

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

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

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

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Abstract

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

Key Words

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

Introduction

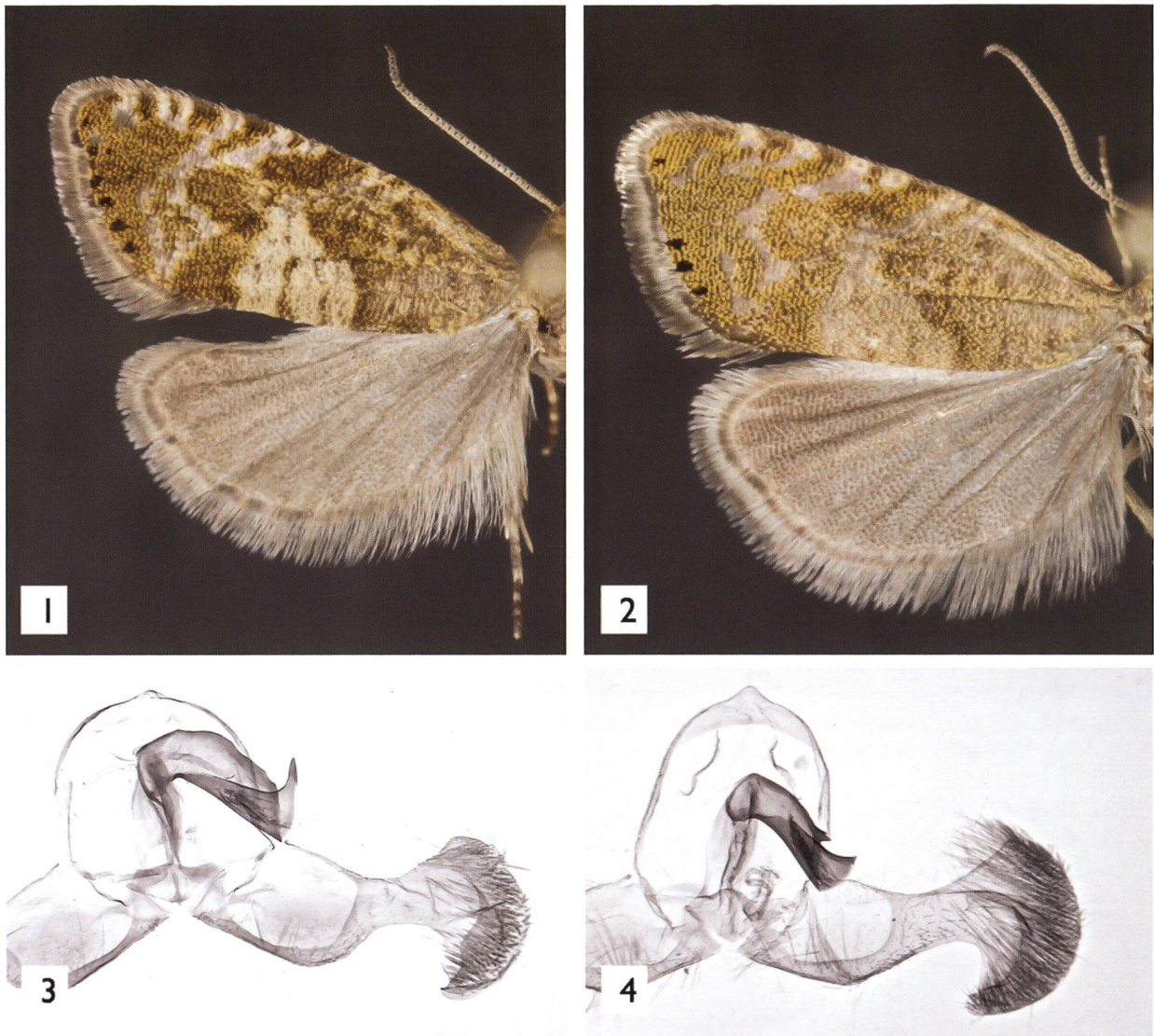
With currently 62 species records *Dichrorampha* Guenée, 1845 is the most diverse genus of European Tortricidae (Razowski 2003; Rennwald and Rodeland 2021). Though occasionally new taxa have been described during the last two decades, the genus can taxonomically be considered as well explored, however,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

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

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

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

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



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

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

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

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

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

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

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

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

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

Materials and methods

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

Specimen repositories:

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

The following specimen characteristics were analyzed:

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

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

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

Results

Wing pattern characteristics

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

Male genital features

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

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

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

Molecular analysis

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

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

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

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

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

Species	Mean Intra-Sp %	Max Intra-Sp %	Nearest species	Nearest Neighbour	Distance to NN %
<i>Dichrorampha acuminatana</i>	0.37	1.87	<i>Dichrorampha petiverella</i>	BTLBP376-11	4.83
<i>Dichrorampha aeratana</i>	1.32	5.08	<i>Dichrorampha sedatana</i>	LON5763-17	0.46
<i>Dichrorampha aguilana</i>	0.39	0.64	<i>Dichrorampha teichiana</i>	LEEU626-11	4.18
<i>Dichrorampha alpestrana</i>	0.72	2.5	<i>Dichrorampha velata</i>	PHLAD201-11	3.96
<i>Dichrorampha alpigenana</i>	1.54	3.1	<i>Dichrorampha inconspiqua</i>	BTLBP451-11	1.4
<i>Dichrorampha alpinana</i>	0.92	1.99	<i>Dichrorampha flavidorsana</i>	FBLMT309-09	2.5
<i>Dichrorampha bugnionana</i>	4.54	9.34	<i>Dichrorampha teichiana</i>	LEEU626-11	4.16
<i>Dichrorampha cacaleana</i>	0.17	0.17	<i>Dichrorampha carpatalpina</i>	LEASV661-19	7.94
<i>Dichrorampha carpatalpina</i>	N/A	0	<i>Dichrorampha alpigenana</i>	PHLAF568-11	5.65
<i>Dichrorampha chavanneana</i>	0.78	1.87	<i>Dichrorampha consortana</i>	FBLMZ645-12	4.92
<i>Dichrorampha cinerascens</i>	1.23	2.44	<i>Dichrorampha acuminatana</i>	LEAST411-17	6.4
<i>Dichrorampha cinerosana</i>	0.86	1.24	<i>Dichrorampha plumbagana</i>	CGUKC685-09	2.76
<i>Dichrorampha consortana</i>	0.27	0.58	<i>Dichrorampha chavanneana</i>	PHLAD710-11	4.92
<i>Dichrorampha dinarica</i>	0.15	0.31	<i>Dichrorampha thomanni</i>	LEASU278-18	4.47
<i>Dichrorampha eximia</i>	N/A	0	<i>Dichrorampha petiverella</i>	LASTS800-15	4.23
<i>Dichrorampha flavidorsana</i>	0.58	1.44	<i>Dichrorampha teichiana</i>	LEEU626-11	2.05
<i>Dichrorampha forsteri</i>	N/A	0	<i>Dichrorampha pentheriana</i>	LEATJ1152-16	5.91
<i>Dichrorampha gueneeana</i>	0.13	0.25	<i>Dichrorampha vancouverana</i>	LPAB581-08	0.15
<i>Dichrorampha heegerana</i>	0.23	0.46	<i>Dichrorampha teichiana</i>	LEEU626-11	3.1
<i>Dichrorampha incognitana</i>	N/A	0	<i>Dichrorampha teichiana</i>	LEEU626-11	3.47
<i>Dichrorampha inconspiqua</i>	N/A	0	<i>Dichrorampha infusata</i>	BTLBP373-11	0.93
<i>Dichrorampha infusata</i>	N/A	0	<i>Dichrorampha inconspiqua</i>	BTLBP451-11	0.93
<i>Dichrorampha ligulana</i>	1.17	1.76	<i>Dichrorampha petiverella</i>	NOELE683-20	4.42
<i>Dichrorampha melaniana</i>	N/A	0	<i>Dichrorampha sedatana</i>	PHLAC013-10	0
<i>Dichrorampha minutiana</i>	N/A	0	<i>Dichrorampha teichiana</i>	LEEU626-11	4.18
<i>Dichrorampha obscuratana</i>	0.83	1.72	<i>Dichrorampha plumbagana</i>	CGUKC685-09	3.6
<i>Dichrorampha pentheriana</i>	0	0	<i>Dichrorampha teichiana</i>	LEEU626-11	2.82
<i>Dichrorampha petiverella</i>	0.73	1.55	<i>Dichrorampha teichiana</i>	LEEU626-11	3.11
<i>Dichrorampha plumbagana</i>	0.32	1.04	<i>Dichrorampha cinerosana</i>	BTLBP382-11	2.76
<i>Dichrorampha plumbana</i>	1.26	3.65	<i>Dichrorampha sedatana</i>	PHLAC013-10	0
<i>Dichrorampha podoliensis</i>	0.89	0.89	<i>Dichrorampha petiverella</i>	TDAAT820-19	4.8
<i>Dichrorampha rejectana</i>	0	0	<i>Dichrorampha inconspiqua</i>	BTLBP451-11	3.64
<i>Dichrorampha rilana</i>	0	0	<i>Dichrorampha teichiana</i>	LEEU626-11	3.82
<i>Dichrorampha sedatana</i>	0.27	1.24	<i>Dichrorampha plumbana</i>	PHLAJ255-14	0
<i>Dichrorampha senectana</i>	N/A	0	<i>Dichrorampha sedatana</i>	PHLAC013-10	0.15
<i>Dichrorampha sequana</i>	0.44	0.92	<i>Dichrorampha teichiana</i>	LEEU626-11	5.31
<i>Dichrorampha simpliciana</i>	1.29	3.46	<i>Dichrorampha teichiana</i>	LEEU626-11	4.92
<i>Dichrorampha sylvicolana</i>	0	0	<i>Dichrorampha teichiana</i>	LEEU626-11	4.57
<i>Dichrorampha tarmanni</i>	0.79	2.18	<i>Dichrorampha sedatana</i>	PHLAC013-10	0
<i>Dichrorampha teichiana</i>	0	0	<i>Dichrorampha flavidorsana</i>	FBLMT309-09	2.05
<i>Dichrorampha thomanni</i>	N/A	0	<i>Dichrorampha dinarica</i>	PHLAE559-11	4.47
<i>Dichrorampha vancouverana</i>	0.11	0.33	<i>Dichrorampha gueneeana</i>	BTLBP389-11	0.15
<i>Dichrorampha velata</i>	0.05	0.31	<i>Dichrorampha alpestrana</i>	PHLAB566-10	3.96

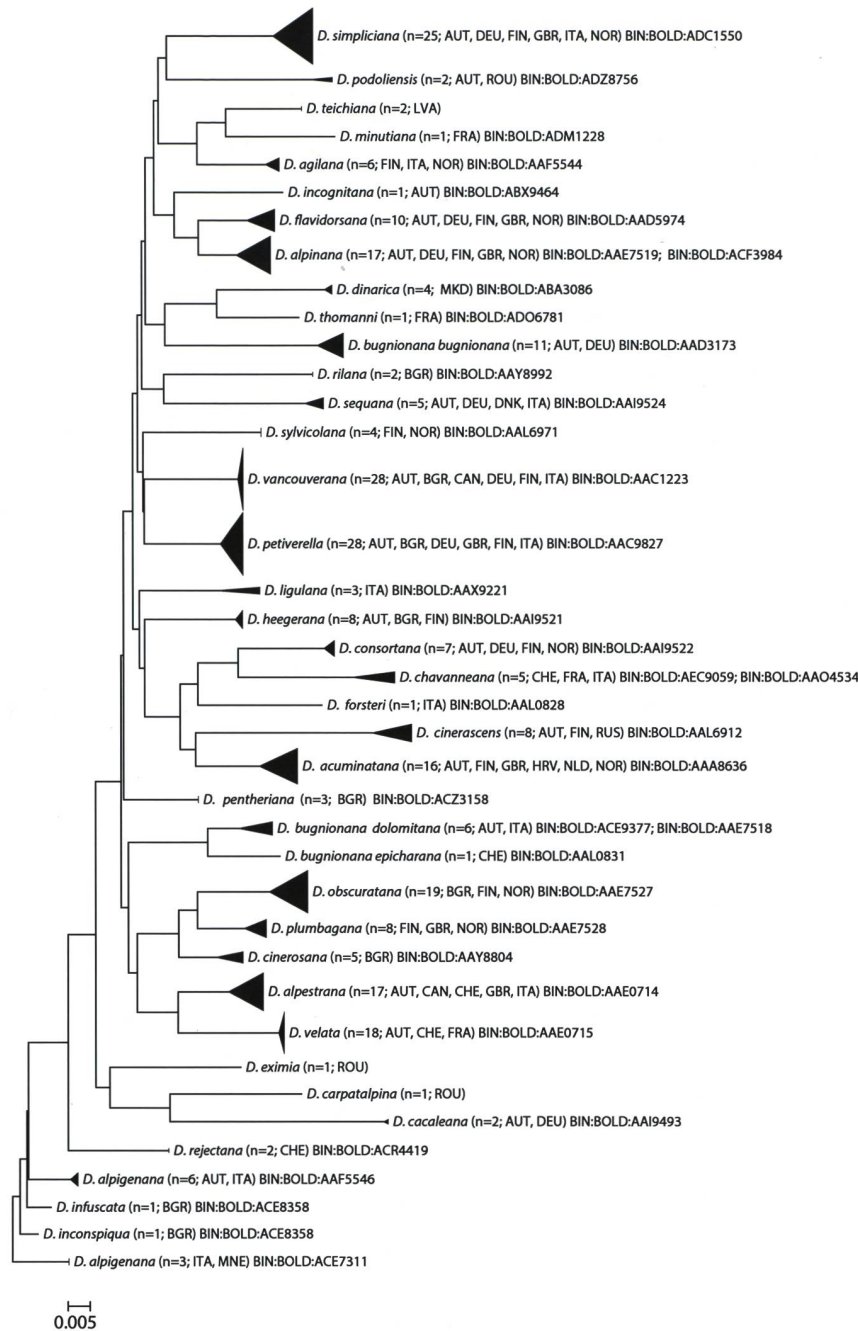


Figure 5. Neighbor-Joining tree of species in European *Dichrorampha* (Kimura 2 parameter, built with MEGA 6 cf. Tamura et al. 2013), only sequences (>500 bp) considered. Note: the scale bar only applies to internal branches between species. Width of triangles represent sample size, depth the genetic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

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

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

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

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



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

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

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

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

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

1) *Grapholitha alpestrana* [Zeller], 1843

Grapholitha alpestrana Herrich-Schäffer, 1851

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

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

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

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

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

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

2) *Dichrorampha tanaceti* Stainton, 1857

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

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

4) *Dichrorampha herbosana* Barrett, 1872

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

5) *Hemimene blasiana* Kennel, 1919

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

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

6) *Hemimene modestana* Müller-Rutz, 1922

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

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

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

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

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

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

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

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

Application of the correct name:

Dichrorampha montanana or *D. alpestrana*?

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

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

Synonymic list

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

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

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

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

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

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

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

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

Dichrorampha velata sp. nov.

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

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

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

Taxonomic part

Dichrorampha velata sp. nov.

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

Figs 2, 9, 11–16, 47

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



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

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

Derivatio nominis. "velatus" Latin, meaning "veiled" with respect to its confused history.

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

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

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

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

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

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

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

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

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



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

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

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

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

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



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

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

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

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

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

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



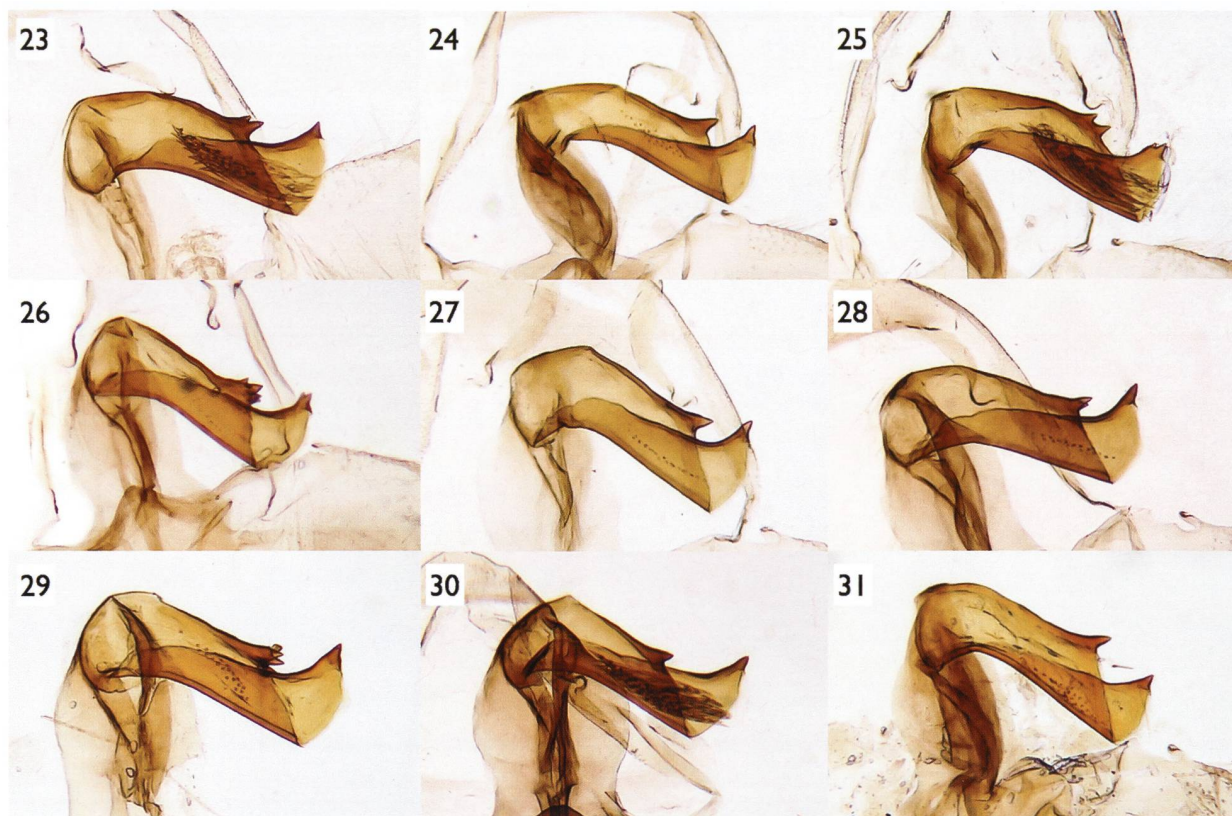
Figures 17–22. *Dichrorampha alpestrana*, variation in wing pattern; all: CH-La Punt, 1820 m, 19.6.2006–26.6.2006 all coll. J. Schmid.

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

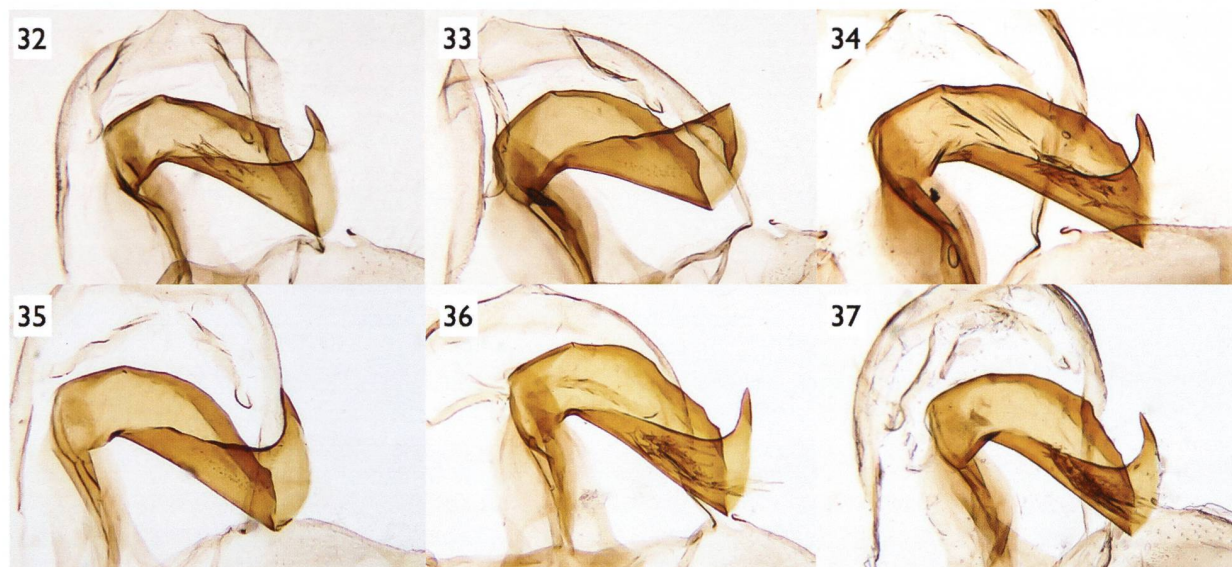
4.7.2009, Huemer/TLMF, DNA Barcode ID TLMF Lep 00818; 1♂: Kärnten, Saualpe, Umg. Wolfberger Hütte [46.83333°N, 14.65°E], 1500–1800 m, 19.6.2000, Wimmer/TLMF; 1♂: Niederösterreich, Seeau S Hollenstein/Ybbs [47.75°N, 14.78°E], 600 m, 1.6.1986, Lichtenberger /TLMF. Italy: 1♂: Südtirol, Vinschgau, Graun,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

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

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



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



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

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

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



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



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



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

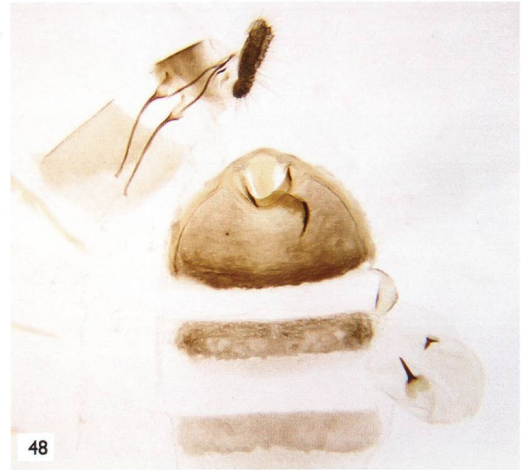
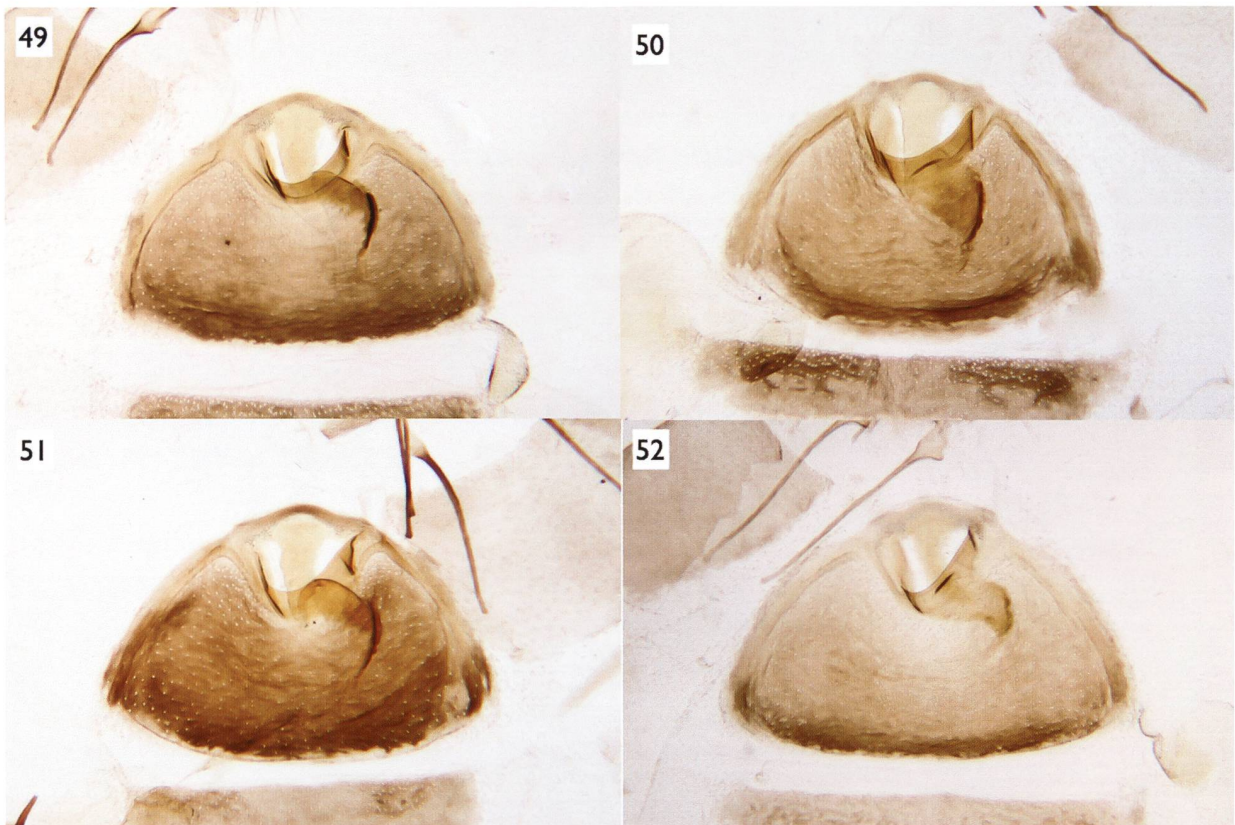


Figure 48. *Dichrorampha velata* sp. nov. paratype, female genitalia, CH-Cormoret BE, leg. Bryner.

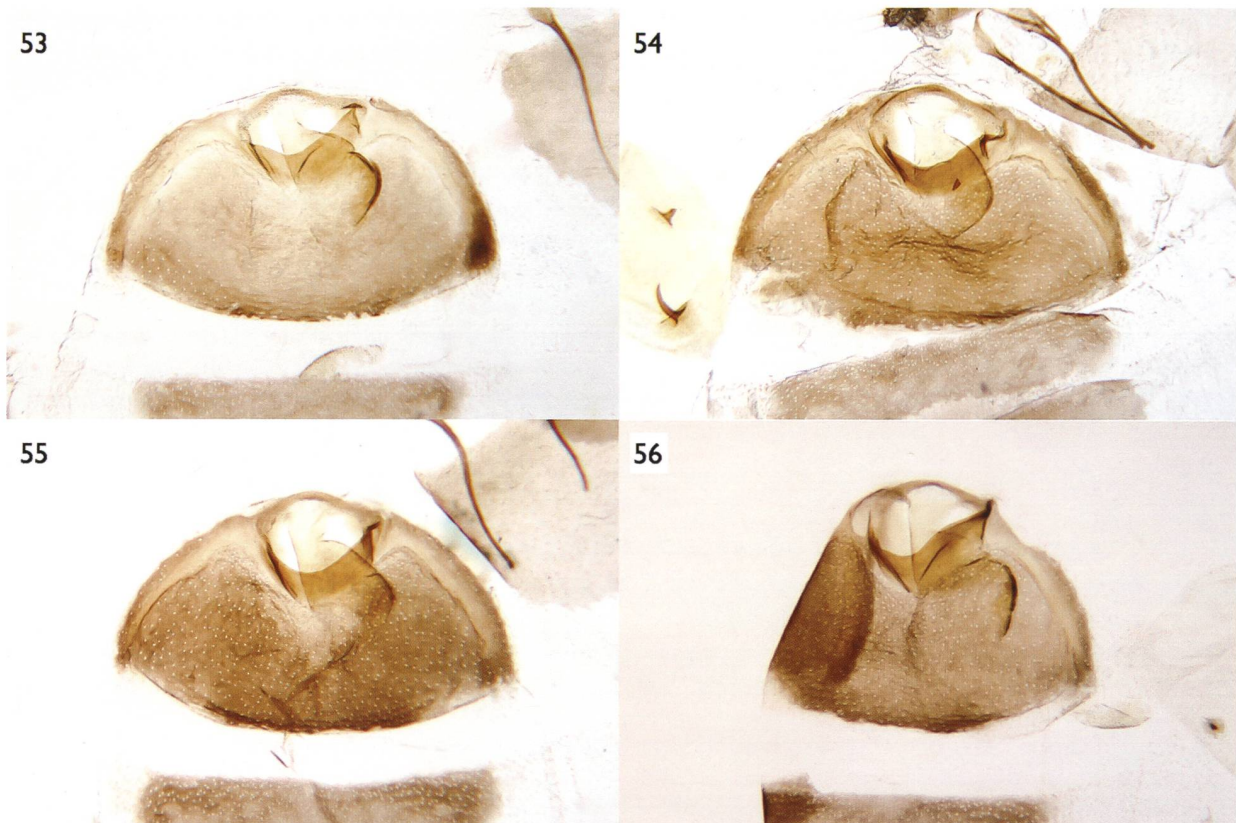


Figures 49–52. CH-Sedrun *Dichrorampha velata* sp. nov., female genitalia, variation in sterigma and ostium; 49. CH-Cormoret BE; 50. CH-Pigniu GR; 51. Sedrun GR; 52. CH-Villeret BE.

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

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

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



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

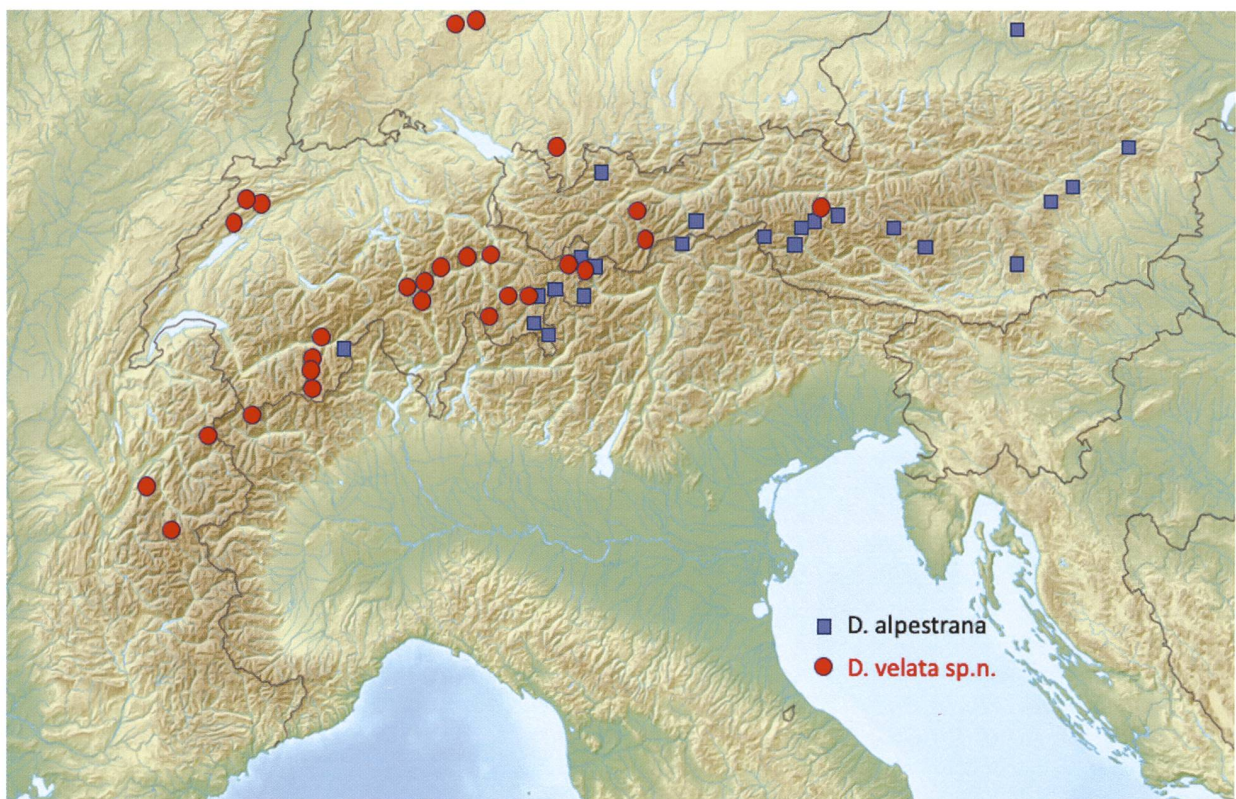


Figure 57. Proved records of *Dichrorampha velata* sp. nov. (red dots) and *D. alpestrana* (blue squares) in European Alps and nearby areas.

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

Discussion

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

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

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

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

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

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