzungen zur Wildbienenfauna Baden-Württembergs (Hymenoptera: Apoidea). Carolinea 50: 173–176.

Dorchin A, López-Uribe MM, Praz CJ, Griswold T, Danforth BN (2018) Phylogeny, new generic-level classification, and historical biogeography of the *Eucera* complex (Hymenoptera: Apidae). Molecular Phylogenetics and Evolution 119: 81–92. https://doi.org/10.1016/j.ympev.2017.10.007.

Dorchin A (2023) Revision of the historical type collections of long-horn bees (Hymenoptera: Apidae: Eucerini) preserved in the Muséum national d'Histoire naturelle, Paris. Annales de la Société Entomologique de France 59: 115–149. https://doi.org/10.1080/00379271.2023.2192693

Ebmer AW (1969) Die Bienen des Genus *Halictus* Latr. *s. l.* im Grossraum von Linz (Hymenoptera, Apidae). Systematik, Biogeographie, Ökologie und Biologie mit Berücksichtigung aller bisher aus Mitteleuropa bekannten Arten. Teil I. Naturkundliches Jahrbuch der Stadt Linz 15: 133–183.

Ebmer AW (1975) Revision der von Brullé, Lucas und Pérez beschriebenen westpaläarktischen *Halictus*-Arten (Halictidae, Halictinae, Apoidea) – Nachtrag. Polskie Pismo Entomologiczne 45: 267–278.

Ebmer AW (1988) Kritische Liste der nicht-parasitischen Halictidae Österreichs mit Berücksichtigung aller mitteleuropäischen Arten (Insecta: Hymenoptera: Apoidea: Halictidae). Linzer biologische Beiträge 20: 527–711.

Ebmer AW (2001) Hymenopterologische Notizen aus Österreich - 14 (Insecta: Hymenoptera: Apoidea). Linzer biologische Beiträge 33: 435–460.

Else GR, Edwards M (2018) Handbook of the Bees of the British Isles, Vol. 1 & 2. Ray Society/The Natural History Museum, London, 775 pp.

Falk SJ, Johannson N, Paxton R (2022) DNA and morphological characterisation of the Bilberry Mining Bee *Nomada glabella sensu* Stöckhert *nec* Thomson in Britain with discussion on the remaining variation within *N. panzeri*. British Journal of Entomology & Natural History 35: 91–111.

Falk S, Lewington R (2015) Field Guide to the Bees of Great Britain and Ireland. Bloomsbury Publishing, London, 432 pp.

Freitas FV, Branstetter MG, Franceschini-Santos VH, Dorchin A, Wright KW, López-Uribe MM, Griswold T, Silveira FA, Almeida EAB (2023) UCE phylogenomics, biogeography, and classification of long-horned bees (Hymenoptera: Apidae: Eucerini), with insights on using specimens with extremely degraded DNA. Insect Systematics and Diversity 7: 1–21. https://doi.org/10.1093/isd/ixad012

Frey-Gessner E (1899–1912) Fauna insectorum Helvetiae I & II. Bolli & Böcherer, Schaffhausen, 393 + 318 pp. [Originally published as supplements to the Mitteilungen der Schweizerischen entomologischen Gesellschaft, X (3–7, 10), XI (1–6), XI (7–10), XII (1–3)]

Friese H (1895) Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Theil I: Schmarotzerbienen. R. Friedländer, Berlin, 218 pp. https://doi.org/10.5962/bhl.title.160173

Friese H (1896) Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Theil II: Solitäre Apiden. Genus *Eucera*. R. Friedländer, Berlin, 216 pp. https://doi.org/10.5962/bhl.title.160173

Friese H (1897) Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Theil III: Solitäre Apiden: Genus *Podalirius*. R. Friedländer, Berlin, 316 pp.

Friese H (1898) Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Theil IV: Solitäre Apiden: Genus *Eriades*, Genus *Trachusa*, Genus *Anthidium*. C. Lampe, Innsbruck und Imst, 302 pp.

Friese H (1899) Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Theil V: Solitäre Apiden: Genus *Lithurgus*, Genus *Megachile* (*Chalicodoma*). C. Lampe, Innsbruck und Imst, 228 pp.

Friese H (1901) Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Theil VI: Solitäre Apiden: Subfam. Panurginae, Melittinae, Xylocopinae. C. Lampe, Innsbruck und Imst, 284 pp.

Ghisbain G, Rosa P, Bogusch P, Flaminio S, Le Divelec R, Dorchin A, Kasparek M, Kuhlmann M, Litman J, Mignot M, Müller A, Praz C, Radchenko VG, Rasmont P, Risch S, Roberts SPM, Smit J, Wood TJ, Michez D, Reverté S (2023) The new annotated checklist of the wild bees of Europe (Hymenoptera: Anthophila). Zootaxa 5327: 1–147. https://doi.org/10.11646/zootaxa.5327.1.1

Gibbs J, Brady SG, Kanda K, Danforth BN (2012) Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). Molecular Phylogenetics and Evolution 65: 926–939. https://doi.org/10.1016/j.ympev.2012.08.013

Gonseth Y, Sartori L (2022) Les régions biogéographiques de la Suisse. 1ère édition actualisée 2022. 1ère parution 2001. Connaissance de l'environnement n° 2214, Office fédéral de l'environnement, Berne, 28 pp.

Gueuning M, Frey JE, Praz C (2020) Ultraconserved yet informative for species delimitation: Ultraconserved elements resolve long-standing systematic enigma in central european bees. Molecular Ecology 29: 4203–4220. https://doi.org/10.1111/mec.15629

Gusenleitner F, Schwarz M (2002) Weltweite Checkliste der Bienengattung *Andrena* mit Bemerkungen und Ergänzungen zu paläarktischen Arten (Hymenoptera, Apidae, Andreninae, Andrena). Entomofauna, Supplement 10: 1–1280.

Kirby W (1802) Monographia Apum Angliae. II. J. Raw, Ipswich, 388 pp.

Kohl PL, Rutschmann B, Steffan-Dewenter I (2022) Population demography of feral honeybee colonies in central European forests. Royal Society Open Science 9: 220565. [12 pp] https://doi.org/10.1098/rsos.220565

Kouakou D, Sattler T, Obrist MK, Duelli P, Moretti M (2008) Recent Swiss records of rare bee species (Hymenoptera, Apidae) with two species new to Switzerland. Mitteilungen der Schweizerischen Entomologischen Gesellschaft - Bulletin de la Société entomologique suisse 81: 191–197.

Kuhlmann M (1997) Zum taxonomischen Status von *Nomada goodeniana* (Kirby, 1802) und *Nomada succincta* Panzer, 1798 (Hymenoptera: Apidae). Entomofauna 18: 521–528.

Leclercq N, Marshall L, Caruso G, Schiel K, Weekers T, Carvalheiro LG, Dathe HH, Kuhlmann M, Michez D, Potts SG, Rasmont P, Roberts SPM, Smagghe G, Vandamme P, Vereecken NJ (2023) European bee diversity: Taxonomic and phylogenetic patterns. Journal of Biogeography 50: 1244–1256. https://doi.org/10.1111/jbi.14614

Litman JR, Fateryga AV, Griswold TL, Aubert M, Proshchalykin MY, Le Divelec R, Burrows S, Praz CJ (2021) Paraphyly and low levels of genetic divergence in morphologically distinct taxa: revision of the *Pseudoanthidium scapulare* complex of carder bees (Apoidea: Megachilidae: Anthidiini). Zoological Journal of the Linnean Society CLXVI: 1–51. https://doi.org/10.1093/zoolinnean/zlab062

Mandery K (1999) Die für Bayern neue Sandbiene *Andrena florivaga* Eversmann, 1852, nun auch in Mittelfranken (Hymenoptera: Apidae). Galathea, Berichte des Kreises Nürnberger Entomologen e.V. 15: 157–164.

Mandery K, Kosuch J, Schuberth J (2008) Untersuchungsergebnisse zum Artstatus von *Andrena decipiens* Schenck, 1861, *Andrena flavilabris* Schenck, 1874, und ihrem gemeinsamen Brutparasiten *Nomada stigma* Fabricius, 1804 (Hymenoptera: Apidae). Nachrichtenblatt der Bayerischen Entomologen 57: 30–41.

McLaughlin G, Gueuning M, Genoud D, Frey JE, Praz C (2023) Why are there so many species of mining bees (Hymenoptera, Andrenidae)? The possible roles of phenology and *Wolbachia* incompatibility in maintaining species boundaries in the *Andrena proxima*-complex. Systematic Entomology 48: 127–141. https://doi.org/10.1111/syen.12566

Michener C (1997) The identity of the type species of the bee genus *Tetralonia* (Hymenoptera: Apidae). Journal of the Kansas Entomological Society 70: 18–20.

Michener CD (2007) The Bees of the World, second edition. Johns Hopkins University Press, Baltimore, Maryland, 953 pp.

Mignot M (2020) Précision sur le statut taxonomique du complexe *Nomada alboguttata* (Herrich-Schäfer, 1839), (Hymenoptera, Apidés). Master Thesis, University of Bourgogne, Dijon, France, 44 pp.

Monnerat C, Chittaro Y, Sanchez A, Gonseth Y (2015) Critères et procédure d'élaboration de listes taxonomiques nationales: le cas des Buprestidae, Cerambycidae, Cetoniidae et Lucanidae (Coleoptera) de Suisse. Mitteilungen der Schweizerischen Entomologischen Gesellschaft - Bulletin de la Société entomologique suisse 88: 155–172.

Morawitz F (1867) Ein Beitrag zur Hymenopteren-Fauna des Ober-Engadins. Horae Societatis Entomologicae Rossicae 5: 39–71.

Müller A (2021) Dr. Erwin Steinmann, 1923–2020. Entomo Helvetica 14: 198.

Müller A (2023) The hidden diet – examination of crop content reveals distinct patterns of pollen host use by Central European bees of the genus *Hylaeus* (Hymenoptera, Colletidae). Alpine Entomology 7: 21–35. https://doi.org/10.3897/alpento.7.102639

Müller A, Mauss V, Prosi R (2017) Unique nest architecture in the North African osmiine bee *Hoplitis* (*Hoplitis*) *mucida* (Hymenoptera, Megachilidae). Journal of Hymenoptera Research 60: 99–109. https://doi.org/10.3897/jhr.60.20218

Müller A, Praz C (in press) Rote Liste der Bienen. Gefährdete Arten der Schweiz, Stand 2022. Bundesamt für Umwelt, Bern & info fauna, Neuchâtel, 85 pp.

Müller A, Prosi R, Praz C, Richter H (2019) Nesting in bark – the peculiar life history of the rare boreoalpine osmiine bee *Osmia* (*Melanosmia*) *nigriventris* (Hymenoptera, Megachilidae). Alpine Entomology 3: 105–119. https://doi.org/10.3897/alpento.3.34409

Neumeyer R (2008) Ausgewählte Ergänzungen und Kommentare zur Artenliste der Faltenwespen (Hymenoptera: Vespidae) in der Schweiz. Entomo Helvetica 1: 27–31.

Neumeyer R (2014) Kommentierte Liste der in der Schweiz vorkommenden Faltenwespen (Hymenoptera: Vespidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft - Bulletin de la Société entomologique suisse 87: 359–369.

Neumeyer R, Merz B (2012) Vespoidea (Vespidae). In: Merz B (Ed.) Liste annotée des insectes du canton de Genève. Instrumenta Biodiversitatis 8: 220–222.

Nieto A, Roberts SPM, Kemp J, Rasmont P, Kuhlmann M, Criado MG, Biesmeijer JC, Bogusch P, Dathe HH, De la Rúa P, De Meulemeester T, Dehon M, Dewulf A, Ortiz-Sánchez FJ, Lhomme P, Pauly A, Potts SG, Praz C, Quaranta M, Radchenko VG, Scheuchl E, Smit J, Straka J, Terzo M, Tomozii B, Window J, Michez D (2014) European red list of bees. International Union for conservation of nature. Luxembourg: Publication Office of the European Union; [I–X +] 84 pp.

Oertli S, Müller A, Dorn S (2005) Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). European Journal of Entomology 102: 53–63. https://doi.org/10.14411/eje.2005.008

Pachinger B, Kratschmer S, Ockermüller E, Neumayer J (2019) Notizen zum Vorkommen und zur Ausbreitung ausgewählter Wildbienenarten (Hymenoptera: Anthophila) in den Agrarräumen Ost-Österreichs. Beiträge zur Entomofaunistik 20: 177–198.

Packer L, Porsa A, Plateaux-Quénu C, Plateaux L (1999) A cryptic species allied to *Evylaeus villosulus* (Kirby) (Hymenoptera: Halictidae). Annales de la Société entomologique de France (N.S.) 35: 165–171.

Parejo M, Dietemann V, Praz C (2020) Der Status freilebender Völker der Dunklen Honigbiene (*Apis mellifera mellifera*) in der Schweiz – Literatursynthese und Expertenempfehlungen. Endebericht. Unveröffentlichter Schlussbericht, Bundesamt für Umwelt, Bern, 41 pp.

Pauly A (1990) Classification des Nomiinae Africains. Annales - Musée Royal de l'Afrique Centrale, Tervuren, Belgique - Sciences Zoologiques 261: 1-206.

Pauly A (2015) Clés illustrées pour l'identification des abeilles de Belgique et des régions limitrophes (Hymenoptera: Apoidea) I. Halictidae. Document de Travail du Projet BELBEES. http://www.atlashymenoptera.net/page.aspx?id=41

Pauly A, Devalez J, Sonet G, Nagy ZT, Boevé J-L (2015) DNA barcoding and male genital morphology reveal five new cryptic species in the West Palearctic bee *Seladonia smaragdula* (Vachal, 1895) (Hymenoptera: Apoidea: Halictidae). Zootaxa 4034: 257–290. https://doi.org/10.11646/zootaxa.4034.2.2

Pauly A, Noël G, Sonet G, Notton DG, Boevé JL (2019) Integrative taxonomy resuscitates two species in the *Lasioglossum villosulum* complex (Kirby, 1802) (Hymenoptera: Apoidea: Halictidae). European Journal of Taxonomy 541: 1–43. https://doi.org/10.5852/ejt.2019.541

Pérez J (1903) Espèces nouvelles de Mellifères (paléarctiques). Procès-verbaux de la Société linnéenne de Bordeaux 58: LXXVIII–XCIII, CCVIII–CCXXXVI.

Pesenko YA (1985) Systematics of the bees of the genus *Halictus* Latreille with a description of the 7th and 8th metasomal sterna of males: Subgenus *Monilapis* Cockerell [in Russian]. Trudy Zoologicheskova Instituta, Akademii Nauk SSSR 132: 77–105.

Pesenko YA (2004) The phylogeny and classification of the tribe Halictini, with special reference to the *Halictus* genus-group (Hymenoptera: Halictidae). Zoosystematica Rossica 13: 83–113. https://doi.org/10.31610/zsr/2004.13.1.83

Praz CJ, Bénon D (2023) Revision of the leachella group of *Megachile* subgenus *Eutricharaea* in the Western Palaearctic (Hymenoptera, Apoidea, Megachilidae): A renewed plea for DNA barcoding type material. Journal of Hymenoptera Research 95: 143–198. https://doi.org/10.3897/jhr.95.96796

Praz C, Genoud D, Vaucher K, Bénon D, Monks J, Wood TJ (2022) Unexpected levels of cryptic diversity in European bees of the genus *Andrena* subgenus *Taeniandrena* (Hymenoptera, Andrenidae): implications for conservation. Journal of Hymenoptera Research 91: 375–428. https://doi.org/10.3897/jhr.91.82761

Praz C, Müller A, Hermann M, Neumeyer-Funk R, Bénon D, Amiet F, Gonseth Y (2022) Swiss National Apoidea Databank. Version 1.5. Swiss National Biodiversity Data and Information Centres – infospecies.ch. Occurrence dataset. https://doi.org/10.15468/ksfmzj [accessed via GBIF.org on 2023-09-08]

Praz C, Müller A, Genoud D (2019) Hidden diversity in European bees: *Andrena amieti* sp. n., a new Alpine bee species related to *Andrena bicolor* (Fabricius, 1775) (Hymenoptera, Apoidea, Andrenidae). Alpine Entomology 3: 11–38. https://doi.org/10.3897/alpento.3.29675

Prost JF Real P, Bordon J, Cornier P, Rolandez JL, De Bros F, Robert JC, Liogier M, Corcelle J, Roncin P, Siffointe R, Burgunder M, Martin R, Contet M (1987) Contribution à la connaissance biologique de la haute chaîne jurassienne principalement du Crêt de la Neige. Mémoires du Comité de Liaison pour les Recherches Ecofaunistiques dans le Jura 3: 1–497.

Rasmont P, Devalez J, Pauly A, Michez D, Radchenko VG (2017) Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea). Annales de la Société entomologique de France (N.S.) 53: 17–32. https://doi.org/10.1080/00379271.2017.1307696

Reder G (2000) Zugewandert oder eingeschleppt? Nachweis von *Osmia latreillei* Spinola, 1806 in Deutschland (Hymenoptera: Megachilidae). Bembix 13: 13–15.

Reverté S, Miličić M, Ačanski J, Andrić A, Aracil A, Aubert M, et al. (in press) National records of 3000 European bee and hoverfly species: A contribution to pollinator conservation. Insect Conservation and Diversity (in press) 1–18. https://doi.org/10.1111/icad.12680

Sann M, Gerth M, Venne C, Tiedemann R, Bleidorn C (2010) Molekulare und morphologische Untersuchungen zum Status des *Nomada alboguttata* (Apiformes) Artkomplexes. Ampulex 2: 65–72.

Saure C, Wagner F (2018) *Heriades rubicola* Pérez 1890, eine für Deutschland neue Bienenart (Hymenoptera: Apiformes). Eucera 12: 3–7.

Schoder S (2018) The *Hylaeus brevicornis* group revisited – an integrative approach to delimit four closely related species of masked bees (Hymenoptera: Apidae). Master Thesis, University of Vienna, Vienna, Austria, 43 pp.

Scheuchl E (2000) Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band I: Anthophoridae. 2. erweiterte Auflage. Eigenverlag, Velden, 158 pp.

Scheuchl E, Schwenninger HR (2015) Kritisches Verzeichnis und aktuelle Checkliste der Wildbienen Deutschlands (Hymenoptera, Anthophila) sowie Anmerkungen zur Gefährdung. Mitteilungen des Entomologischen Vereins Stuttgart 50: 1–225.

Scheuchl E, Schwenninger HR, Burger R, Diestelhorst O, Kuhlmann M, Saure C, Schmid-Egger C, Silló N (2023) Die Wildbienenarten Deutschlands – Kritisches Verzeichnis und aktualisierte Checkliste der Wildbienen Deutschlands (Hymenoptera, Anthophila). Critical Inventory and Checklist of the Wild Bees of Germany (Hymenoptera, Anthophila). Anthophila 1: 25–138.

Scheuchl E, Willner W (2016) Taschenlexikon der Wildbienen Mitteleuropas. Quelle & Meyer, Wiebelsheim, 920 pp.

Schmid-Egger C (2005) *Proxiandrena* subgen. nov. and revision of the *Andrena proxima* group in the western and central palaearctic region (Hymenoptera, Apidae). Revue Suisse de Zoologie 112: 1029–1044. https://doi.org/10.5962/bhl.part.80335

Schmid-Egger C (2012) Die taxonomischen Situation der Gattung *Andrena* (Apidae) in Mitteleuropa – Kommentar zu: Amiet et al. (2010): Fauna Helvetica, Apidae 6. Ampulex 4: 55–60.

Schmid-Egger C, Patiny S (1997) Anmerkungen zur *Andrena-pillipes*-Gruppe (=*carbonaria* auct.). Bembix 8: 37–42.

Schmid-Egger C, Scheuchl E (1997) Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs unter Berücksichtigung der Arten der Schweiz, Band III, Andrenidae. Eigenverlag, Velden/Vils, 180 pp.

Schmidt S, Schmid-Egger C, Morinière J, Haszprunar G, Hebert PD (2015) DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Molecular Ecology Resources 15: 985–1000. https://doi.org/10.1111/1755-0998.12363

Schmiedeknecht O (1907) Die Hymenopteren Mitteleuropas. Nach ihren Gattungen und zum grossen Teil auch nach ihren Arten analytisch bearbeitet. Gustav Fischer, Jena, 804 pp. https://doi.org/10.5962/bhl.title.10481

Schmiedeknecht O (1930) Die Hymenopteren Nord- und Mitteleuropas. Gustav Fischer, Jena, 1062 pp.

Schwarz M, Gusenleitner F (1997) Neue und ausgewählte Bienenarten für Österreich Vorstudie zu einer Gesamtbearbeitung der Bienen Österreichs (Hymenoptera, Apidae). Entomofauna 18: 301–372.

Schwarz M, Gusenleitner F, Westrich P, Dathe HH (1996) Katalog der Bienen Österreichs, Deutschlands und der Schweiz (Hymenoptera, Apidae). Entomofauna, Supplement 8: 1–398.

Schwenninger HR (2007) Eine neue Art der *Andrena taraxaci*-Gruppe aus Italien und der Schweiz (Hymenoptera, Andrenidae, *Andrena*, Subgenus *Chlorandrena*). Linzer Biologische Beiträge 39: 637–650.

Schwenninger HR (2009) Zum taxonomischen Status von *Andrena anthrisci* Blüthgen 1925 (Hymenoptera, Andrenidae, *Andrena*, *Micrandrena*). Linzer Biologische Beiträge 41: 2025–2038.

Schwenninger HR (2013) Festlegung von Typen für *Andrena nitidiuscula* Schenck 1853 und *Andrena fulvicornis* Schenck 1861 sowie Erstnachweis von *Andrena curvana* Warncke 1965 für Deutschland (Hymenoptera, Andrenidae, *Andrena*, Subgenus *Notandrena*). Linzer biologische Beiträge 45: 1945–1962.

Smit (2018) Identification key to the European species of the bee genus *Nomada* SCOPOLI, 1770 (Hymenoptera: Apidae), including 23 new species. Entomofauna, Monographie 3, 253 pp.

Steinmann E (2002) Die Wildbienen (Apidae, Hymenoptera) einiger inneralpiner Trockentäler. Jahresbericht der Naturforschenden Gesellschaft Graubünden 111: 5–26.

Straka J, Bogusch P (2011) Contribution to the taxonomy of the *Hylaeus gibbus* species group in Europe (Hymenoptera, Apoidea and Colletidae). Zootaxa 2932: 51–67. https://doi.org/10.11646/zootaxa.2932.1.6

Tischendorf S (2020) Anmerkungen zu früheren Vorkommen von *Nomada numida* Lep. (Hymenoptera, Apiformes) in Süddeutschland mit Hinweisen zur aktuellen Verbreitung im mediterranen Raum. Eucera 15: 11–19.

Warncke K (1972a) Beitrag zur Systematik und Verbreitung der Bienengattung *Prosopis* F. in der Westpaläarktis (Hymenoptera, Apoidea, Colletidae). Bulletin des Recherches agronomiques de Gembloux 5: 745–768.

Warncke K (1972b) Westpaläarktische Bienen der Unterfamilie Panurginae (Hymenoptera, Apidae). Polskie Pismo Entomologiczne 42: 53–108.

Warncke K (1986) Die Wildbienen Mitteleuropas, ihre gültigen Namen und ihre Verbreitung (Insecta: Hymenoptera). Entomofauna, Supplement 3, 1–128.

Warncke K, Desmier de Chenon R, Leclercq J (1974) Atlas provisoire des insectes de France. Hymenoptera: Apoidea. Andrenidae: *Andrena* (Fabricius 1775). Faculté des sciences agronomiques de l'état, zoologie générale et faunistique, Gembloux (Belgique) & Office pour l'information entomologique (O.P.I.E), Versailles (France), 58 pp.

Wermeille E, Chittaro Y, Gonseth Y (2014) Liste rouge Papillons diurnes et Zygènes. Espèces menacées en Suisse, état 2012. L'environnement pratique n° 1403, Office fédéral de l'environnement, Berne et CSCF, Neuchâtel, 97 pp.

Westrich P (2018) Die Wildbienen Deutschlands. Ulmer, Stuttgart, 824 pp.

Wood TJ (2023a) The genus *Andrena* Fabricius, 1775 in the Iberian Peninsula (Hymenoptera, Andrenidae). Journal of Hymenoptera Research 96: 241–484. https://doi.org/10.3897/jhr.96.101873

Wood TJ (2023b) The genus *Andrena* in Belgium: revisions, clarifications, and a key for their identification (Hymenoptera: Andrenidae). Belgian Journal of Entomology 135:1–63.

Wood TJ, Hogan J, Edwards M, Paxton R, Praz C, Seidel M, Schmid-Egger C (2022) *Andrena scotica* Perkins is the valid name for the widespread European taxon previously referred to as *Andrena carantonica* Pérez (Hymenoptera: Andrenidae). British Journal of Entomology & Natural History 35: 393–408.

Wood TJ, Le Divelec R (2022) Cryptic diversity revealed in a revision of West Palaearctic *Nomiapis* and *Systropha* (Hymenoptera: Halictidae). Diversity 14: 1–32. https://doi.org/10.3390/d14110920

Wood TJ, Monfared A (2022) A revision of the *Andrena* (Hymenoptera: Andrenidae) fauna of Iran, with the description of 16 new species. European Journal of Taxonomy 843: 1–136. https://doi.org/10.5852/ejt.2022.843.1947

Supplementary material 1

Locality labels from important historical bee collections in Switzerland

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: tif

Explanation note: **fig. S1**: **A.** Original, hand-written label by E. Frey-Gessner (Genthod, 20.vi). **B.** Original, printed and hand-written label by E. Frey-Gessner (Genthod, 5.v). **C.** Recopied label from the collection E. Frey-Gessner, associated with a specimen of Epeolus alpinus supposedly collected in Genthod near Genève; this (in Switzerland) alpine species is probably absent from the Geneva Region. **D.** Original label by M. Paul (Sierre, 29.v.[18]85). **E.** Printed label from the Chevrier Collection; the hand-writing, presumably from E. Frey-Gessner, has likely been added after Chevrier's death. **F.** Printed label from the W. Schmidt collection. **G.** Original label from the H. Tournier Collection (P[eney]. 27.vi.[18]89); **H.** Original label from the Jabob Collection (Serroux [Le Landeron, Serroue], 1.ix.[19]05); **I.** Original label from the T. Steck Collection (Wallis, Useigne [Euseigne], 21.vi.1925).

Link: https://doi.org/10.3897/alpento.7.112514.suppl1

Supplementary material 2

Primers used to amplify and sequence the mitochondrial gene Cytochrome oxidase I

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: xlsx

Link: https://doi.org/10.3897/alpento.7.112514.suppl2

Supplementary material 3

Locality, collection data and BOLD accession numbers for specimens sequenced in this study

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: xlsx

Link: https://doi.org/10.3897/alpento.7.112514.suppl3

Supplementary material 4

Checklist of the Swiss bees and presence of each species in each canton

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: xlsx

Explanation note: Open circles indicate records before 2000, closed circles after 1999. Abbreviations: AG: Aargau; AI: Appenzell Innerrhoden; AR: Appenzell Ausserrhoden; BE: Bern; BL: Basel-Landschaft; BS: Basel-Stadt; FR: Fribourg; GE: Geneva; GL: Glarus; GR: Graubünden; JU: Jura; LU: Luzern; NE: Neuchâtel; NW: Nidwalden; OW: Obwalden; SG: St. Gallen; SH: Schaffhausen; SO: Solothurn; SZ: Schwyz; TG: Thurgau; TI: Ticino; UR: Uri; VD: Vaud; VS: Valais; ZG: Zug.

Link: https://doi.org/10.3897/alpento.7.112514.suppl4

Supplementary material 5

Distance-based tree

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: pdf

Explanation note: Distance-based tree build using the unweighted pair group method with arithmetic mean (UPGMA) based of the mitochondrial gene Cytochrome Oxidase I for all individuals sequenced in this project. Previously published sequences (Praz et al. 2019, 2022; Gueuning et al. 2020, McLaughlin et al. 2023) are also included.

Link: https://doi.org/10.3897/alpento.7.112514.suppl5

Alpine Entomology 7 2023, 269–273 | DOI 10.3897/alpento.7.108448

Alpine Entomology

Parvapila lyncispinnae new genus and new species (Coleoptera, Melandryidae) from South Africa

Vivien Cosandey[1]

1 *Muséum d'histoire naturelle, Malagnou 1, 1206 Genève, Switzerland*

https://zoobank.org/1E892669-A346-457A-AA4C-277862E54019

Corresponding author: Vivien Cosandey (vivien.cosandey@bluewin.ch)

Academic editor: Stève Breitenmoser ♦ **Received** 3 July 2023 ♦ **Accepted** 30 October 2023 ♦ **Published** 13 November 2023

Abstract

The first Orchesiini of South Africa, *Parvapila lyncispinnae* **gen. nov.** and **sp. nov.**, is described. Specimens were collected at the foot of the Langeberg Range and of the Kogelberg, mountains of Western Cape. Individuals were collected by sifting soil litter in Afromontane forests, an endemic vegetation community of Afrotropical mountainous areas.

Key Words

False darkling beetles, Orchesiini, taxonomy, Afrotropical realm, Afromontane region

Introduction

Orchesiini are characterized by their saltatory posterior legs bearing metatarsal spurs longer than the metatibiae and having trilobate genitalia (Nikitsky and Pollock 2011). They are mostly associated with fungi (Hammond and Lawrence 1989) and therefore often occur in moist habitats. In Africa, Orchesiini are represented by nine species in three genera, namely *Eucinetomorphus* Perris, 1875, *Microscapha* LeConte, 1866 and *Orchesia* Latreille, 1807. Three species are recorded from the Afrotropical region (Pic 1942, 1946; Nikitsky and Below 1982), all belonging to the genus *Microscapha* (see comment in Nikitsky and Pollock 2011), while six species occur in North Africa (Nikitsky 2020).

Unidentified specimens of Melandryidae originating from nature reserves situated at the foot of the Langeberg Range and of the Kogelberg, Western Cape, South Africa, were discovered to be an undescribed species of Orchesiini. As it cannot be accommodated in any Orchesiini genera, a new genus is also here established.

Material and methods

Fifty-two specimens were examined. They are housed in the museums listed below.

MHNG	Muséum d'histoire naturelle, Geneva, Switzerland
OKZC	Ondřej Konvička collection, Zlín, Czech Republic
PBPC	Petr Bulirsch collection, Praha, Czech Republic
TMSA	Ditsong (= Transvaal) Museum, Pretoria, South Africa

The images were taken with a Leica DFC425 camera in conjunction with a Leica M205–C compound microscope, stacked with Zerene Stacker (version 1.04) and processed with GIMP (version 2.10.30.).

Results

Parvapila gen. nov.

https://zoobank.org/356123C2-5B45-45AD-996B-DB34B1063E60

Type species. *Parvapila lyncispinnae* sp. nov., by present designation and monotypy.

Diagnosis. *Parvapila* has a distinct scutellar shield unlike most of the Orchesiini: *Eucinetomorphus*, *Lederia* Reitter, 1880, *Lederina* Nikitsky & Belov, 1982, *Lyperocharis* Broun, 1914. It can be distinguished from the three Orchesiini genera with visible scutellar shield, *Orchesia*, *Hylobia* Broun, 1880, and *Microscapha* by the following combination of characters: scutellar shield small with rounded posterior margin (Fig. 1), suture dividing metanepisterna and metaventrite evanescent posteriad (Fig. 2), and metacoxae directed antero-laterally.

Etymology. The name of this genus refers to its small (“parva” lat.) and convex shape (“pila” lat.: ball).

Description. Body oval, small, ca. 1.5–2.5 mm long. Body convex in lateral view; sides regularly curved in dorsal view. Pubescence on head directed anteriad, on dorsal surface of pronotum, elytra and abdomen directed posteriad.

Head embedded in pronotum and directed downward, hardly visible in dorsal view; delimited posteriorly by carina. Neck surface with strong microreticulation. Distance between dorsal margin of eyes two times eyes width. Antennae long, as long as ca. half of body length, antennomeres progressively widening apicad, without distinct antennal club; insertion point of antennae hidden by lateral margins of frons. Maxillary palpi with strongly transverse articles II and III, apical article cultriform.

Pronotum transverse, regularly convex in lateral view, without impressions; lateral margins with lateral bead in posterior half, anterior and posterior margins not edged; anterior angles broadly rounded, posterior angles orthogonal with rounded tip, pointing posteriad. Scutellum visible, with rounded posterior margin. Elytra elongate; humeral stria marked, forming small gutter with completely edged lateral border. Epipleura well marked on most of elytral length, evenly narrowed posteriad. Elytra fused. Hind wings not developed. Prosternal process triangular, wide. Mesoventral process thin and elongate, triangular. Metaventrite separated from metanepisterna by incomplete suture, evanescent posteriad. Metanepisterna ca. 3 times longer than wide. Metacoxae directed antero-laterally and narrowed.

Legs robust, with wide, short tibiae. Metatarsal spurs and metatarsomeres wide.

Male: Metaventrite with a medial depression.

Parvapila lyncispinnae sp. nov.

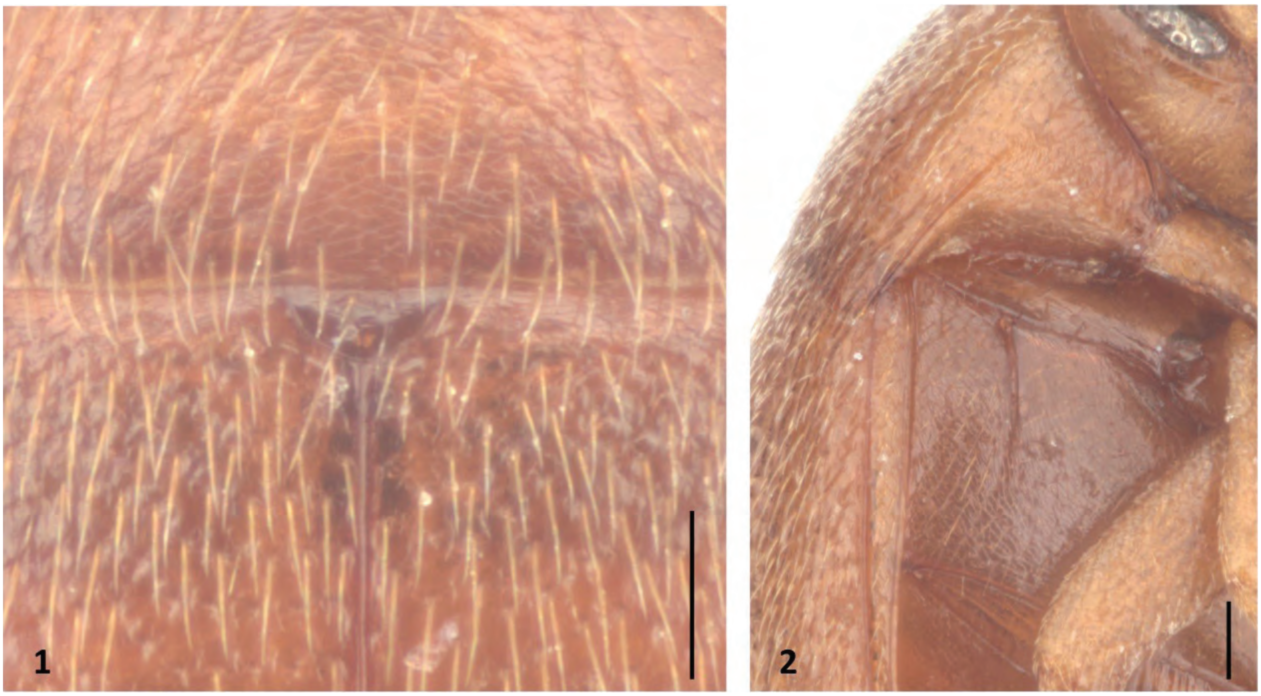
https://zoobank.org/21000D3B-D5C5-415A-84C1-EE447BCD1158
Figs 1–9

Type material. ***Holotype*** (housed in MHNG): MHNG-ENTO-0119356; 1♂; RSA, Western Cape, Grootvadersbosch N.R., 33°59.39'S, 20°48.32'E, 25–26.I.2004; 350 m, sifting, lgt. P. Hlaváč.

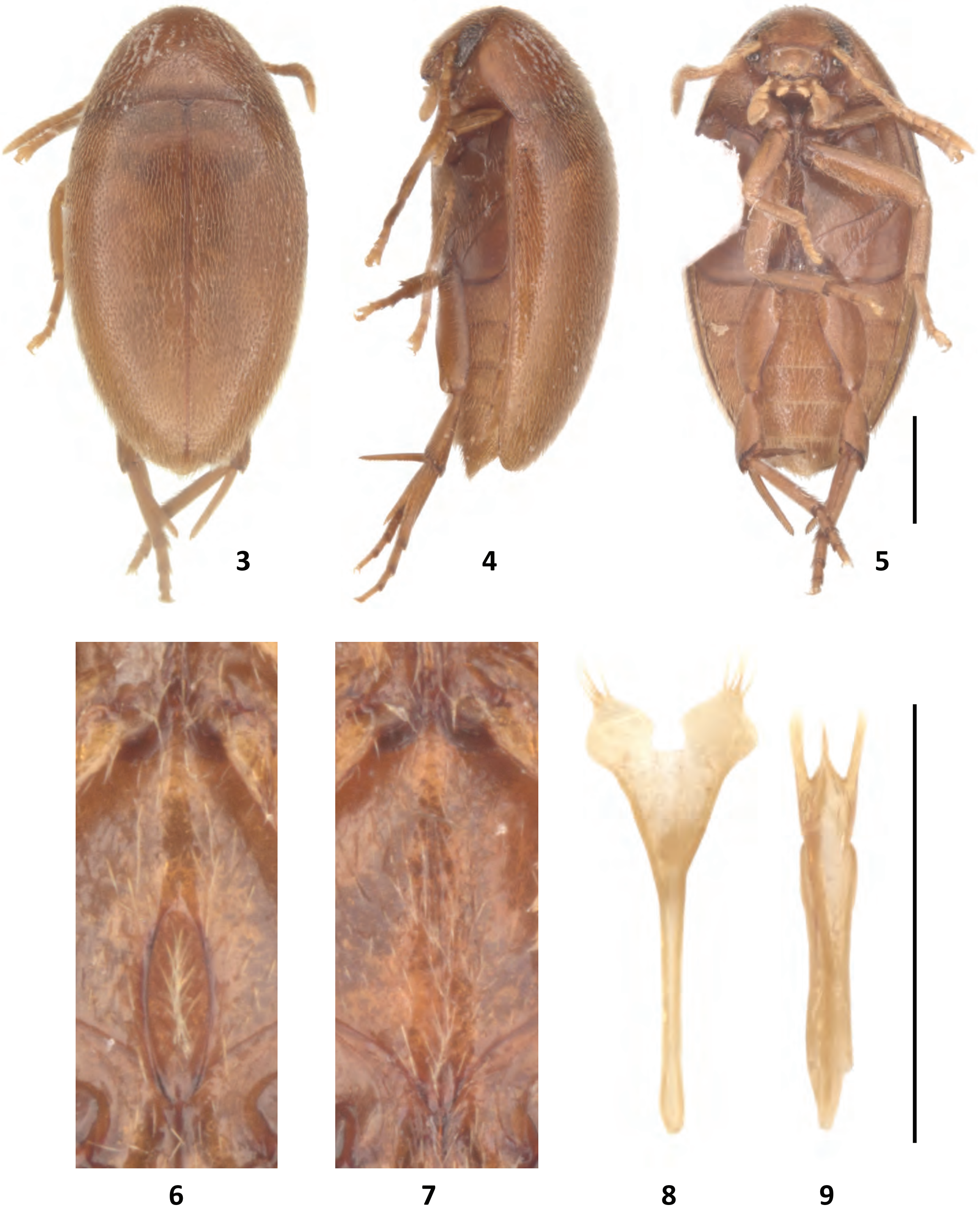
Paratypes (3): MHNG; MHNG-ENTO-0119357 - MHNG-ENTO-0119359; 1♂, 2♀; same data as holotype. - 1♂; OKZC; South Africa, Western Cape, Kogelberg NR, Platbos for., 34°20.1'S, 18°56.0'E, 14.i.2020, P. Bulirsch lgt. - 18♂ and ♀; MHNG, TMSA, PBPC, OKZC; South Africa, Western Cape, Marloth NR, Duiwelsbos for., 33°59.6'S, 20°27.6'E, 25.x.2019, P. Bulirsch lgt. - 5♂ and ♀; MHNG, OKZC: South Africa, Western Cape, Marloth NR, Koloniesbos for., 33°59.5'S, 20°27.1'E, 26.x.2019, P. Bulirsch lgt. - 14♂ and ♀; MHNG, OKZC: South Africa, Western Cape, Marloth NR, Duiwelsbos indig. forest, 33°59.6'S, 20°27.6'E, 22.x.2013, P. Bulirsch lgt. - 10♂ and ♀; MHNG, OKZC: South Africa, Western Cape, Marloth NR, Wamakersbos, ca. 33°59.5'S, 20°28.6'E, 23.i.2020, P. Bulirsch lgt.

Diagnosis. For now, *Parvapila lyncispinnae* is the only known species of this genus. It can be easily distinguished from other Orchesiini by characters given in the diagnosis of *Parvapila*.

Etymology. The specific epithet refers to the shape of the sternite IX of males, which bears two patches of setae, recalling the tufted ears of the Eurasian lynx.



Figures 1, 2. *Parvapila* gen. nov. **1.** Scutellar shield; **2.** Metanepisternum. Scale bars: 0.1 mm.



Figures 3–9. *Parvapila lyncispinnae* sp. nov. **3–5.** Habitus; **6.** Male metaventrite; **7.** Female metaventrite; **8.** Male sternite IX; **9.** Aedeagus. Scale bars: 0.5 mm.

Description. Length: 1.48–2.51 mm; width: 0.78–1.28 mm; depth: 0.57–0.91.

Body (Figs 3–5) oval, ca. twice longer than wide, widest at middle; sides regularly arcuate in dorsal view; body convex in lateral view, slightly elongated posteriorly. Body yellowish to orange-reddish. Pubescence regular and dense, yellowish.

Head with strong setiferous punctation; surface covered by homogeneous transverse microreticulation. Clypeus with strong and rough punctation; surface lacking microreticulation. Antennae long, reaching posteriorly ca. middle of body; antennomeres progressively widening toward apex, not forming distinct club; length ratios of antennomeres: 22-16-13-8-11-12-10-11-14-13-29; antennomere I and XI ca. twice longer than wide, antennomeres II, III, V, VI, and VII slightly elongate, antennomeres IV, VIII, and X slightly transverse, antennomere IX as long as wide. Basal maxillary palpomere small, as long as wide; second article transverse; penultimate article transverse, three times wider than long; distal maxillary palpomere 1.2 times longer than wide, widest at base, with inner margin slightly concave, outer margin widely rounded.

Pronotum ca. 0.4 times as long as wide, widest at base; surface covered by fine punctation, two times denser anteriorly than at base; elytral surface covered by microreticulation formed of transverse to polyhedral meshes. Elytra 1.5 times longer than wide; homogeneously covered with small granules except for elytral base, and with dense confluent rough punctation; lacking microreticulation, shining; pubescence long and dense directed posteriad. Scutellar shield small, 0.07 mm wide, ca. twice longer than wide, with rounded posterior margin, surface smooth and shining, bearing a few hairs. Metaventrite shining, homogeneously covered by shallow microreticulation and fine punctation and pubescence. Length of both metatarsal spurs subequal, almost as long as metatarsomere I; first metatarsomere seven times longer than wide; length ratio of metatarsomeres: 38-12-9-11.

Abdomen bearing dense pubescence on ventral side; surface smooth, shining, finely punctured, without microreticulation.

Male: Metaventrite (Fig. 6) with a deep oval medial depression occupying slightly more than posterior half of metaventrite and three to four times longer than wide, widest at middle, with margins clearly edged; inner area of medial depression bearing long pubescence; metaventral area anterior of depression with long erected hairs.

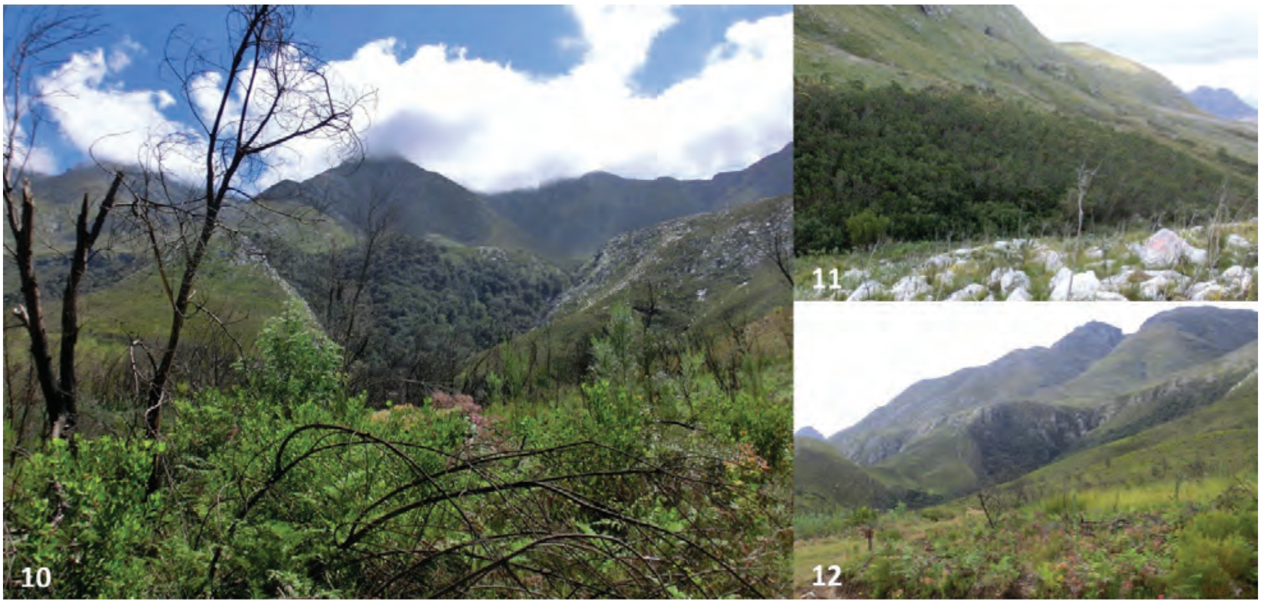
Sternite IX (Fig. 8) 0.51 mm long, formed by two tubular pieces joining anteriorly and linked by a thin membrane, strait on anterior 2/3, diverging in apical third, prolonged by quadratic membranous pieces with pubescent tips. Aedeagus (Fig. 9) 0.43 mm long; phallobase slightly sinuate around its midlength, 0.6 times as long as total aedeagal length; parameres straight, divergent posteriad, in basal half not distinct from median lobe; median lobe extremely thin, narrowed posteriad.

Female: Metaventrite (Fig. 7) with shallow lineiform groove directed longitudinally occupying 0.6 times of metaventral length, surrounded by strong hairs directed posteriad.

Discussion

The specimens of *Parvapila lyncispinnae* sp. nov. were collected by sifting floor litter in Afromontane forests (P. Hlaváč pers. comm.) and on the foot of big trees (P. Bulirsch pers. comm.) in a few localities of the Western Cape (Figs 10–12). Most of them are situated in the Grootvadersbosch and Marloth Nature Reserves at the foot of the Langeberg Range. This mountain chain, situated in Western Cape, is directed east-west and reaches an elevation of 1710 m a.s.l. It is mostly covered by fynbos, endemic shrublands of the Cape region, while patches of Afromontane forests grow in deep gorges (McDonald 1993). Additionally, a single individual of *P. lyncispinnae* was collected at the foot of the Kogelberg, a mountain chain culminating at almost 1300 m a.s.l.

The Afromontane region is an archipelago-like endemism centre distributed on reliefs of tropical Africa (White 1983). Three quarters of its flora is endemic (ca. 3000 spp.), and it shares a restricted number of plant species with the forests of lower elevation (White 1978). Afromontane vegetation shows a disjunct distribution, mostly occurring at high elevations (only above 2000 m a.s.l. in the tropics) (White 1983). However, in South Africa the effect of latitude compensate the elevation,



Figures 10–12. Habitat of *P. lyncispinnae* sp. nov. Specimens were collected in the patches of Afromontane forests. **10.** Duweilsbos; **11.** Platbos; **12.** Koloniesbos. Pictures: Jiří Janák.

making it possible for enclaves of Afromontane forests to grow at low elevations (down to ca. 100 m a.s.l.). They are mostly found on southern slopes, in moist or cloudy conditions, and with water-retaining soils (White 1978).

Parvapila lyncispinnae may be endemic to both South Africa and specifically to Afromontane forests. It is probable that more species of *Parvapila* and of other Orchesiini are still to be discovered in moist areas of Afrotropical regions, of which the knowledge concerning Melandryidae is extremely limited.

The apparent restricted distribution of *Parvapila* may indicate a Gondwanian origin. In this case, its closest relative may be *Lyperocharis*, from New Zealand and the Chilean subgenera of *Lederia*, *Fuscatelia* Nikitsky & Belov, 1982 and *Macrolederia* Nikitsky & Belov, 1982, all of them being apterous. However, the residual scutellar shield may suggest a more recent loss of the flight ability. Possibly, *Parvapila* is more closely related to *Hylobia* from New Zealand. The subdivision of Orchesiini into genera is based on the patterns of the metasternal sutures, the direction of the metacoxae, and the presence or absence of scutellum, and of wings. These characters do not necessarily reflect evolutionary relationships. Phylogenetic studies and taxonomic revisions are needed to better understand the relationships of the Orchesiini genera, and more generally, the systematics of Melandryidae. Synthetic works and identification tools are also needed.

Acknowledgements

I thank Giulio Cuccodoro for providing the photographic material, Peter Hlaváč and Petr Bulirsch for transmitting additional information on the sampling stations as well as Jiří Janák for the pictures of localities. I also acknowledge Ivan Löbl for his comments on an early version of the manuscript. Finally, I thank the Ondřej Konvička and Darren Pollock for their helpful advice on the manuscript.

References

Hammond PM, Lawrence JF (1989) Appendix: Mycophagy in Insects: a Summary. In: Wilding N, Collins NM, Hammond PM, Weber JF (Eds) Insect-fungus interactions, 14th Symposium of the Royal Entomological Society of London in collaboration with the British Mycological Society. Academic Press, London, 275–324. https://doi.org/10.1016/B978-0-12-751800-8.50018-5

McDonald DJ (1993) The vegetation of the southern Langeberg, Cape Province. 1. The plant communities of the Boosmansbos Wilderness Area. Bothalia 23(1): 129–151. https://doi.org/10.4102/abc.v23i1.798

Nikitsky NB (2020) Family Melandryidae Leach, 1815. In: Iwan D, Löbl I (Eds) Catalogue of Palearctic Coleoptera Volume 5. Tenebrionoidea. Revised and Updated Second Edition. Brill, Leiden/Boston, 47–59.

Nikitsky NB, Below VV (1982) The false darkling beetles genus *Microscapha* LeConte (Coleoptera, Melandryidae). Annales historico-naturales Musei Nationalis Hungarici 74: 141–150.

Nikitsky NB, Pollock DA (2011) 11.6. Melandryidae Leach, 1815. In: Leschen RAB, Beutel RG, Lawrence JF (Eds) Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles, Volume 2, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, New York, 520–533. https://doi.org/10.1515/9783110911213.520

Pic M (1942) Coléoptères nouveaux du Cameroun. Échange 58: 1–3. https://doi.org/10.3406/bsef.1942.15613

Pic M (1946) Coléoptères nouveaux de la Côte d'Ivoire. Bulletin de la Société entomologique de France 51(6–7): 107–108. https://doi.org/10.3406/bsef.1946.15906

White F (1978) The Afromontane Region. In: Werger MJA (Ed.) Biogeography and Ecology of Southern Africa. Junk, The Hague, 463–513. https://doi.org/10.1007/978-94-009-9951-0_11

White F (1983) The Vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. UNESCO, Natural Resources Research 20: 1–356.

Alpine Entomology 7 2023, 275–277 | DOI 10.3897/alpento.7.108429

Bernhard Merz (29.VII.1963–14.II.2023)

Giulio Cuccodoro[1], Bernard Landry[1]

1 *Muséum d'histoire naturelle de Genève, Geneva, Switzerland*

https://zoobank.org/BBE8F976-E36F-4090-A0B6-8C995BDD1A78

Corresponding author: Giulio Cuccodoro (giulio.cuccodoro@ville-ge.ch)

Academic editor: Jessica Litman ♦ **Received** 21 June 2023 ♦ **Accepted** 8 November 2023 ♦ **Published** 15 November 2023

Born on July 29, 1963 in Basel, Switzerland, Bernhard Merz attended school in the canton of Basel-Landschaft (BL). He studied biology at the ETH Zürich (1982–86), graduating with a Bachelor's thesis entitled "Vegetationszusammensetzung von Trespen-Halbtrockenrasen nach 10-jähriger Brache, Mahd- und Brandbewirtschaftung bei Merishausen (Kt. Schaffhausen)" under the supervision of Prof. Elias Landolt.

After a trip to the USA, New Zealand and Australia from January to April 1987, he was employed from May 1 to September 30, 1987 as a technical collaborator at the entomological collection of the Institute of Entomology of the ETH Zürich. He later continued his work in the collection of the ETH Zürich as a PhD student of Prof. Willy Sauter, where he worked from March 1, 1988 to September 30, 1992.

He received his doctorate at the ETH Zürich on September 11, 1992 with a PhD thesis entitled "Revision der westpalaearktischen Gattungen und Arten der *Paroxyna*-Gruppe und Revision der Fruchtfliegen der Schweiz (Diptera, Tephritidae)".

On October 1, 1992, he became curator of the entomological collection at the ETH Zürich, a position he held until November 30, 1998. At the same time, he also worked as a teaching assistant and lecturer at the Institute of Entomology of ETH Zürich from October 01, 1993 to September 30, 1993, then in Applied Entomology (former Institute of Entomology) at the Institute of Plant Science of ETH Zürich from October 01, 1993 to November 30, 1998, where he became also Senior scientist from March 1, 1996 to November 30, 1998. On December 1,

Figure 1. Bernhard Merz in his office at the Natural History Museum in Geneva on July 30, 2005.

Figure 2. Bernhard Merz during a Wednesday animation on Diptera on January 14, 2009.

1998, Bernhard Merz was hired as a research scientist at the Department of Entomology of the Natural History Museum of Geneva. He was later promoted to the position of curator on December 1, 1999.

Bernhard Merz was a passionate and dedicated entomologist who focused his interests on Diptera, in particular the Tephritidae, Pallopteridae and Clusiidae of the world (taxonomy, nomenclature, phylogeny and biogeography), the Lauxaniidae of the West Palearctic region (taxonomy), as well as on the faunistics of the Diptera of Switzerland in general and of Geneva in particular. He was involved in various academic societies, including the Swiss Entomological Society (member: 1988—2015), the Entomological Society of Zurich (member: 1988–1999; committee 1993–1999; president: 1995–1999), Pronatura Zürich (committee: 1994–1998), the Entomological Society of Geneva (member: 1999–2014; committee: 1999–2008, president: 2003–2008), and the Entomological Society of Basel (member: 2002–2015).

In addition to countless excursions in Switzerland in search of Diptera, his interests also led him to go prospecting with his net in Sweden (30.VII–11. VIII.2001), England (2–13.IX.1998), Holland (23.VIII–28.VIII.1995), Austria and Czechia (22.VIII–4.IX.1990), Hungary (9–25.VI.1991), mainland Italy (7–17.V.199; 25–27.V.2001; 30.VIII–3.IX.2004), Sardinia (10–24. VI.2002), Sicily (3–17.VI.1999), France (25.VIII–1. IX.1988; 2–7.VI.1990; 3–7.VI.1993; 30.V–5.VI.1995; 6–15.VI.2007), Andorra (5–18. IX. 1999), mainland Spain (3–24.IV.1989; 26.VII–3.VIII.1995), Canary Islands (28. IV–5.V.1988; 3–17.III.1990; 21.IX–4.X.1998), Malta (3–17.VI.1999; 1–7.V.2001; 21.IV–7.V.2002), Crete (16–23.IV.1991), Cyprus (21.IV–7.V.2002), Turkey (20–27. IX.1990 25.IV–3.V.2000), Israel (9–23.IV.1992; 10–18. III.1995; 7–18.VI.1996; 26.VI–3.VII.2000), Kyrgyzstan (27.IV–28.V.1994), South Korea (12.VI–1.VII.2005), Thailand (15.X–5.XI.2000), Australia (4–31.X.2002), Canada (15–23.VIII.1994) and Kenya (28.II–21.III.1993). The fruits of his work increased the size of the Diptera collection at the Museum of Geneva from barely 10’000 specimens to nearly 100’000 specimens, including more than 30’000 Lauxaniidae and Tephritidae. During his career, he described 96 taxa (five genera and 91 species; Suppl. material 2), and 30 taxa (two genera and 28 species; Suppl. material 1) were dedicated to him. His 236 published scientific papers on the taxonomy and faunistics of Diptera and other insects make him undoubtedly one of the greatest Swiss entomologists of his generation.

For health reasons, he was forced to give up his research, as well as his position as curator at the Museum in Geneva, which he left definitively on January 31, 2014 at the age of 50. Despite his great courage in the face of illness, he passed away on Tuesday, February 14, 2023 at the Cantonal Hospital in Chur, Switzerland. He was a generous man with great qualities and abilities, including a prodigious memory, which he put to use in his work and other passions, especially tea, which he could discuss for hours.

We thank Betty Oudomsouk and Philippe Wagneur (MHNG) as well as Tommy Andriollo (Annemasse), Patrick Graff (Basel) and Valery Korneyev (National Academy of Sciences of Ukraine, Kiev) for providing relevant information, and Jean Wüest (Geneva) for his comments and suggestions.

Giulio Cuccodoro et Bernard Landry,
Muséum d’histoire naturelle de Genève.

Supplementary material 1

Merz's patronymic taxa (2 genera and 28 species)

Authors: Giulio Cuccodoro, Bernard Landry
Data type: docx

Link: https://doi.org/10.3897/alpento.7.108429.suppl1

Supplementary material 2

Taxa described by Bernhard Merz (5 genera and 91 species)

Authors: Giulio Cuccodoro, Bernard Landry
Data type: docx

Link: https://doi.org/10.3897/alpento.7.108429.suppl2

Supplementary material 3

List of the scientific publications of Bernhard Merz (236)

Authors: Giulio Cuccodoro, Bernard Landry
Data type: docx

Link: https://doi.org/10.3897/alpento.7.108429.suppl3

Alpine Entomology 7 2023, 279–283 | DOI 10.3897/alpento.7.114602

PENSOFT.

Alpine Entomology

Protokoll der Jahresversammlung der Schweizerischen Entomologischen Gesellschaft vom 3., 4. und 27. März 2023 an der ETH Zürich und via Videokonferenz

Marc Neumann[1]

1 *Naturmuseum Solothurn, Solothurn, Switzerland*

https://zoobank.org/30439247-2177-49D7-8805-D76EEAEA1440

Corresponding author: Marc Neumann (marc.neumann@solothurn.ch)

Academic editor: Jessica Litman ♦ **Received** 23 October 2023 ♦ **Accepted** 6 November 2023 ♦ **Published** 15 November 2023

Die Jahresversammlung der SEG fand diesmal auf Einladung der Eidgenössischen Technischen Hochschule Zürich am 3. und 4. März in Zürich statt. Da die Traktanden der GV im Vorfeld zu spät an die Mitglieder versendet worden waren, entschied man, die Vorstandswahlen auf einen späteren Termin auszulagern. Sie fanden daher am 27. März per Videokonferenz statt.

Der Themenschwerpunkt am Freitag lag einerseits bei Projekten zur Erforschung der Biodiversität der Schweizer Insektenfauna, andererseits bei Parasitoiden in der angewandten Forschung. Den Einstieg zum Thema Artenvielfalt gab Glenn Litsios, Direktor von info fauna in Neuchâtel. Durch die langjährigen Tätigkeiten im Bereich Biodiversitätsmonitoring, Datensammlung und -verarbeitung sind einige Insektengruppen in der Schweiz gut erfasst und es konnten Modelle bei den Veränderungen der Artzusammensetzung erstellt werden. Daraus resultieren auch Checklisten und Rote Listen, die wiederum wichtig für politische Entscheidungen sein können, etwa wenn der Anteil gefährdeter Arten aufgezeigt werden kann. Für viele Gruppen und seltene Arten ist die Datengrundlage aber noch unzureichend, weil sie schwer zu erfassen sind, oder schlicht Experten und Expertinnen mit dem nötigen Wissen fehlen. Ein weiterer wichtiger Aspekt, den Litsios anführt, ist die Vernetzung.

Einerseits von Fachpersonen und Bevölkerung, da etwa die Hälfte der Biodiversitätsdaten von Privatpersonen geliefert wird. Eine Verbesserung der Dateneingabe via Internet und Apps ist daher ein wichtiger Schritt. Andererseits sollen die Schweizer Daten auch global eingebettet sein und werden daher von info fauna an die «Global Biodiversity Information Facility» (GBIF) weitergeleitet.

Folgende acht Vorträge wurden am Freitag gehalten:

- Le suivi des insectes en Suisse, défis et opportunités.
  Glenn Litsios, info fauna, Neuchâtel
- 20 Jahre Biodiversitätsmonitoring Schweiz: Erkenntnisse aus den Erhebungen der Tagfalter und Gewässerinsekten.
  Pascale Hutter, Hintermann & Weber AG, Reinach
- eBioDiv: linking specimens with literature, or to what is known about a specimen.
  Donat Agosti, Plazi, Bern
- Wie Klima- und Landnutzungsänderungen zu Veränderungen der Insektenverbreitung in der Schweiz seit 1980 beigetragen haben.
  Felix Neff, WSL, Birmendsorf
- Nutzen und Risiken von Parasitoiden im Pflanzenschutz.
  Jana Collatz, Agroscope, Zürich-Reckenholz
- Interaction between beneficial insects and pests in sugar beets.
  Angela Studer, Agroscope, Zürich- Reckenholz
- Using parasitoids in biological control of invasive insects.
  Lukas Seehausen, CABI, Delémont
- Contribution au catalogue des coléoptères de Suisse.
  Andreas Sanchez, info fauna, Neuchâtel

Am Samstag wurde zunächst noch einmal der Themenbereich Parasitoide aufgegriffen. Einen spannenden

Aspekt zeigte Christoph Vorburger von der Eawag in Dübendorf & der ETHZürich in seinem Hauptvortrag. Darin ging es um den Einfluss von Symbionten auf WirtParasitoid-Interaktionen. Blattläuse besitzen etwa endosymbionte Bakterien, die einen gewissen Schutz vor parasitoiden Brackwespen bieten, indem sie die Eier der Wespen abtöten. Dieser Schutz scheint aber auch vom Genotyp der Parasitoiden und der Symbionten abhängig zu sein. Mit fortschreitender Generationsdauer steigt im Experiment die Infektionsrate der Parasitoiden, die sich offenbar an den Genotyp der Endosymbionten anpassen können. Die Vielfalt der Genotypen beeinflusst sich also gegenseitig. Da die Wirte nicht beliebig viele Varianten von Endosymbionten beherbergen können (verringerte Lebensdauer durch Kosten der Symbionten) sollte eine erhöhte genetische Vielfalt bei den Parasitoiden zu einer stärkeren Reduzierung der Wirtspopulation führen. Dies kann für die biologische Schädlingsbekämpfung relevant sein, da in Zukunft potenziell „massgeschneiderte“ Parasitoide besonders gut an die Genotypen der Wirts-Endosymbionten angepasst wären.

Folgende sieben Vorträge wurden am Samstag gehalten:

- Versteckte Helfer: Symbionten und ihr Einfluss auf Wirt-Parasitoid-Interaktionen.
  Christoph Vorburger, Eawag Dübendorf & ETH Zürich

- Parasitoids of oil seed rape and crop pests – investigating biocontrol potential of hymenopterans in Switzerland.
  Maura Ganz, Agroscope, Zürich-Reckenholz

- Parasitoide in Gebäuden.
  Marcus Schmidt, Fachstelle Schädlingsprävention der Stadt Zürich

- DNA barcoding of the stoneflies in Switzerland: an update of the reference database.
  Laurent Vuataz, Muséum cantonal des sciences naturelles Lausanne

- Population density affects sexual selection in an insect model.
  Lennart Winkler, Technische Universität Dresden

- Influence of climate change and infection on thermal preferences of mosquitos.
  David Hug, National Centre for Vector Entomology, Universität Zürich

- Fitness consequences of heatwaves in *Drosophila melanogaster*.
  Abhishek Meena, Department of Evolutionary Biology and Environmental Studies, Universität Zürich

Oliver Martin, seinem Team und dem Departement Biologie der ETH Zürich sei für die hervorragende Organisation und Verpflegung während der Jahresversammlung herzlich gedankt.

Generalversammlung

Begrüssung

Der Präsident Oliver Martin eröffnet die Generalversammlung um 9:30 Uhr und begrüsst die anwesenden 21 Mitglieder und einen Gast (total 22 Personen).

Protokoll der Generalversammlung 2022 in Lugano

Das Protokoll wird kommentarlos und unverändert genehmigt.

Bericht des Präsidenten, Oliver Martin

Administratives

Im administrativen Bereich wurde die SEG 2022 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 wurde dort von der Leiterin der Plattform Claudia Rutte betreut. https://biol.scnat.ch/de.

Finanzielle Unterstützung

Die Gesuche des Präsidenten um finanzielle Unterstützung wurden von den angefragten Institutionen vollumfänglich bewilligt: Akademie der Naturwissenschaften Schweiz (SCNAT) in Bern: CHF 7’700.– und Biedermann-Mantel-Stiftung in Zürich: CHF 6‘000.–. Wir sind diesen beiden Geldgebern für ihre wichtigen Beiträge sehr dankbar.

Jahresversammlung, Generalversammlung und Vorstandssitzungen

Die Jahresversammlung entomo.ch 2022 inkl. Generalversammlung (GV) der SEG konnte nach der Online-Version im Jahr 2021 wieder in Präsenz durchgeführt werden und fand als zweitägige Tagung am 20. & 21. Mai 2022 am Museo cantonale di storia naturale in Lugano statt. Pandemiebedingt wurde die Jahrestagung allerdings auf Mai anstelle des traditionellen Zeitpunkts anfangs März verschoben. Es fanden zwei Vorstandssitzungen statt: Freitag, 20.

Mai in Lugano (1. reguläre halbjährliche Sitzung während der entomo.ch 2022), und Mittwoch, 2. November 2022 am Naturhistorischen Museum in Bern (2. reguläre halbjährliche Sitzung).

Website

Die Website der SEG, u.a. mit Informationen zur Jahrestagung entomo.ch, war auch dieses Jahr wieder im Portal Naturwissenschaften Schweiz der Akademie der Naturwissenschaften Schweiz (SCNAT) abrufbar: https://entomo.ch/de.

Für die Betreuung danke ich besonders Mariella Hobi, Nicola Frieden (beide Administration, Geschäftsstelle SCNAT), Marcel Falk (Leiter Kommunikation) und Andres Jordi (Chefredaktor Web).

Digitalisierung von entomologischen Zeitschriften

In Partnerschaft mit dem DigiCenter der ETH-Bibliothek arbeitet die SEG seit einigen Jahren intensiv an verschiedenen Digitalisierungsprojekten. Sobald ein Projekt zu Ende geführt wird, sind alle Bänder der vollständig digitalisierten Zeitschrift im pdf-Format online via der Webseite e-periodica frei zugänglich: www.e-periodica.ch.

Diese Digitalisierungsprojekte der SEG entstehen in Zusammenarbeit mit der ETH-Bibliothek in Zürich und dank der grosszügigen finanziellen Unterstützung der SCNAT. Unsere Ansprechpartnerin bei der ETH-Bibliothek war weiterhin Regina Wanger, die Leiterin des DigiCenters. Eine Unterseite der SEG-Webpage liefert eine Übersicht der bisher digitalisierten Zeitschriften sowie der laufenden Projekte inkl. Details zum Zugang via eperiodica: https://entomo.ch/en/publications/digitalisierungsprojekte.

Neben den verschiedenen Zeitschriften konnte die SEG ebenfalls in Zusammenarbeit mit dem DigiCenter zusätzlich das vergriffene Werk von Peter Sonderegger «Die Erebien der Schweiz (Lepidoptera: Satyrinae, Genus *Erebia*)» digitalisieren lassen. Dieses Buch ist nun via Zenodo verfügbar: https://zenodo.org/record/7409160#.Y5C43C3Mx3l.

Insekt des Jahres

In Zusammenarbeit mit entomologischen Gesellschaften in Deutschland und Österreich wurde für das Jahr 2023 das Landkärtchen (*Araschnia levana*, Nymphalidae) zum Insekt des Jahres 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_2023.

Im Namen des Vorstandes und der SEG-Mitgliedschaft bedanke ich mich nochmals besonders herzlich bei allen genannten Institutionen, Gremien und Personen für ihre wertvolle Unterstützung und ihren Einsatz!

Bericht des Bibliothekars, Philippe Jeanneret

En 2022, 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. Band 33, Ökologie und Atlas der Staphylinidae (ohne Pselaphinae und Scydmaeninae), liegt als fertiges PDF-Buch vor, konnte aber noch nicht veröffentlicht werden. Da dies der erste Band von Fauna Helvetica ist, der digital publiziert wird, muss der Shop von info fauna entsprechend angepasst werden. Gegenwärtig wird die Webseite von info fauna aber überarbeitet und der Verkauf des Buches kann erst integriert werden, wenn die neue Website eingerichtet ist. Das Manuskript über die Bombyliidae ist abgeschlossen und beim Layouter. Es ist geplant, dass der Band in der ersten Hälfte 2023 herauskommt. Ein Manuskript über die Singzikaden ist weit fortgeschritten und weitere Arbeiten sind in Vorbereitung. Für die gute Zusammenarbeit möchte ich Dr. Yves Gonseth und den Mitarbeiterinnen und Mitarbeitern von info fauna ganz herzlich danken. Die jetzt meist vergriffenen Bände von Insecta Helvetica wurden von der ETH-Bibliothek digitalisiert und stehen seit Kurzem unter www.e-periodica.ch zur freien Verfügung. Wir danken dem Digitalisierungsteam der ETH-Bibliothek.

Bericht des Chefredaktors von Alpine Entomology, Thibault Lachat

The sixth edition of Alpine Entomology was delivered in January 2023. This issue included 18 articles spanning 160 pages: eleven research articles, three short communications/news, one checklist, one *in memoriam*, one editorial, and the yearly report of the SES. A second topical collection has been launched about the impacts of alien insects in alpine ecosystems. Oliver Martin, Stève Breitenmoser and Dominique Mazzi are the editors of this collection. Authors invited to submit a manuscript will be granted a fee waiver.

This issue is the last for Thibault Lachat, the redactor in chief of Alpine Entomology since 2017. A successor will be elected by the committee of the SES; the new redactor in chief will be responsible for the seventh issue of Alpine Entomology.

Bericht des Quästors, Yohan Collaud

Aus der Jahresrechnung 2022 von Herrn Collaud ist folgende Tabelle entnommen:

Positionen / Objets	**Ausgaben / Dépenses**	**Einnahmen / Revenus**
Publikationskosten / Charges de publications:		
Publikation AE - Druck / Impression	6‘673.07	
Pensoft: Website, Open access	15‘072.75	
Publikation «Fauna Helvetica»	5.00	
Honorare Hauptreferenten / Honoraires des conférenciers principaux	1‘360.20	
ETH-Digitalisierungsprojekte / Projets de digitalisation ETH	4‘027.98	
Verwaltung / Administration	7‘899.80	
Beitrag sc|nat / Cotisation sc|nat	1‘533.00	
Arbeitsgruppenförderung / Groupes soutien de travail	1‘668.05	
Verkäufe Zeitschriften / Ventes magazines		0.00
Mitgliederbeiträge / Cotisations		15‘099.16
Verkäufe «Fauna Helvetica» / Ventes «Fauna Helvetica»		3’719.65
Beiträge / Subventions:		
sc|nat		10‘056.23
Biedermann-Mantel-Stiftung		6‘000.00
Spenden und sonstige Einnahmen / Dons et autres produits		90.00
Zinsen / Intérêts:		
SEG-Konten / Comptes SEG	98.92	
Wechselkursdifferenz / Différence de change	34.31	
«Fauna Helvetica»-Konto / Compte «Fauna Helvetica»	55.00	
Erhöhung von Rücklagen / Augmentation de réserve (résultat «Fauna Helvetica»)	1‘991.60	
Total / Totaux	**40‘419.68**	**34‘965.04**
Jahresverlust / Perte annuelle 2022	**-5‘454.64**	
	34‘965.04	34‘965.04

Die Erfolgsrechnung für das Jahr 2022 schloss mit einem Verlust von CHF 5‘454,64 und einem Vermögen von CHF 107‘452,92.

Bericht der Rechnungsrevisoren, Andreas Sanchez und Yannick Chittaro

Sehr geehrte Damen und Herren

Als Kontrollstelle der Schweizerischen Entomologischen Gesellschaft und der Entomo Helvetica haben wir die Jahresrechnung 2022 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.

Dem Quästor wird von den anwesenden Mitgliedern einstimmig Decharge erteilt. Michel Sartori, der seine Tätigkeit als Revisor niederlegt, wird für sein langjähriges Engagement im Amt verdankt.

Budget und Mitgliederbeiträge

Budget

Der Präsident stellt das Budget für 2023 vor, welches einen Verlust von CHF 4’750.- vorsieht.

Mitgliederbeiträge 2023

Die Beiträge bleiben erneut gleich: Mitglieder in der Schweiz zahlen CHF 60.-, Studierende oder sich anderweitig in Ausbildung befindende Mitglieder zahlen nur die Hälfte des ordentlichen Beitrags (CHF 30.-). Der Zeitrahmen für diesen reduzierten Beitrag wird von drei auf fünf Jahre erweitert. 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.

Statutenrevision

Der Präsident stellt die Beweggründe für die Revision vor. Die wichtigsten Punkte betreffen:

- Die explizite Bezeichnung unserer Zeitschrift als «Alpine Entomology».
- Die Beziehung der SEG zu den assoziierten Lokalgesellschaften und deren Zusammenarbeit mit der SEG und unserem Vorstand.
- Die Umwandlung des Amtes des Bibliothekars in das Amt des Medienverantwortlichen.

Alle weiteren kleineren Anpassungen von Formulierungen werden anschliessend umfassend präsentiert.

Die Statutenrevision wird ohne Anmerkungen einstimmig angenommen. Die aktuelle Version kann hier eingesehen werden: https://entomo.ch/de/portrait/steering_committee.

Personelles

Todesfälle

Den verstorbenen SEG-Mitgliedern Jacques Derron (Agrarwissenschaftler, Abteilungsleiter Entomologie am Agroscope Changins; 1945–2022) und Bernhard Merz (Experte für Diptera, Kurator Naturhistorisches Museum Genf; 1963–2023) wird mit einer Schweigeminute gedacht.

Vorstandswahlen für die Amtsperiode 2023–2026

Da alle Mitglieder der SEG genug Zeit haben sollen, sich auf die Wahlen und eine allfällige Kandidatur vorzubereiten, werden die Vorstandswahlen in eine ausserordentliche Sitzung via Videokonferenz ausgelagert (siehe oben). Die Sitzung findet am 27. März um 17:15 Uhr statt. Es sind zwölf Mitglieder anwesend.

- Dominique Mazzi vom Agroscope Cadenazzo wird einstimmig zur neuen Präsidentin gewählt und ist damit die erste Tessinerin in diesem Amt. Der bisherige Präsident Oliver Martin wechselt gemäss den Statuten zum Amt des Vizepräsidenten. Der bisherige Vizepräsident Hannes Baur verlässt den Vorstand.
- Yohan Collaud von info fauna in Neuchâtel übernimmt das Amt des Quästors, das er zuvor bereits ad interim geführt hatte.
- Jessica Litman vom Naturhistorischen Museum in Neuchâtel übernimmt den Posten der Chefredaktorin von «Alpine Entomology» von Thibault Lachat.
- Claudia Buser von der Eawag in Dübendorf übernimmt das neu geschaffene Amt der Medienverantwortlichen. Dafür wurde das Amt des Bibliothekars gestrichen; der ehemalige Bibliothekar Philippe Jeanneret wird Beisitzer im Vorstand.
- Jean-Luc Gattolliat von der Universität Lausanne stellt sich neben Andreas Sanchez neu als zweiter Revisor zur Verfügung.
- Bei den Vertretungen der assoziierten Lokalgesellschaften gibt es zwei Änderungen: Christophe Praz von der Universität Neuchâtel übernimmt von Yves Gonseth die
- Vertretung der «Société Neuchâteloise d’Entomologie» (SNE) und Bärbel Koch vom «Museo cantonale di storia naturale» in Lugano ist Vertreterin der neu gegründeten «Società entomologica della Svizzera italiana» (SENSI).

Neben der Wahl der neuen Präsidentin werden alle weiteren Änderungen im Vorstand gemeinsam einstimmig angenommen. Die Vertretungen der assoziierten Lokalgesellschaften im Vorstand der SEG werden einstimmig bestätigt.

Ende der ausserordentlichen Sitzung um 17:27 Uhr

Prix Moulines 2023

Der diesjährige Preisträger des Prix Moulines ist Christian Roesti, dessen hochattraktives Buch «Die Steinfliegen der Schweiz» (2021, Haupt Verlag, Bern) die Jury überzeugt hat. Das umfassende Werk enthält einen Bestimmungsschlüssel und stellt alle 126 derzeit bekannten Schweizer Steinfliegenarten im Portrait vor. Zahlreiche vom Autor selbst erstellte Fotos und Zeichnungen erleichtern Neulingen den Einstieg in diese oft vernachlässigte Insektengruppe.

Jahresversammlung 2024

Die nächste Jahresversammlung, die entomo.ch 2024, soll am 8. und 9. März am Naturhistorischen Museum Neuchâtel stattfinden.

Ende der Generalversammlung um 10:58 Uhr.

Zuchwil im Oktober 2023,
der Sekretär Marc Neumann.