

Observations on the *Isturgia limbaria* (Fabricius, 1775) / *roraria* (Fabricius, 1776) complex (Lepidoptera, Geometridae, Ennominae)

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Abstract. The *Isturgia limbaria* (Fabricius, 1775)/*roraria* (Fabricius, 1776) complex is analyzed, taking into consideration the external morphology of the adults (coloration and pattern of upperside and underside of wings), the morphology of the female genitalia (signum and lamella postvaginalis), of the tympanal organs and of the preimaginal stages, as well as molecular data. Based on the molecular data and morphology of signum and tympanic organs, the populations of this complex can be divided into two groups, one more western (with the taxa *limbaria* s. str. and *delimbaria*), distributed east to north-western Italy and part of Germany, and one more eastern (with the taxa *roraria* s. str., *rablensis* and *anzascaria*), distributed west to northern and eastern Piedmont (Italy) and north-eastern and south-eastern Germany. However, there are no consistent differences between the two groups in the diagnostic characters used until now to identify the two taxa (pattern of the wing upperside and underside). Although there is a considerable genetic distance between these two groups, the correlation between molecular differences and morphological characters (size of the signum and presence—or absence—of a roundish lobe in the bullae tympani) is not completely constant and the two groups of populations are not completely separated from each other: some populations of the northern Apennines (taxon *delimbaria*) cannot be clearly attributed to one or the other group. In the absence of constant morphological characters associated with the molecular differences and in the presence of Italian populations with intermediate characters, we suggest that the different taxa of this complex be considered as subspecies of the same species, as already proposed by Povolný and Moucha (1957, 1959). However, the data available do not allow definitive clarification of the taxonomic problem and further research is necessary.

Introduction

Fabricius described *Phalaena limbaria* and *P. roraria* respectively in 1775 and 1776. Zeller (1868) described *Fidonia limbaria* var. *rablensis* (from the Julian Alps), as intermediate between *roraria* and *limbaria*, but attributed it to the latter based on the characteristics of the wing underside. Prout (1915) and Wehrli (1940) treated this taxon as *Isturgia limbaria* var. *rablensis*, distributed from northern Italy to Albania and to the southern Carpathians. Povolný and Moucha (1957, 1959) downgraded *roraria* to a subspecies of *limbaria*: in their opinion the former is distributed in central and south-eastern Europe, the latter mainly in western Europe, but the populations from the Balkans and the southern Alps (taxon *rablensis*) have mixed characters and cannot be attributed objectively to one or the other; in addition, both *limbaria* and *roraria* are very variable and there are no differences in the genitalia, habitat and foodplant. According to these authors in the Riss-

Würm interglacial period there would still have been a single species, which during the Würm glaciation would have been divided into two groups of populations, confined to different glacial refuges (south-western and south-eastern European). Later, after long isolation, the two groups of populations would have come into contact again. In Central Europe the differentiation due to the isolation period would have been sufficient to prevent hybridization between the two forms, while to the south of the Alps the isolation would have been shorter (or would not have been complete) and therefore hybridization would have been possible. According to the same authors a similar example would be represented by *Polyommatus eros eros* (Ochsenheimer, 1808) and *Polyommatus eros eroides* (Frivaldsky, 1835) (Lycaenidae).

Also Patočka (2004) considered *roraria* as a subspecies of *limbaria*. In contrast, Lehmann (1990) transferred *rablensis* from a subspecies of *limbaria* to a subspecies of *roraria*, based on Gelbrecht's research, who examined mainly the characteristics of the larvae and pupae and the size of the signum in female genitalia (Gelbrecht, pers. comm.); however, Gelbrecht did not examine specimens from the Julian Alps (locus typicus of *rablensis*), but only from Bulgaria (Vitosha). His point of view was accepted by Viidalepp (1996) and Beshkov (2001), while Huemer and Tarmann (1993), Flamigni et al. (2007) and Leraut (2009) continued to treat this taxon as *Isturgia limbaria rablensis*. Hausmann (2001) mentioned and figured southern Alpine populations as a model case for hybridization in the evolutionary history of species complexes.

Based on genetic data, Skou and Sihvonen (2015) attributed the populations from the Balkans and the Julian Alps to *roraria*, but not those from South Tyrol (Monte Baldo), which grouped in a different genetic cluster but are practically identical to those from the Julian Alps in the wing pattern. Without transferring *rablensis* from the status of subspecies of *limbaria* to a subspecies of *roraria*, they suggested that the *limbaria/roraria* species complex needs a thorough detailed analysis.

The present study aims to provide a contribution to the clarification of the taxonomic problems still unresolved, through an analysis of the different populations that make up this complex.

Material and methods

The study is based on material deposited in the collections listed in Table 1 (see section Taxonomy for details on specimens examined). These observations were also supplemented by the examination of images in the literature and on websites. Unpublished information on the morphology of larvae and pupae have been provided by Jörg Gelbrecht (Königs Wusterhausen, Germany).

Taxon delimitation was based on the combined study of external morphology of the adults (coloration and pattern of the upperside and underside wings), morphology of the female genitalia (signum and lamella postvaginalis) and tympanal organs, as well as of molecular data.

For the extraction of the female genitalia and tympanal organs the abdomen was macerated cold in a 20% KOH solution for 12 hours. Then the longitudinally sectioned abdomen was stained using chlorazol black-alcohol mixture for two minutes. Genitalia were cleaned in water and mounted on a slide in dimethyl hydantoin formaldehyde (DMHF). Tympanal organs were removed from the abdomen, cleaned and mounted on a slide.

Because the signum is stellate with a more or less elliptical shape, in each specimen the smaller diameter and the larger diameter of this ellipse were measured (both up to the ends of the tips), averaging the two diameters.

Table 1. Abbreviations of the collections.

KLM: Landesmuseum Kärnten, Klagenfurt, Austria	RCEF: Research Collection of Egbert Friedrich
MNC: Museum für Naturkunde, Chemnitz, Germany	RCGF: Research Collection of Gabriele Fiumi
MSNB: Museo civico di Scienze Naturali “E. Caffi”, Bergamo, Italy	RCGG: Research Collection of Guido Govi
NHMW: Museum of Natural History of Vienna	RCJV: Research Collection of Joachim Viehmann
RCAH: Research Collection of Alfred Haslberger	RCSB: Research Collection of Stoyan Beshkov
RCBD: Research Collection of Bernard Dardenne	TLMF: Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
RCCF: Research Collection of Claudio Flamigni	ZSM SNSB: Bavarian State Collection of Zoology, Munich
RCCM: Research Collection of Carlo Morandini	(Zoologische Staatssammlung München)

For the DNA analyses, one leg was removed from dried specimens. DNA extraction, amplification, and sequencing of the barcode region of the mitochondrial cytochrome c oxidase I (COI) gene (658 base pairs) were carried out in the Canadian Centre for DNA Barcoding, Ontario, Canada, using standard protocols (Ivanova et al. 2006; deWaard et al. 2008). Unfortunately, the barcoding of only one of our specimens (BC ZSM Lep 97046, from Lombardy) was successful. For this research all the data in the BOLD database (Ratnasingham and Hebert 2007) were also used: data on utilized sequences are summarized in Table 2.

The Barcode Index Number (BIN) is an online framework of BOLD database that clusters barcode sequences algorithmically (Ratnasingham and Hebert 2007).

Information on molecular data was provided by A. Hausmann (SNSB-Bavarian State Collection of Zoology, Munich, Germany), who also examined the specimens from the ZSM collection. Sequence divergence was calculated by Hausmann using the Kimura 2-parameter model (Kimura 1980) and the neighbour-joining algorithm (Saitou and Nei 1987), as implemented in BOLD.

Results

Molecular data

The results from the molecular analysis are shown in Figure A1 (see Appendix I).

The *limbaria/roraria* complex genetically splits up into three genetic clusters. BOLD:AAF3598 corresponds to the taxa *limbaria* s. str. and *delimbaria*; BOLD:ACX8520 to the westernmost populations of the taxon *rablensis* (Lombardy and Monte Baldo in Italy, Carinthia in Austria); BOLD:AAF3597 to the remaining populations of *rablensis* (from the Julians Alps to Bulgaria and Romania) and to the taxon *roraria* s. str.. The minimum distance of AAF3598 from the other two BINs is 3.95%, while that between AAF3597 and ACX8520 is 2.0%. Further information is given in the treatment of single taxa.

Figure 1 shows the distribution of the barcode clusters of the complex *limbaria/roraria* in northern Italy and southern Austria; Figure 2 the distribution of the taxa of the same complex in northern Italy.

Morphological characters

The diagnostic characters of *I. limbaria* and *I. roraria* are illustrated by Skou and Sihvonen (2015: 98, text-figs 37–40): wings, upperside irrorated with brown scales, terminal area dark brown in *limbaria*; wings, upperside striated with brown scales, terminal area light brown in *roraria*; hindwings, underside with radiating whitish lines in *limbaria*, without whitish lines in *roraria*. On the basis of these characters, the taxa *limbaria* s. str. (Figs 3, 8, 13, 18), *delimbaria* (Figs 4, 9, 14, 19), *anzascaria* (Figs 5, 10, 15, 20) and *roraria* s. str. (Figs 7, 12, 17, 22) can be identified without prob-

Table 2. Barcoded specimens (from BOLD data systems).

Taxon	Country	Region	Locality and date	Collector and collection	Specimen ID	Barcode Index Number (BIN)
<i>limbaria</i> s. str.	Germany	Hesse	Lahn-Dill-Kreis, Hirzenhain, 4.vii.2002	D. Feierabend leg., RCJV	BC ZFMK Lep 00683	BOLD:AAF3598
<i>limbaria</i> s. str.	Germany	Thuringia	Gumpelstadt, Jauchsentäl, 11.vi.2006	U. Buechner leg., MNC	SE MNC Lep 00599	BOLD:AAF3598
<i>limbaria</i> s. str.	Germany	Thuringia	Wahlhausen, 22.v.1998	R. Rommel leg., MNC	SE MNC Lep 00600	BOLD:AAF3598
<i>limbaria</i> s. str.	Germany	Bavaria	Oberpfalz, Schwarzenbach, 11.v.1994	G. Nowak leg., MNC	SE MNC Lep 00601	BOLD:AAF3598
<i>limbaria</i> s. str.	France	Upper Normandy	Seine Maritime, Anneville-Ambourville, 22.v.1995	B. Dardenne leg., RCBD	LN-BD1103	BOLD:AAF3598
<i>delimbaria</i>	Italy	Liguria	Ligurian Alps, Ventimiglia, 600 m, 27.v.2001	E.O. Bonora leg., RCJV	BC ZFMK Lep 00684	BOLD:AAF3598
<i>delimbaria</i>	Italy	Tuscany	Apuan Alps, under Monte Corchia, Passo Croce, 18.vi.1999	L. Dapporto leg., ZSM	BC ZSM Lep 63447	BOLD:AAF3598
<i>rablensis</i>	Italy	Lombardy	Bergamasque Prealps, Camerata Cornello, towards Passo Griaieggio, 23.vii.2010	M. Massaro and W. Zucchelli leg., MSNB	BC ZSM Lep 97046	BOLD:ACX8520
<i>rablensis</i>	Italy	Trentino-Alto Adige	Monte Baldo, 1550 m, 8.vi.1994	S. Erlacher leg., MNC	SE MNC Lep 00609	BOLD:ACX8520
<i>rablensis</i>	Austria	Carinthia	[Gitschtal], 46.678N, 13.313E, 1020 m, 29.v.2015	Ch. Wieser leg., KLM	KLM Lep 03479	BOLD:ACX8520
<i>rablensis</i>	Italy	Friuli-Venezia Giulia	Julian Prealps, Val Venzonassa, Jof Ungarina SW side – Malga Confin W, 1280 m, 12.vi.2007	P. Huemer leg., TLMF	TLMF Lep 00212, TLMF Lep 04447, TLMF Lep 04448	BOLD:AAF3597
<i>rablensis</i>	Bulgaria	W Stara Planina Mts	between Gorni Lom Village and Midzhur Top, 1425 m, 14.vii.2009	S. Beshkov leg., RCSB	BC SB Lep 0017	BOLD:AAF3597
<i>rablensis</i>	Romania	Buzău County	Eastern Carpathians, Nemira Mountains, Lassuag, 1100 m, 22.vi.1996	S. and Z. Kovacs leg., ZSM	BC ZSM Lep 73989	BOLD:AAF3597
<i>rablensis</i>	Romania	Dâmbovița County	Southern Carpathians, Bucegi Mountains, Valea Jepii, 1800 m, 7.vi.2007	S. and Z. Kovacs leg., ZSM	BC ZSM Lep 73986, BC ZSM Lep 73987	BOLD:AAF3597
<i>roraria</i> s. str.	Germany	Thuringia	Erlau, Zeltplatz, 4.vii.1999	S. Erlacher leg., MNC	SE MNC Lep 00605	BOLD:AAF3597
<i>roraria</i> s. str.	Germany	Saxony-Anhalt	Bitterfeld, Marke: 0.5 km east the motorway exit Dessau-Süd, 85 m, 24.v.2012	J. Gelbrecht leg., ZSM	BC ZSM Lep 91967	BOLD:AAF3597
<i>roraria</i> s. str.	Germany	Bavaria	Spalt, 6.v.1997	A. Zoglauer leg., RCJV	BC ZFMK Lep 00685	BOLD:AAF3597
<i>roraria</i> s. str.	Germany	Bavaria	Mittelfranken, Roth, Spalt, 400 m, 17.vii.2007	A. Zoglauer leg., RCAH	BC ZSM Lep 24010	BOLD:AAF3597
<i>roraria</i> s. str.	Germany	Bavaria	Mittelfranken, Nuernberger Land, Leinburg, Wolfgrube Ost 405 m, 20.vii.2010	A. H. Segerer leg., ZSM	BC ZSM Lep 51392	BOLD:AAF3597

lems (the first three as *limbaria* s. l.). In contrast, the identification of the taxon *rablensis* is problematic: on the basis of the wing underside (Figs 16, 21) it should belong to *limbaria* (hindwing with radiating whitish lines), but the upperside (Figs 6, 11) of some specimens matches *roraria*, while that of others matches *limbaria* (above all in the most western part of its range). According

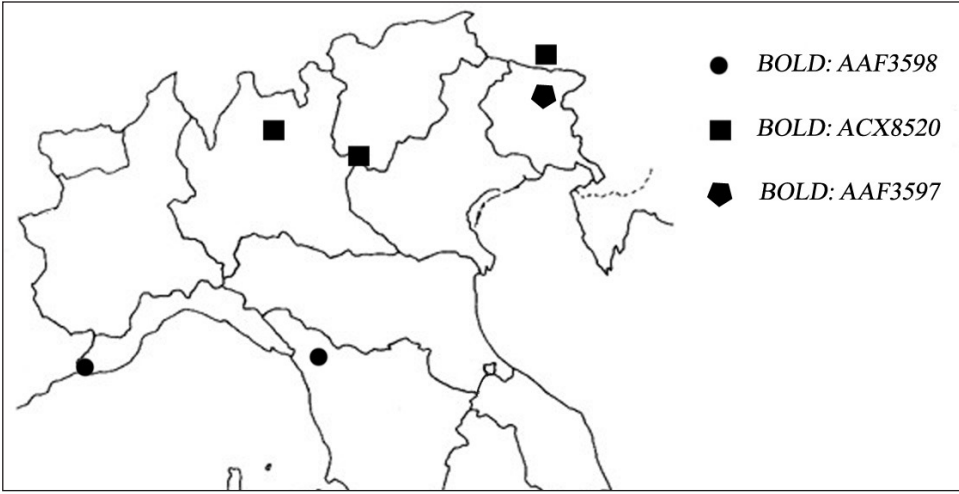


Figure 1. Distribution of the BINs of the complex *limbaria/roraria* in northern Italy and southern Austria.

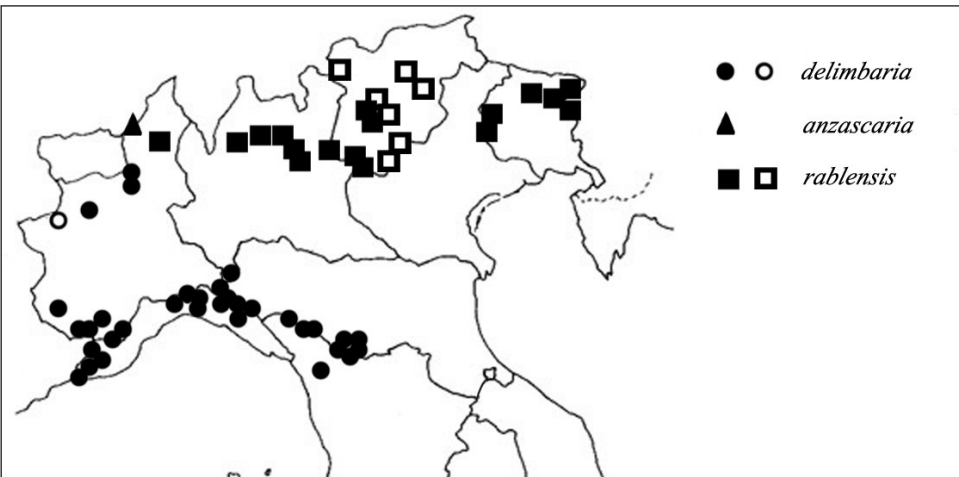
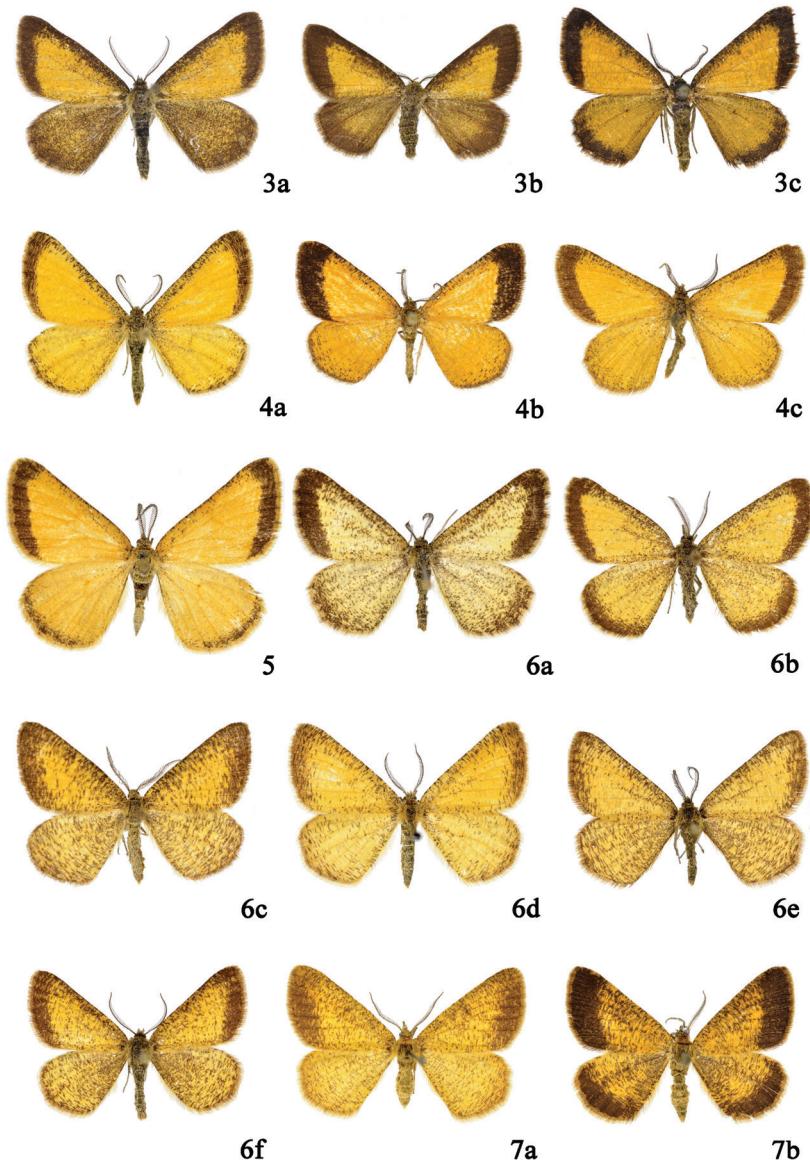


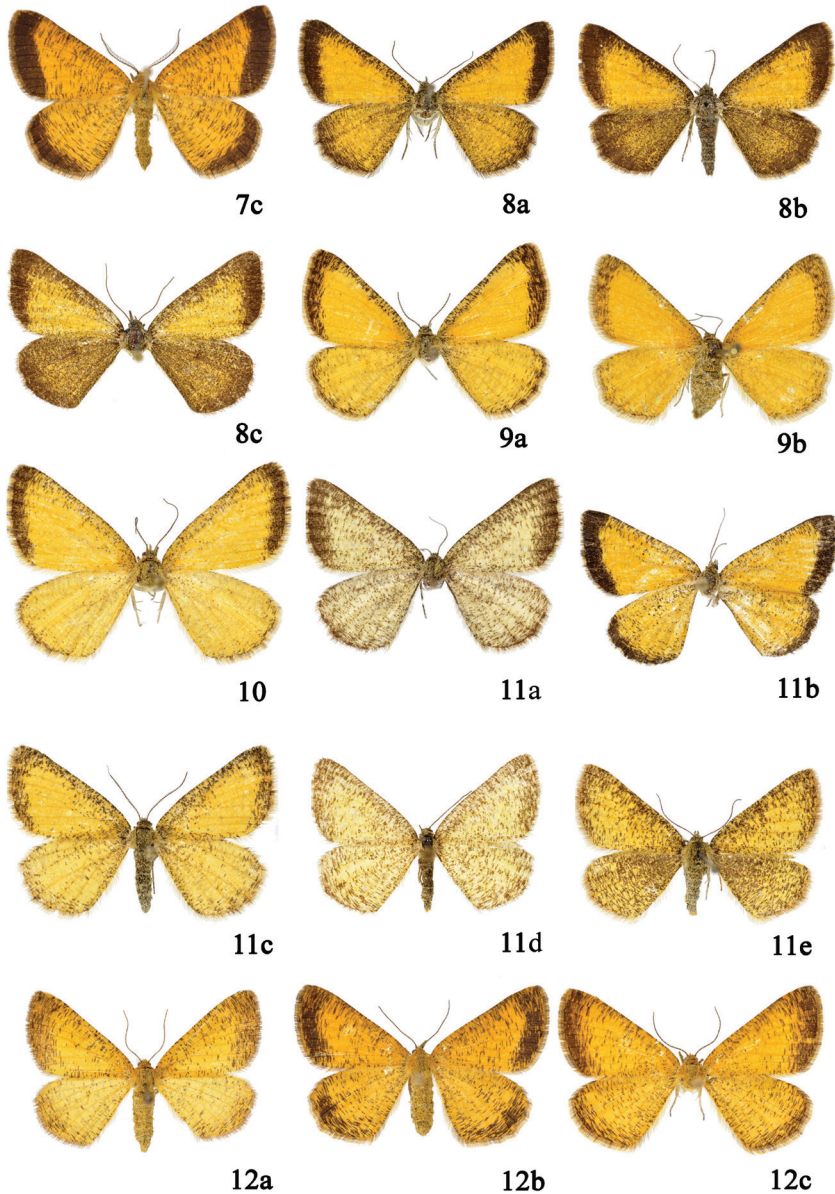
Figure 2. Distribution of the taxa of the complex *limbaria/roraria* in northern Italy (the open symbols refer to records not verified by the authors).

to Fajčík and Slamka (1996) the width of the dark terminal fascia is also a diagnostic character; wider in *roraria* (when it is present), narrower in *limbaria*.

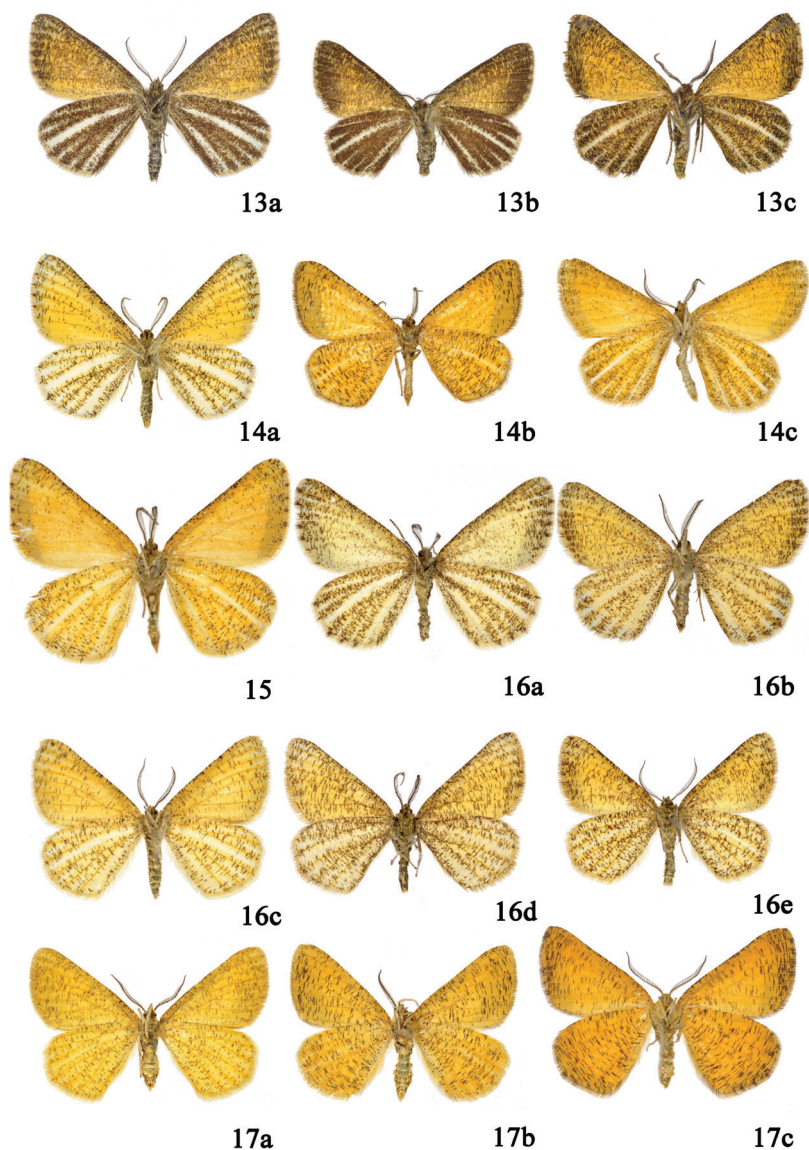
According to Skou and Sihvonen (2015) there are no differences in the male and female genitalia of *limbaria* and *roraria*, but in the female of *roraria* the lamella postvaginalis is often more sclerotized, with the posterior margin round, but they state that these differences are not clear-cut. According to the same authors the bullae tympani have a roundish lobe in *limbaria*, but not in *roraria*; however, they suggest that the reliability of this character needs to be tested on more extensive material from the whole distribution range of the complex.



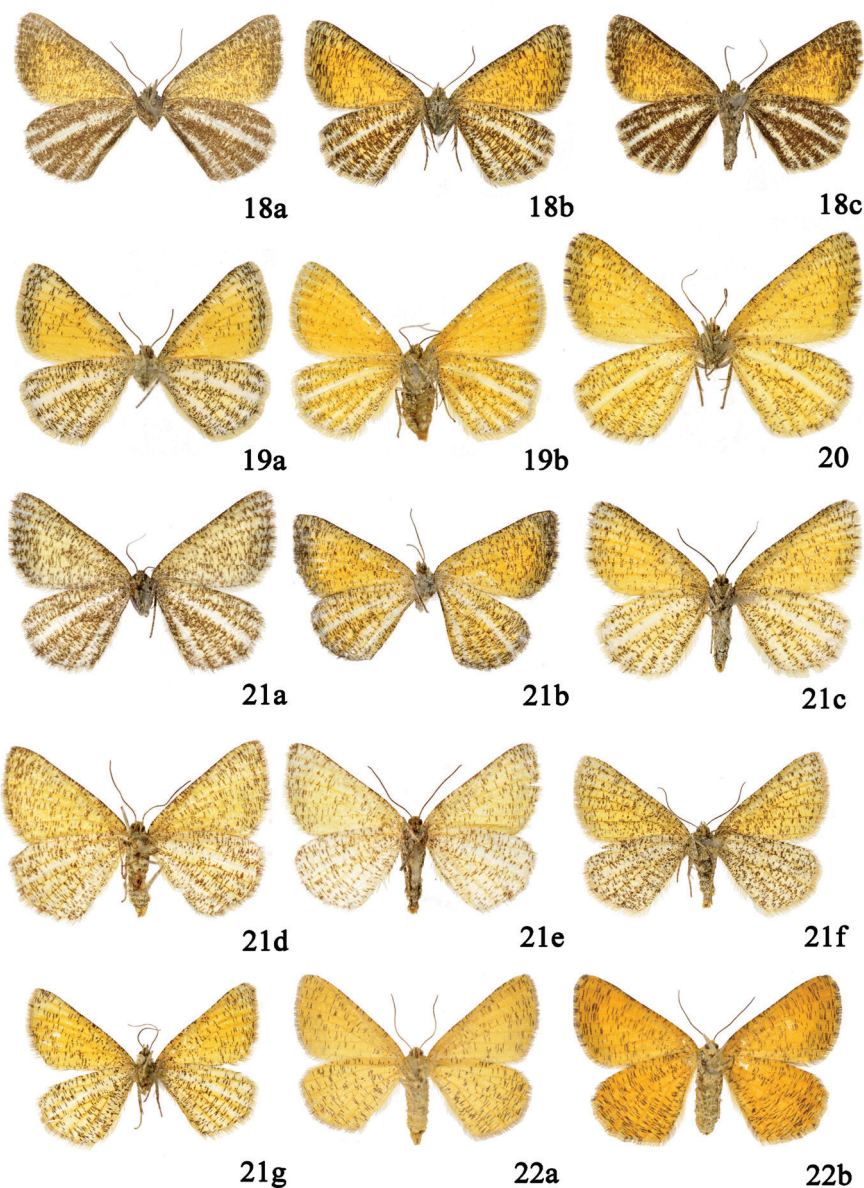
Figures 3–7. Upperside of males (3–7) and females (8–12). **3a.** *I. l. limbaria* ♂, Germany: North Rhine-Westphalia, Wuppertal. **3b.** *I. l. limbaria* ♂, Switzerland: Valais, district of Sierre, Val d’Anniviers. **3c.** *I. l. limbaria* ♂, Spain: Aragon, province of Huesca, Fanlo. **4a.** *I. l. delimbaria* ♂, France: Vaucluse, Gignac. **4b.** *I. l. delimbaria* f. *pedemontaria* ♂, Italy: Piedmont, Ligurian Apennines, Capanne Superiori di Marcarolo. **4c.** *I. l. delimbaria* ♂, Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Monte Pizzo. **5.** *I. l. anzascaria* ♂, Italy: Piedmont, Monte Rosa, Macugnaga, under Alpe Bill. **6a.** *I. l. rablensis* ♂, Italy: Piedmont, province of Verbania-Cusio-Ossola, Valstrona, Campello Monti. **6b.** *I. l. rablensis* ♂, Italy: Trentino-Alto Adige/Veneto, Monte Baldo, Cima Valdritta. **6c.** *I. l. rablensis* ♂, Italy: Friuli-Venezia Giulia, Carnic Prealps, Barcis, Prescudin. **6d.** *I. l. rablensis* ♂, Italy: Friuli-Venezia Giulia, Julian Prealps, Matajur. **6e.** *I. l. rablensis* ♂, Macedonia: Baba Planina [Baba Mountain], Pelister, Golemozero [Large Lake]. **6f.** *I. l. rablensis* ♂, Bulgaria: Sofia, Vitoša [Vitosha]. **7a.** *I. l. roraria* ♂, Czech Republic: Moravia, Bílé Karpaty [White Carpathians], Machová. **7b.** *I. l. roraria* ♂, Czech Republic: Moravia, Vápenky.



Figures 7c–12. Upperside of males (3–7) and females (8–12). **7c.** *I. l. roraria* ♂, Germany: Bavaria, surroundings of Spalt. **8a.** *I. l. limbaria* ♀, Belgium: Comblain[-au-Pont]. **8b.** *I. l. limbaria* ♀, Switzerland: Valais, district of Sierre, Val d’Anniviers. **8c.** *I. l. limbaria* ♀, Spain: Aragon, province of Huesca, Fanlo. **9a.** *I. l. delimbaria* ♀, France: Alpes-Maritimes, Grasse above Gourdon. **9b.** *I. l. delimbaria* ♀, Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Monte Grande. **10.** *I. l. anzascaria* ♀, Italy: Piedmont, Monte Rosa, Macugnaga, under Alpe Bill. **11a.** *I. l. rablensis* ♀, Italy: Piedmont, province of Verbania-Cusio-Ossola, Valstrona, Campello Monti. **11b.** *I. l. rablensis* ♀, Italy: Lombardy, Bergamasque Prealps, Camerata Cornello, towards Passo Grialeggio. **11c.** *I. l. rablensis* ♀, Italy: Trentino-Alto Adige, Brentonico, [Monte Baldo]. **11d.** *I. l. rablensis* ♀, Italy: Friuli-Venezia Giulia, Julian Alps, Jof Montasio. **11e.** *I. l. rablensis* ♀, Bulgaria: Sofia, Vitoša [Vitosha]. **12a.** *I. l. roraria* ♀, Slovakia: Handlová. **12b.** *I. l. roraria* ♀, Germany: Bavaria, surroundings of Spalt. **12c.** *I. l. roraria* ♀, Germany: Bavaria, Spalt.



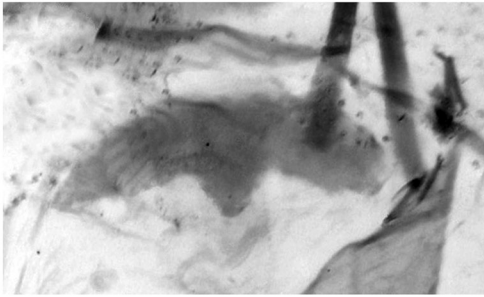
Figures 13–17. Underside of males (13–17). **13a.** *I. l. limbaria* ♂, Germany: North Rhine-Westphalia, Wuppertal. **13b.** *I. l. limbaria* ♂, Switzerland: Valais, district of Sierre, Val d’Anniviers. **13c.** *I. l. limbaria* ♂, Spain: Aragon, province of Huesca, Fanlo. **14a.** *I. l. delimbaria* ♂, France: Vaucluse, Gignac. **14b.** *I. l. delimbaria* f. *pedemontaria* ♂, Italy: Piedmont, Ligurian Apennines, Capanne Superiori di Marcarolo. **14c.** *I. l. delimbaria* ♂, Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Monte Pizzo. **15.** *I. l. anzascharia* ♂, Italy: Piedmont, Monte Rosa, Macugnaga, under Alpe Bill. **16a.** *I. l. rablensis* ♂, Italy: Piedmont, province of Verbania-Cusio-Ossola, Valstrona, Campello Monti. **16b.** *I. l. rablensis* ♂, Italy: Trentino-Alto Adige/Veneto, Monte Baldo, Cima Valdritta. **16c.** *I. l. rablensis* ♂, Italy: Friuli-Venezia Giulia, Julian Prealps, Matajur. **16d.** *I. l. rablensis* ♂, Macedonia: Baba Planina [Baba Mountain], Pelister, Golemo ezero [Large Lake]. **16e.** *I. l. rablensis* ♂, Bulgaria: Sofia, Vitoša [Vitosha]. **17a.** *I. l. roraria* ♂, Czech Republic: Moravia, Bílé Karpaty [White Carpathians], Machová. **17b.** *I. l. roraria* ♂, Czech Republic: Moravia, Vápenky. **17c.** *I. l. roraria* ♂, Germany: Bavaria, surroundings of Spalt



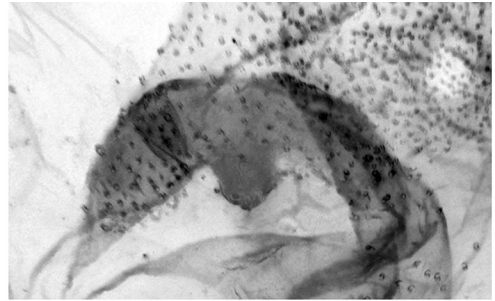
Figures 18–22. Underside of females (18–22). **18a.** *I. l. limbaria* ♀, Belgium: Comblain[au-Pont]. **18b.** *I. l. limbaria* ♀, Switzerland: Valais, district of Sierre, Val d’Anniviers. **18c.** *I. l. limbaria* ♀, Spain: Aragon, province of Huesca, Fanlo. **19a.** *I. l. delimbaria* ♀, France: Alpes-Maritimes, Grasse above Gourdon. **19b.** *I. l. delimbaria* ♀, Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Monte Grande. **20.** *I. l. anzascaria* ♀, Italy: Piedmont, Monte Rosa, Macugnaga, under Alpe Bill. **21a.** *I. l. rablensis* ♀, Italy: Piedmont, province of Verbania-Cusio-Ossola, Valstrona, Campello Monti. **21b.** *I. l. rablensis* ♀, Italy: Lombardy, Bergamasque Prealps, Camerata Cornello, towards Passo Grialeggio. **21c.** *I. l. rablensis* ♀, Italy: Trentino-Alto Adige, Brentonico, [Monte Baldo]. **21d.** *I. l. rablensis* ♀, Italy: Friuli-Venezia Giulia, Carnic Prealps, Barcis, Prescudin. **21e.** *I. l. rablensis* ♀, Italy: Friuli-Venezia Giulia, Julian Alps, Jof Montasio. **21f.** *I. l. rablensis* ♀, Bulgaria: Sofia, Vitoša [Vitosha]. **21g.** *I. l. rablensis* ♀, Bulgaria: Sofia, Vitoscha [Vitosha]. **22a.** *I. l. roraria* ♀, Slovakia: Handlová. **22b.** *I. l. roraria* ♀, Germany: Bavaria, surroundings of Spalt.

J. Gelbrecht (pers. comm.) found differences in the size of the signum in the female genitalia.

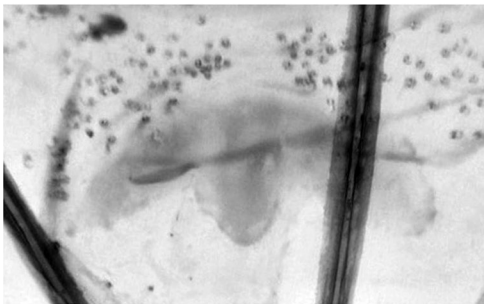
The morphological characters observed in the material examined by us are summarized in Table 3 (further information in the treatment of single taxa in the section Taxonomy). Some examples of variability of the lamella postvaginalis, of the tympanic organs and of the signum are illustrated respectively in Figures 23–34.



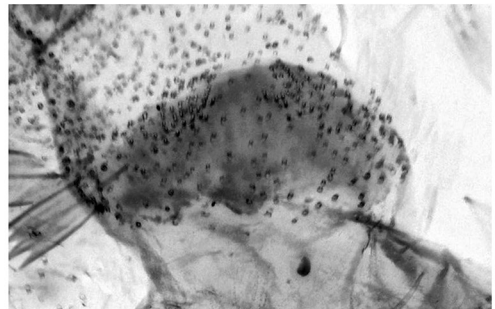
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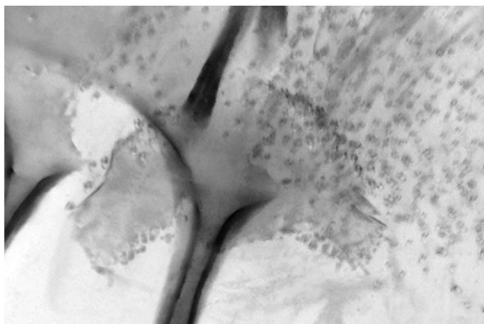
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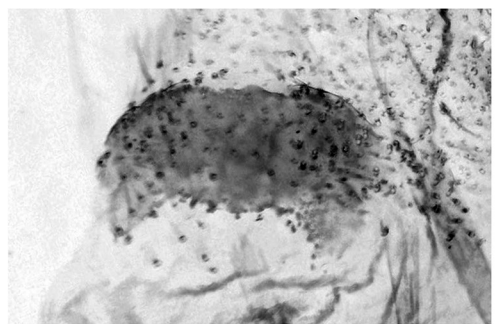
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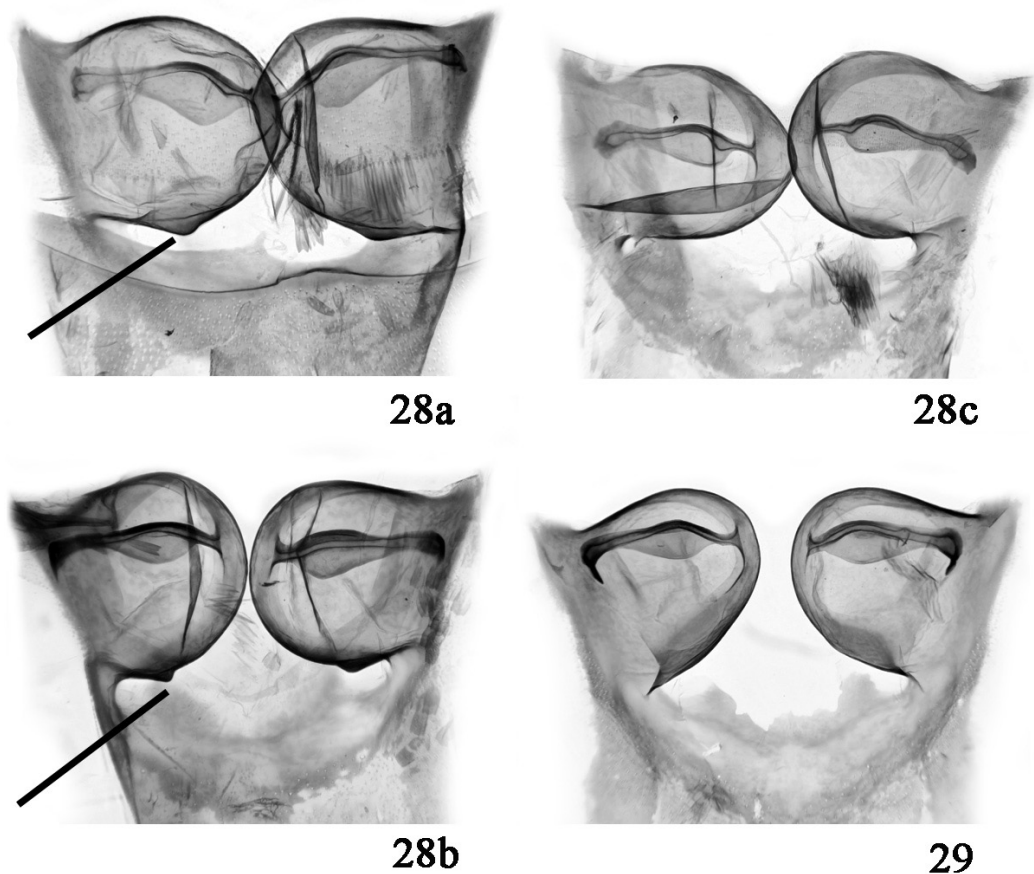


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Figures 23–27. Variability of the lamella postvaginalis. **23.** *I. l. limbaria*, Belgium: Comblain[-au-Pont]. **24a.** *I. l. delimbaria*, Italy: Liguria, Ligurian Alps, Rocchetta Nervina, Passo del Cane. **24b.** *I. l. delimbaria*, Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Bologna, Corno alle Scale, Passo del Vallone. **25.** *I. l. anzascaria*, Italy: Piedmont, Monte Rosa, Macugnaga, under Alpe Bill. **26.** *I. l. rablensis*, Bulgaria: Sofia, Vitoscha [Vitosha]. **27.** *I. l. roraria*, Germany: Bavaria, Spalt.



Figures 28, 29. Variability of the bullae tympani (bars point at the rounded lobes). **28a.** *I. l. delimbaria* ♀, France: Alpes-Maritimes, Grasse above Gourdon. **28b.** *I. l. delimbaria* ♀, Italy: Liguria, Ligurian Apennines, Maissana, road to Passo del Bocco di Bargone. **28c.** *I. l. delimbaria* ♀, Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Bologna, Corno alle Scale, Passo del Vallone. **29.** *I. l. rablensis* ♀, Italy: Piedmont, province of Verbania-Cusio-Ossola, Valstrona, Campello Monti.

Our observations confirm that the posterior margin of the lamella postvaginalis is often more curved in *roraria* and *rablensis* than in *limbaria*, but this character is variable, especially in the Italian populations, and it does not allow to identify the various taxa with certainty.

Preimaginal stages

J. Gelbrecht (pers. comm.) has bred material of the taxa *limbaria* s. str. (from Lüneburg Heath in Lower Saxony, Germany), *delimbaria* (from southern France), *rablensis* (from Vitosha, Bulgaria) and *roraria* s. str. (from Dessau in Saxony-Anhalt, Germany). Based on his observation, the larvae of *limbaria* and *delimbaria* are identical, darker green than *roraria* and *rablensis*, with brownish markings, the head capsule is more marked with black than in *roraria* and *rablensis*; the larvae of *roraria* and *rablensis* are mostly completely green, rarely with a brownish ground colour (in

Table 3. Analysis of the morphological characters observed in the material examined.

Taxon	Upperside	Underside	Female genitalia and tympanal organs
BIN			
place of origin of the material			
<i>limbaria</i> s. str. BOLD:AAF3598 Spain, Belgium, Germany (North Rhine-Westphalia), Switzerland	(♂♀) Forewing more or less irrorated with brown scales (sometimes almost absent except in the costa and in the terminal fascia). Width of the forewing dark terminal fascia about 2 mm (rarely 1 mm), hindwing dark terminal fascia generally well developed, rarely reduced; hindwing often densely covered with dark scales.	(♂♀) Forewing scattered with dark vertical stripes or more densely sprinkled with dark scales. Hind wing more or less densely covered with dark scales, except the whitish radiating streaks.	Signum: 0.7–1 mm (n=2, from Spain and Belgium). Bullae tympani with a roundish lobe (visible only in one bulla in a female from Spain).
<i>delimbaria</i> BOLD:AAF3598 France SE, Italy (Ligurian Alps, Northern Apennines)	(♂♀) Forewing almost free of dark scales (except the costa and the terminal fascia). Hindwing with more dark scales. Width of the forewing dark terminal fascia generally just over 1 mm (rarely 2 mm, 3 mm in the form <i>pedemontaria</i>), hindwing dark terminal fascia absent or very reduced.	(♂♀) Hindwing scattered with dark vertical stripes (much less numerous on the forewing). Whitish radiating streaks of the hindwing present and generally well evident (barely perceptible in the form <i>pedemontaria</i>).	Signum: 0.8–0.9 mm (exceptionally 1.2 mm in a female from the Apennines near Bologna; 0.9 mm in another female from the same locality) (n=5, from France and Italy: Alpes-Maritimes, Ligurian Alps, Ligurian Apennines and Tuscan-Emilian Apennines). Bullae tympani with a roundish lobe (France SE, Ligurian Alps, Ligurian Apennines); a female from the Tuscan-Emilian Apennines (near Bologna) lacks it, in a male from the same locality it is barely visible.
<i>anzascaria</i> not barcoded Italy (northern Piedmont: Macugnaga)	(♂♀) Forewing almost free of dark scales (except the costa and the terminal fascia). Hindwing with a few dark scales. Width of the forewing dark terminal fascia 1.5–2 mm, hindwing dark terminal fascia narrow or reduced to a few scales.	(♂♀) Hindwing scattered with dark vertical stripes (much less numerous on the fore wing). Whitish radiating streaks of the hindwing present.	Signum: 1.4 mm (n=1). Bullae tympani without roundish lobe.
<i>rablensis</i> BOLD:ACX8520 Italy (northeastern Piedmont, Lombardy, Monte Baldo)	(♂♀) Forewing often with only a few dark scales (except the costa and the terminal fascia), a little more dense in the hindwing; sometimes both wings scattered with dense groups (or short stripes) of dark scales. Width of the dark terminal fascia generally just over 1 mm.	(♂♀) Fore- and hindwing scattered with dark vertical stripes; ground colour of the wings almost identical or more orange in the fore wing. Whitish radiating streaks of the hindwing present.	(altogether in the taxon <i>rablensis</i>) Signum: 1.1 mm (exceptionally 1.6 mm in a female from Lombardy) (n=6, from northeastern Piedmont, Lombardy, Monte Baldo, Carnic Prealps, Italian Julian Alps and Bulgaria). Bullae tympani without roundish lobe.
<i>rablensis</i> BOLD:AAF3597 Julian Alps (Italy and Slovenia)	(♂♀) Wings scattered with sparse groups (or short stripes) of dark scales, sometimes with more dense dark vertical stripes. Width of the dark terminal fascia just over 1 mm.	(♂♀) Fore- and hindwing scattered with dark vertical stripes (more dense on the hindwings); ground colour of forewing more orange than the hindwing. Whitish radiating streaks of the hindwing present.	
<i>rablensis</i> not barcoded (most likely BOLD:AAF3597) Macedonia	(♂) Forewing scattered with sparse groups (or short stripes) of dark scales, hindwing with dense dark vertical stripes. Width of the dark terminal fascia just over 1 mm.	(♂) Fore and hindwing scattered with dense dark vertical stripes; ground colour of forewing more orange. Whitish radiating streak of the hindwing present.	

Taxon BIN place of origin of the material	Upperside	Underside	Female genitalia and tympanal organs
<i>rablensis</i> BOLD:AAF3597 Bulgaria (Vitosha)	(♂♀) Ground colour yellowish scattered with irregular dark vertical stripes and groups of dark scales, often more dense in the hindwing. Width of the dark terminal fascia just under 2 mm.	(♂♀) Fore- and hindwing scattered with dark vertical stripes; ground colour of fore wing slightly more orange. Whitish radiating streak(s) of the hindwing present but generally not very evident (sometimes barely perceptible).	(altogether in the taxon <i>rablensis</i>) Signum: 1.1 mm (exceptionally 1.6 mm in a female from Lombardy) (n=6, from northeastern Piedmont, Lombardy, Monte Baldo, Carnic Prealps, Italian Julian Alps and Bulgaria). Bullae tympani without roundish lobe.
<i>rablensis</i> BOLD:AAF3597 Romania (Buzău and Dâmbovița Counties)	(♂♀) Very similar to the Bulgarian specimens.	(♂♀) Very similar to the Bulgarian specimens.	
<i>roraria</i> s. str. BOLD:AAF3597 Czech Republic, Slovakia	(♂♀) Ground colour deep yellow with irregular dark vertical stripes, sometimes divided into groups of scales (especially in the forewing) or thickened one to the other. Width of the dark terminal fascia 2–3 mm.	(♂♀) Fore- and hindwing with identical pattern: ground colour orange yellow scattered with dark vertical stripes (a little more dense on the hind wings). Hindwing without a trace of whitish radiating streaks.	(altogether in the taxon <i>roraria</i> s. str.) Signum: 1.2–1.4 mm (n=3, from Slovakia and Germany). Bullae tympani without roundish lobe.
<i>roraria</i> s. str. BOLD:AAF3597 Germany (Bavaria)	(♂♀) Fore- and hindwing with identical pattern: ground colour orange scattered with dark vertical stripes. Width of the dark terminal fascia 2–2.5 mm, rarely less in very small specimens.	(♂♀) Fore- and hindwing with identical pattern: ground colour orange scattered with dark vertical stripes (a little more dense on the hind wings). Hindwing without a trace of whitish radiating streaks.	

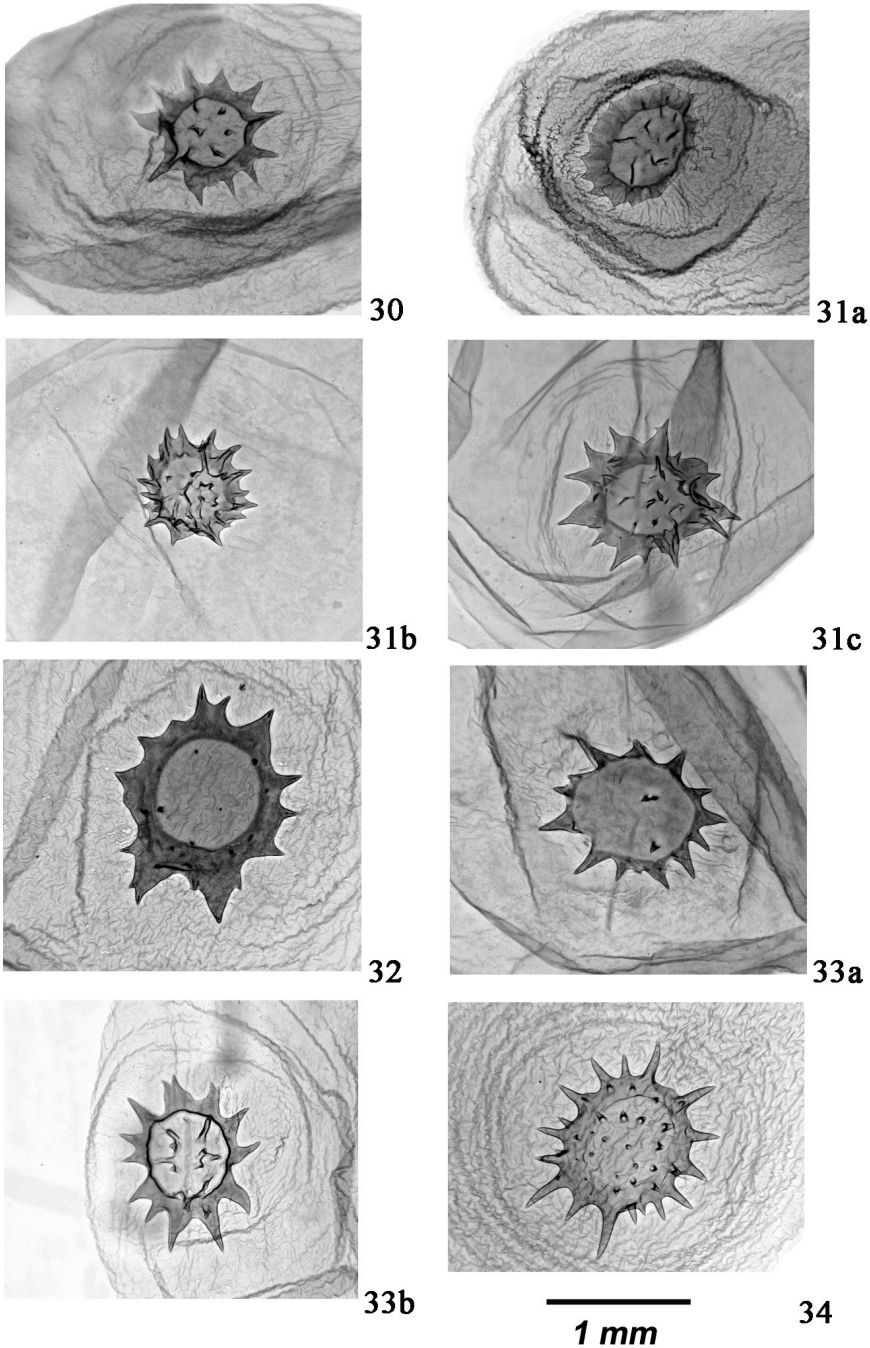
rablensis), the markings of the head capsule are weak. The shape of the pupal cremaster of *delimbaria* is similar to *limbaria* (thinner and a little longer), that of *rablensis* is similar to *roraria* (shorter and thicker) (Figs 35–38). Buckler (1897) shows green and brown larvae, both from Great Britain (taxon *limbaria* s. str.). The morphology of the larval and pupal stages of *roraria* s. str. is described and illustrated in detail by Blaik and Malkiewicz (2003) (material from south-western Poland): their images of the cremaster match rather well those of Gelbrecht, but not those of Patočka (1986) (from Slovakia, as *I. limbaria roraria*). Images of the preimaginal stages of the complex *limbaria/roraria* can also be found on the web: larvae from Netherlands (UKmoths 2019), France (Mazzei et al. 2019: Ariège; LepiNet 2019: Lot), eggs, larvae and pupae from Germany (Lepiforum 2019: *limbaria* from Rhineland-Palatinate, *roraria* from Saxony-Anhalt).

Gelbrecht also did breeding experiments (pers. comm.). The taxa *limbaria* and *delimbaria* crossbred easily; he managed to rear some adults also from the crossing between *rablensis* (from Bulgaria) and *roraria*. In laboratory conditions he also obtained a pairing between *delimbaria* and *rablensis*: the few eggs hatched but the larvae died immediately.

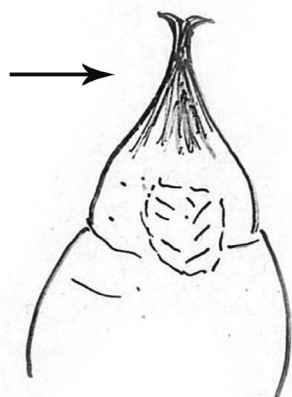
We have not found any images of the preimaginal stages of the Italian populations and we do not believe that breeding experiments have ever been carried out between them.

Discussion and conclusions

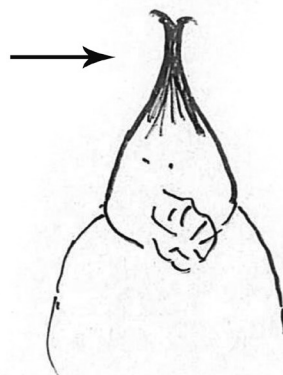
Populations delineated on the basis of molecular data, the size of the signum and the presence (or absence) of a roundish lobe in the bullae tympani, can be divided into two groups: one including



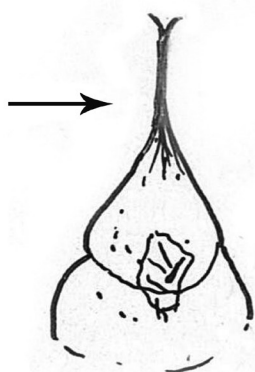
Figures 30–34. Variability of the signum. **30.** *I. l. limbaria*, Belgium: Comblain[-au-Pont]. **31a.** *I. l. delimbaria*, France: Alpes-Maritimes, Grasse above Gourdon. **31b.** *I. l. delimbaria*, Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Bologna, Corno alle Scale, Passo del Vallone. **31c.** Italy: Emilia-Romagna, Tuscan-Emilian Apennines, Bologna, Bologna, Corno alle Scale. **32.** *I. l. anzascaria*, Italy: Piedmont, Monte Rosa, Macugnaga, under Alpe Bill. **33a.** *I. l. rablensis*, Italy: Veneto, Monte Baldo, Bocca di Navene. **33b.** *I. l. rablensis*, Bulgaria: Sofia, Vitosha [Vitosha]. **34.** *I. l. roraria*, Germany: Bavaria, Spalt.



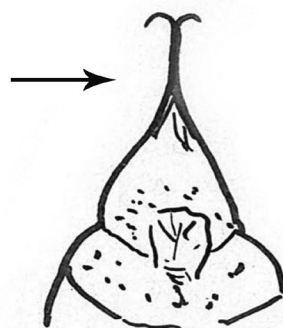
35



36



37



38

Figures 35–38. Pupal cremaster (drawings by J. Gelbrecht). **35.** *I. l. rablensis*, Bulgaria: Sofia, Vitosha. **36.** *I. l. roraria*, Germany: Saxony-Anhalt, Dessau. **37.** *I. l. delimbaria*, southern France. **38.** *I. l. limbaria*, Germany: Lower Saxony, Lüneburg Heath.

the taxa *limbaria* s. str. and *delimbaria*, and the other the taxa *roraria* s. str. and *rablensis*. The taxon *anzascaria* (not yet barcoded) can also be attributed to the latter group as it shares with *rablensis* and *roraria* a larger signum (see Table 3) and the absence of a roundish lobe in the bullae tympani; most of the populations of *rablensis* (from the Julian Alps to Romania) share the same BIN with *roraria*, while the most western ones (northern Italy, excluding the Julian Alps, and southern Austria) share their own barcode cluster which is much closer to *roraria* than to *delimbaria* and *limbaria* s. str.. This population is, however, not morphologically distinguishable from that from the Julian Alps. However, the diagnostic wing pattern characters until now used to identify the two species

limbaria and *roraria* do not correlate with these two groups: the taxa *rablensis* and *anzascaria* are more similar to *limbaria* in the hindwing underside (whitish radiating streaks present); the pattern of the upperside wing is variable and often intermediate between *limbaria* and *roraria* in *rablensis* (especially in the Italian populations), while in *anzascaria* it is rather similar to *delimbaria* (forewing upperside almost free of dark scales, except the costa and the terminal fascia).

Furthermore, the two groups of populations are not completely separated from each other. Some populations of the northern Apennines (taxon *delimbaria*) cannot be clearly attributed to one or the other group: a barcoded specimen from the “Apuan Alps” in Tuscany (northern Apennines) shares the same BIN with *delimbaria* and *limbaria* s. str. (diverging by 1.6% from both the cluster of *limbaria* s. str. and the specimen of *delimbaria* from the Ligurian Alps). However, in the Apennines near Bologna there are females with a large signum (as in *roraria* s. str. and *rablensis*) and females with a small signum; in the latter area a female lacks the roundish lobes in the bullae tympani (like in *roraria* s. str. and *rablensis*), in the single male examined they are barely visible.

The genetic distance between the two groups of populations of the *I. limbaria/roraria* complex is considerable. However, the correlation between molecular differences and morphological characters is not completely constant, as shown by the example of the Apennine populations just mentioned. In the absence of constant morphological characters associated with the molecular differences and in the presence of Italian populations with intermediate characters, we believe it better, in the current state of knowledge, to consider the different taxa of this complex as subspecies of the same species, as already proposed by Povolný and Moucha (1957, 1959). However, the available data do not allow a definitive clarification of the taxonomic problem and further research is necessary to consider the conspecificity of the clusters of the different taxa. Additional genetic data are necessary (in particular from northern Piedmont and the Apennines), as well as an in-depth study of the preimaginal stages of the Italian populations, with breeding experiments between them to check their interfertility.

Gelbrecht’s breeding experiments suggest the conspecificity between *limbaria* s. str. and *delimbaria* on the one hand and between *rablensis* (from Bulgaria) and *roraria* s. str. on the other. However, they do not exclude the possible interfertility between Italian populations belonging to different taxa: other experiments would be necessary for this purpose. Also the immutability of differences in the larva and in the pupal cremaster should be confirmed through the study of the Italian populations.

These results emphasize the need to further investigate the patterns of mitochondrial DNA in “hybrid” populations. In our research on Ennominae (cf. Flamigni et al. 2016) we have met other cases of mismatch between DNA barcodes and morphological characters: specimens from southern Piedmont (north-western Italy) are closer to the genetic cluster of *Yezognophos serotinaria serotinaria* (Denis & Schiffermüller, 1775) even though their genitalia are similar to those of *Y. serotinaria serotinoides* (Wehrli, 1922); in addition, in the northern Apennines the male genitalia and sometimes also the female ones, although clearly attributable to the “western” taxon *serotinoides*, show some elements of transition towards the “eastern” nominate *serotinaria*, showing a parallelism with the above comments on the taxa *delimbaria* and *rablensis*. The taxon *Psodos chalybaeus* Zerny, 1916 (valid at subspecies rank according to Flamigni et al. (2016), downgraded to a synonym of *Psodos alticolaria alticolaria* Mann, 1853 by Müller et al. (2019), but with the need for further investigations) occurs in a well defined area of the Rhaetian Alps, with a different BIN and a characteristic wing pattern; however, specimens collected in the surroundings of Oberurgl (Austria: North Tyrol) in two very close localities are very similar to each other in wing

pattern (intermediate between *alticolaria alticolaria* and *chalybaeus*), but they have two different BINs (corresponding to those of these two taxa). The specimens of *Hylaea* Hübner, 1822, from Molise (central Italy) are often more similar in wing pattern to *H. fasciaria* (Linnaeus, 1758) (with minimal differences in variable female genitalia), but they share the same BIN as *H. mediterranea* Sihvonen, Skou, Flamigni, Fiumi & Hausmann, 2014. Also the status of subspecies could be a possible alternative for the taxon *mediterranea*.

Summary

Our findings indicate that the relation of barcodes to morphology is a complicated issue, and a ‘correct’ taxonomic interpretation may be impossible to reach solely with these approaches. The case of *Isturgia* taxonomy is an illustrative example of a complicated taxonomic pattern that we observe, potentially showing an example of the current situation resulting from an historical biogeographical pattern initiated during the glaciation eras of Europe.

Taxonomy

Isturgia limbaria limbaria (Fabricius, 1775)

Phalaena limbaria Fabricius, 1775, Syst. Ent. 624, Anglia [England].

Geometra conspicuata [Denis & Schiffermüller], 1775, Ankündigung syst. Werkes Schmett. Wienergegend: 316, [Germany, Hesse: Frankfurt am Main]. Syntype(s) from the collection Gerning (Frankfurt a. M., 1745–1802). The taxon *limbaria* s. str. is not recorded from Vienna; in Lower Austria and in neighbouring Moravia only the taxon *roraria* occurs.

Ph[alaena] Geom[etra] auroraria Hübner, [1787], Beitr. Gesch. Schmett. 1 (2): 27, pl. 4, fig. Y, 1, 2. According to Scoble (1999) it is a synonym both of *limbaria* and *roraria*: Hübner’s figures clearly show that it is *limbaria*.

Phal[aena] Geom[etra] circumdata Villers, 1789, Linn. ent. 2: 330, pl. 6, fig. 10, Europe, Gallia [France].

Phalaena Geometra conspicuaria Borkhausen, 1794, Natur. eur. Schmett. 5: 465, Europe.

Geometra spartariaria Hübner, [1799], Samml. Eur. Schmett. 5 Geometrae (1): pl. 22, fig. 116, Europe.

Ph[alaena] Geom[etra] conspicuaria Esper, [1801], Die Schmett. 5 (5): 124, pl. 24, figs 5–7, Syntype(s), [Germany, Hesse]: Frankfurt am Main, Darmstadt; Switzerland; Hungary [patria falsa?]. Junior primary homonym of *conspicuaria* Borkhausen, 1794. Synonym of *roraria* according to Scoble (1999) and Skou and Sihvonen (2015); the syntypes were identified by Hacker (1999) as *I. limbaria limbaria*; the same author designated as paralectotype a male from the Esper collection (ZSM Munich) and as lectotype one from the Gerning collection (LMW Wiesbaden). In Hungary only the taxon *roraria* occurs.

Fidonia limbaria ab. *quadripunctaria* Fuchs, 1899, Jb. Nassau. Ver. Naturk. 52: 150, [Germany], [Rhineland-Palatinate]: Loreley district [infrasubspecific: each wing with black discal spot].

Fidonia conspicuata ab. *fumata* Mathew, 1907, Entomologist’s Rec. J. Var. 19: 21, [England]: Suffolk [infrasubspecific].

Fidonia limbaria ab. *nigricaria* Bubacek, 1915, Verh. zool.-bot. Ges. Wien 65: (109), [France], Pyrénées-Orientales: surroundings of Vernet-les-Bains 2200 m [infrasubspecific].

Fidonia limbaria var. *infusca* Thierry-Mieg, 1916, *Miscnea. ent.* 23: 50, Europe [infrasubspecific].

Fidonia limbaria f. *nigrostriata* Heydemann, 1938, **syn. n.**, Ent. Z. Frankf. a. M. 52 (3): 23, pl. 1, figs 21, 22, [Germany]: southern Holstein [infrasubspecific]. Valid at subspecies rank according to Scoble (1999); however, according to the original description it co-exists with f. *quadripunctaria* [“it appears here in a percentage up to almost 45% among the *quadripunctaria* Fuchs”]; also Lempke (1952) considers it an individual form, frequent in the Netherlands.

Isturgia limbaria f. *postnigrescens* Lempke, 1952, Tijdschr. Ent. 95: 208, Netherlands: Harendermolen, Nijmegen, Roermond, Steenwijk, Winterswijk, Montferland, Veenendaal [infrasubspecific: “hind wings unicolorous blackish”].

Isturgia limbaria f. *postclara* Lempke, 1952, Tijdschr. Ent. 95: 208, Netherlands: Wehl, Tilburg [infrasubspecific: “hind wings as clear as the fore wings”].

Isturgia limbaria f. *postdemarginata* Lempke, 1952, Tijdschr. Ent. 95: 208, Netherlands: Roermond [infrasubspecific: “hind wings without the dark marginal band”].

Material examined. Spain: 1 ♂, 1 ♀, Aragon: province of Huesca, Fanlo, 1.vi.2007, Perez leg. (RCCF). **Belgium:** 1 ♂, 1 ♀, Comblain[au-Pont], 14.v.2000, Evrard leg. (RCCF). **Germany:** 1 ♂, 1 ♀, North Rhine-Westphalia: Wuppertal

12.v.2006, Hager leg. (RCCF); 1 ♂, Thuringia: Treffurt, Eichsfeld, ex l. 12.ix.1992/2.iii.1993, E. Friedrich leg. (RCEF) (digital images of both sides on Lepiforum). **Switzerland:** 1 ♂, 1 ♀, Valais: district of Sierre, Val d'Anniviers, 1.vii.2005, Chapelle leg., (RCCF).

Colour images of specimens from Great Britain are shown in Ford (1972: pl. 29, figs 13–15): from Ipswich in England (upperside and underside) and from Achanalt in Scotland (upperside).

Diagnosis (Figs 3, 8, 13, 18). Dark terminal fascia almost always well developed on the four wings. Hindwing often densely covered with dark scales, sometimes unicolorous blackish. Hindwing underside more or less densely covered with dark scales, except the whitish radiating streaks.

In the female genitalia signum small (0.7–1 mm). Bullae tympani with a roundish lobe (visible only in one bulla in a female from Spain).

Distribution. Great Britain (Scotland and eastern England, now extinct), part of Germany (cf. Skou and Sihvonen 2015: map on page 97), Benelux, France (excluding the southern Alps), northern Spain (eastern Aragonese, Andorran and Catalan Pyrenees). Our specimens from Valais confirm the occurrence of the species in Switzerland, where only old records existed (cf. Reser 2010).

Remarks. According to Skinner (1984) the specimens from Ross-shire (Scotland) are larger and paler than those from southern England; the difference is also evident in the images in Ford (1972).

Isturgia limbaria delimbaria (Staudinger, 1892)

Fidonia limbaria var. *delimbaria* Staudinger, 1892, Dt. ent. Z. Iris 5: 198, [France]: Basses Alpes [Alpes-de-Haute-Provence], near Castellane and Digne.

Fidonia limbaria var. *pedemontaria* Staudinger, 1892, Dt. ent. Z. Iris 5: 198, [France]: Alpes-Maritimes, [Italy]: Piedmont. Synonymy according to Flamigni et al. (2007, 2016).

Fidonia limbaria var. *ligurica* Fuchs, 1899, Jb. nassau. Ver. Naturk. 52: 151, [Italy]: Liguria. Synonym of *pedemontaria* according to Wehrli (1940).

Material examined. **France:** 1 ♂, Vaucluse: Gignac, 21.iv.1979, F. Coenen leg. (RCCM); 1 ♂, Alpes-Maritimes: Gréolières 950 m, 21.iv.1997, G. Govi leg. (RCGG); 1 ♀, Alpes-Maritimes: Grasse above Gourdon, 750 m, 4.v.1998, G. Govi leg. (RCGG); 1 ♂, 1 ♀, Alpes-de-Haute-Provence: St-Étienne-les-Orgues, Montagne de Lure, 1620 m, 24.v.2014, E. Friedrich and P. Peuker leg. (RCEF) (digital images of both sides on Lepiforum). **Italy:** 1 ♂, Piedmont: Maritime Alps, Limonetto, 1000 m, 24.v.1998, G. Fiumi leg. (RCGF); 1 ♂, Piedmont: Ligurian Alps, Piaggia, 1300 m, 29.vi.1986, G. Bastia leg. (RCCF); 1 ♂, Liguria: Ligurian Alps, le Salse, 1800 m, 17.vii.1974, M. Guidi leg. (RCGF); 1 ♂, Liguria: Ligurian Alps, Ventimiglia, Villatella, Monte Grammondo, 1150 m, 9.v.2015, M. Guaschino leg. (RCCM); 1 ♂, Liguria: Ligurian Alps, Ventimiglia, 600 m, 27.v.2001, E.O. Bonora leg. (RCCM); 4 ♂, 2 ♀, Liguria: Ligurian Alps, Rocchetta Nervina, Passo del Cane, 600 m, 23.v.1998, G. Fiumi leg. (RCGF); 1 ♀, Liguria: Ligurian Alps, Cosio di Arroscia, 1000 m, E.O. Bonora leg., 4.v.2006 (RCCM); 1 ♂, Piedmont: Ligurian Apennines, Capanne Superiori di Marcarolo, 900 m, 21.vii.2003, L. Baldizzone leg. (RCGF); 3 ♀, Liguria: Ligurian Apennines, Maissana, road to Passo del Bocco di Bargone, 635–960 m, 18.v.2015, M. Guaschino leg. (RCCM); 1 ♂, Emilia-Romagna: Tuscan-Emilian Apennines, Bologna, Monte Pizzo, 1000 m, 5.vii.1970, A. Bastia leg. (RCCF); 1 ♂, 3 ♀ Emilia-Romagna: Tuscan-Emilian Apennines, Bologna, Monte Grande, 1530 m, 8.vii.1987, C. Flamigni leg. (RCCF); 2 ♂, 2 ♀, Emilia-Romagna: Tuscan-Emilian Apennines, Bologna, Corno alle Scale, Passo del Vallone, 1650–1750 m, 31.vii.1986, C. Flamigni leg. (RCCF); 2 ♂, 2 ♀, Emilia-Romagna: Tuscan-Emilian Apennines, Bologna, Corno alle Scale, 1650 m, 4.vii.1984, 10.vii.1986, 1945 m, 10.vii.1986, C. Flamigni leg. (RCCF); 1 ♂, Tuscany: Apuan Alps, under Monte Corchia, Passo Croce, 18.vi.1999, L. Dapporto leg. (ZSM).

Diagnosis (Figs 4, 9, 14, 19): Forewing almost free of dark scales (except the costa and the terminal fascia). Hindwing with more dark scales than forewing, but lighter than in most specimens of the nominate subspecies. The dark terminal fascia is generally narrow in the forewing (wide in the form *pedemontaria*), absent or very reduced in the hindwing (also in the form *pedemontaria*). The underside is variable, but less contrasted and less sprinkled with black than in most specimens of the nominate subspecies. The taxon *pedemontaria* (Figs 4b, 14b) is an individual form, sometimes prevalent in some places: it shows a wide, dark terminal fascia on the forewing and a weakly marked underside on the hindwing, which is orange-yellow, scattered with dark vertical stripes, with barely perceptible lighter radiating streaks.

In the female genitalia signum small (0.8–0.9 mm, exceptionally 1.2 mm in a female from the Apennines near Bologna: see Table 3). Bullae tympani with a roundish lobe (absent in a female from the same locality: see Table 3). The specimens from northern Piedmont (Graian and Pennine Alps) were not dissected.

Distribution. France SE, Italy (Piedmont, Liguria, Tuscany, Emilia-Romagna: see Fig. 2). According to Leraut (2009) its distribution in France is limited to the southern Alps; we have confirmation for the following departments: Drôme: Montagne de Chamouse (Skou and Sihvonen 2015: pl. 2, fig. 18c, e), Vaucluse, Alpes-de-Haute-Provence, Alpes-Maritimes, Var. In Piedmont it occurs mainly in the south, from the Maritime Alps to the Apennines; according to Flamigni et al. (2007) it occurs also further north, up to the Graian Alps and the surroundings of Biella (Pennine Alps); the specimens from the Biella area were examined (without dissection of the genitalia) by the first author during the preparatory work on the first volume on the Italian Ennominae. The geographic position would suggest that specimens from Corsica also belong to this subspecies: this will need to be verified through the examination of the collected material.

Molecular data. The two barcoded specimens (both from Italy) diverge from those of the taxon *limbaria* s. str. (from Germany and Upper Normandy) respectively by 1.2% (Ligurian Alps) and 1.6% (northern Apennines); however, they diverge from one another by 1.6% and cannot be regarded as a “common separate cluster”.

Remarks. The distribution of the taxa *delimbaria* and *rablensis* in the northern Piedmont is similar to that of *Crocota pseudotinctaria* Leraut, 1999 and *C. tinctaria* (Hübner, 1799): *delimbaria* and *pseudotinctaria* occur in the surroundings of Biella, while *rablensis* and both *pseudotinctaria* and *tinctaria* occur further to the north-east, in Campello Monti (*tinctaria* also occurs in Lombardy, like *rablensis*). The analysis of the DNA of the northern Piedmontese populations could help to better understand the relationship between the three taxa present in this area (*delimbaria*, *anzascaria*, *rablensis*); the barcoding of a specimen from Campello Monti was unfortunately not successful.

Isturgia limbaria anzascaria (Staudinger, 1892)

Fidonia limbaria var. *anzascaria* Staudinger, 1892, Dt. ent. Z. Iris 5: 198, [Italy, northern Piedmont]: Val d’Anzasca near Macugnaga.

Material examined. Italy: 1 ♂, Piedmont: Monte Rosa, Macugnaga, near Pecetto, 1400 m, 21.vii.1984, C. Flamigni leg. (RCCF). 1 ♂ 1 ♀, Piedmont: Monte Rosa, Macugnaga, under Alpe Bill, 1400–1600 m, 26.vii.1984, C. Flamigni leg. (RCCF).

Diagnosis (Figs 5, 10, 15, 20). Large, light yellow. Forewing upperside almost free of dark scales (except the costa and the terminal fascia), hindwing upperside with a few dark scales. Forewing dark terminal fascia narrow in the male and reduced to a few blackish dots in the female according to the original description; this fascia is present in both sexes in our specimens, but it is relatively narrow in relation to their size. Hindwing dark terminal fascia rather narrow or reduced to a few scales, especially in the female. Hindwing underside yellow, scattered with a few dark vertical stripes; whitish radiating streaks present but not very evident. Although Prout (1915) and Wehrli (1940) reported also the ssp. *rablensis* from Macugnaga, our specimens from this locality correspond well with the description of Staudinger, differing from *rablensis* by the larger size (wingspan 27–30 mm in *anzascaria*, 23–26 mm in the Italian specimens of *rablensis*) and by the purest yellow, almost without dark scales; it will be possible to definitively confirm the validity of the subspecies examining a greater number of specimens.

In the only female examined signum large (1.4 mm). Bullae tympani without roundish lobe.

Distribution. Valle Anzasca (Italy: northern Piedmont), on the southern side of the Monte Rosa massif (Fig. 2).

Remarks. Not yet barcoded. The size of the signum and the absence of a roundish lobe in the bullae tympani indicate a greater similarity with *rablensis* and *roraria*, but the wing upperside is closer to *delimbaria*, but the hindwing has a dark terminal fascia.

Isturgia limbaria rablensis (Zeller, 1868)

Fidonia limbaria var. *rablensis* Zeller, 1868, Verh. zool.-bot. Ges. Wien 18: 587, [Italy, Friuli-Venezia Giulia]: Grafenlahn above Raibl [Cave del Predil] and below along the stream. At the time the locality Raibl was situated in Austria (Upper Carinthia). *Fidonia limbaria styriaca* Schwingenschuss, 1911, Verh. zool.-bot. Ges. Wien 61 (1/2): (46), [Austria], Styria: Polster, near Prebichl [Präbichl], 1400–1600 m. Synonymy follows Huemer and Tarmann (1993). Also Huemer (2013) attributes the population of Styria to the taxon *rablensis*.

Material examined. Italy: 1 ♂, 1 ♀, Piedmont: province of Verbania-Cusio-Ossola, Valstrona, Campello Monti, 1700 m, 13.vi.2003 (♂), 3.vii.2004 (♀), A. Floriani leg. (RCGF); 1 ♂, Lombardy: Bergamasque Prealps, Oltre il Colle, Monte Menna, 1600 m, 22.vi.2013, R. Taverna leg. (RCCF); 1 ♀, Lombardy: Bergamasque Prealps, Camerata Cornello, towards Passo Grialegg, 23.vii.2010, M. Massaro and W. Zucchelli leg. (MSMB); 1 ♂, Lombardy: Bergamasque Alps, Ardesio, 1400 m, 28.iv.2007, W. Zucchelli leg. (MSMB); 1 ♂, Trentino-Alto Adige: Monte Baldo, San Valentino, 1300 m, 30.vi.1980, S. Camporesi leg. (RCGF); 3 ♀, Trentino-Alto Adige: Monte Baldo, Monte Altissimo, Rifugio Graziani, about 1600 m, 3.vii.2005, Morandini leg. (RCCM); 1 ♀, Trentino-Alto Adige: Brentonico, [Monte Baldo], 1700 m, 8.vii.2001, E.O. Bonora leg. (RCCM); 1 ♂, Trentino-Alto Adige/Veneto: Monte Baldo, Cima Valdritta, 1400–1600 m, mid v.1966, J. Wolfsberger leg. (RCCM); 1 ♀, Veneto: Monte Baldo, Bocca di Navene, 14.vi.1969 (RCCF, ex coll. S. Zangheri); 3 ♂, 2 ♀, Veneto: Monte Baldo, Rifugio Novezza, 1600 m, 2.vi.2000/17–22.v.2001 ex ovo, 1550 m, 3.vi.1999, E. Friedrich leg. (RCEF) (digital images of both sides on Lepiforum); 2 ♂, 2 ♀, Friuli-Venezia Giulia: Carnic Prealps, Barcis, Prescudin, 600 m, 6.vi.1973, 8.vi.1976, 800 m, 9.vi.1973, Morandini leg. (RCCM); 1 ♂ 3 ♀, Friuli-Venezia Giulia: Carnic Prealps, Monte Festa, 1200 m, 7.vi.1972, C. Morandini leg. (RCCM); 1 ♂, 1 ♀, Friuli-Venezia Giulia: Carnic Prealps, Monte San Simeone, 1200 m, 22.vi.1972, Morandini leg. (RCCM); 1 ♂, Friuli-Venezia Giulia: Julian Prealps, Matajur, 1600 m, 17.vi.1989, L. Morin leg. (RCCM); 1 ♂, Friuli-Venezia Giulia: Julian Prealps, Matajur, 1500 m, 19.vi.2014, photo H. Deutsch (digital images of both sides on Lepiforum); 3 ♀, Friuli-Venezia Giulia: Julian Alps, Jof Montasio, 1700 m, 18.vii.1972, 1600 m, 1.vii.1973, C. Morandini leg. (RCCM). **Slovenia:** 2 ♂, 1 ♀, Julian Alps, Bovec, Mangart, 1700 m, 28.vi.2003, E. Friedrich leg. (RCEF) (digital images of both sides on Lepiforum). **Macedonia:** 2 ♂, Baba Planina [Baba Mountain], Pelister, Golemozero [Large Lake], 22–25.vi.1965, J. Karneluti leg. (RCCM). **Greece:** 2 ♂, 2 ♀, Western Macedonia: surroundings of

Pisoderi, 1950 m, 2–3.vii.2019, V. Valenta leg. (RCCF). **Bulgaria:** 1 ♂, 1 ♀, Sofia: Vitoša [Vitosha], 1500 m, 11.vi.1972, V. Felix leg. (RCCM); 1 ♂, 1 ♀, Sofia: Vitosha [Vitosha], 2.vii.2002 (RCGF). **Romania:** 1 ♂, 1 ♀, Dâmbovița County: Southern Carpathians, Bucegi Mountains, Valea Jepii, 1800 m, 7.vi.2007, S. and. Z. Kovacs leg. (ZSM); 1 ♂, Buzău County: Eastern Carpathians, Nemira Mountains, Lassuag, 1100 m, 22.vi.1996, S. and.Z. Kovacs leg. (ZSM).

The underside of a male from Gitschtal (Austria: Carinthia) is figured by Wieser (2008: fig. 16); colour images of specimens from Serbia (as *I. limbaria* and as *I. roraria*) are shown on the website Alciphron (2019).

Diagnosis (Figs 6, 11, 16, 21). Upperside more or less scattered with groups of dark scales (or dark lines short or longer), scattered or more dense; in some specimens (mainly in the westernmost part of the distribution area) there are only a few dark scales in the forewing (except on the costa and in the terminal fascia), a little more dense in the hindwing; in other specimens (also among the most western ones) both wings are scattered with dense groups of dark scales; dark terminal fascia generally narrow, wider in Bulgarian specimens, in the hindwing it can be present or absent. Underside with fore- and hindwings more or less different in pattern and colour (identical in *roraria* s. str.): both wings scattered with dark vertical lines, but colour generally more orange-yellow in the forewing, more whitish yellow in the hindwing, whitish radiating streak(s) of the hindwing present (sometimes barely perceptible).

In the female genitalia signum large (1.1 mm, exceptionally 1.6 mm). Bullae tympani without roundish lobe.

Distribution. Northern Italy (see Fig. 2), Austria (Huemer, 2013: Carinthia, Styria), Slovenia, Serbia, Macedonia, Kosovo, Albania, Greece (Western Macedonia), Bulgaria, Romania. The taxon *rablensis* was recorded from Albania (Djalica e Lumës) by Rebel and Zerny (1934) and by Povolný and Moucha (1957: fig. 57); the first two authors also mention Žljeb in Kosovo; its occurrence in Romania is confirmed from the Bucegi Mountains (see also Popescu-Gorj (1995)) and the Nemira Mountains; the records of *I. roraria* s.l. from other areas of Romania (in particular from the Cluj-Napoca area: cf. Rákossy et al. (2016)) must be verified by examining the underside of the specimens. The species also occurs in Croatia and Bosnia and Herzegovina (Skou and Sihvonen 2015), but we have not examined material from these countries. Viidalepp (1996) attributes the populations from Transcaucasus (Georgia) to this subspecies (as *I. roraria rablensis*).

Molecular data. The westernmost populations (Lombardy and Monte Baldo in Italy, Carinthia in Austria) correspond to a separate BIN, at a distance of 2.0%, while all the others (from the Julian Alps to Bulgaria and Romania) share the same BIN of the following subspecies; however, no constant morphological character corresponds to these genetic differences and it is not possible to distinguish the specimens of the more western regions from those of the Julian Alps (both populations are very variable). The exact border between these two BINs is not known, since no specimens from the Carnic Prealps have been barcoded. Three specimens from Romania diverge into a separate cluster, but they are morphologically very similar to those from Bulgaria.

Isturgia limbaria roraria (Fabricius, 1776) stat. nov.

Phalaena roraria Fabricius, 1776, Genera Insect. 285, Europe.

Phalaena adpersaria Fabricius, 1787, Mantissa Insect. 2: 189, [Germany], [Saxony-Anhalt]: Halae Saxonum [Halle (Saale)]. *Fidonia spartiaria* Treitschke, 1827, Schmett. Eur. 6 (1): 270, [Germany]: river Rhine [patria falsa?]. The original description (upperside and underside) corresponds to *roraria*, but in the locality indicated only the taxon *limbaria* occurs.

Fidonia roraria ab. *aequestriga* Hirschke, 1910, Verh. zool.-bot. Ges. Wien 60: 416, [Czech Republic], Silesia: near Trop-

pau [Opava] [infrasubspecific: form without dark terminal fascia].

Fidonia roraria ab. *nigrescens* Preissecker, 1923, Verh. zool.-bot. Ges. Wien 72: (95), [Lower Austria]: Dunkelsteinerwald, near Ernstshof [infrasubspecific].

? *Cleogene ostrogovichii* CARADJA, 1930, Bull. Sect. scient. Acad. roum. 13 (3): 52, [Romania], Siebenbürgen [Transylvania]: Cluj, [Galişer Hill]. Synonym of *roraria* according to Rákossy et al. (2016), but it could instead be synonym of *rablensis* if the occurrence of this taxon in the Cluj-Napoca area was ascertained.

Isturgia roraria ab. *stehliki* Bretschneider, 1954, Ent. Z. 64: 41, Germany, [Saxony-Anhalt], Dessau [infrasubspecific: almost completely black form, obtained from a F2 generation, bred from normal-coloured *roraria* parents].

Material examined. Germany: 1 ♂, Saxony-Anhalt: Bitterfeld, Marke, 0.5 km east the motorway exit Dessau-Süd, 85 m, 24.v.2012, J. Gelbrecht leg. (ZSM); 3 ♂ 3 ♀, Saxony-Anhalt: Dessau, Möst W, 80 m, 19.V.2016, 19.v.2016/31.iii–14. iv.2017 ex ovo, E. Friedrich leg. (RCEF) (digital images of both sides on Lepiforum); 3 ♂, 3 ♀, Bavaria: Spalt (and surroundings), 18.v.2004, 26.v.2005 ex ovo, 22.vi.2007 ex ovo, 3.v.2008 ex ovo, 6.v.11 ex ovo, 27.iv.2012 ex ovo, A. Zoglauer leg. (RCCF, RCCM); 1 ♂, Bavaria: Mittelfranken, Nürnberger Land, Leinburg, Wolfgrube Ost, 405 m, 20.vii.2010, A. H. Segerer leg. (ZSM). **Austria:** 1 ♂, 1 ♀, Lower Austria: Pottenstein, 31.v.1930, 21.vi.1930, R. Kitschelt leg. (NHMW) (digital images of both sides on Lepiforum). **Czech Republic:** 1 ♂, Moravia: Vápenky, 13.v.2006 ex ovo, J. Uňčář leg. (RCCM); 1 ♂, Moravia: Bílé Karpaty [White Carpathians], Machová, 1996 ex ovo, E. Lohočka leg. (RCCM). **Slovakia:** 1 ♀, Handlová, iv-2003 ex ovo on *Genista*, I. Richter leg. (RCCM).

Colour images of specimens from Poland are shown by Blaik (2003) (variability of upperside), Blaik and Malkiewicz (2003) (upperside and underside) and on the website Lepidoptera Mundi (2019).

Diagnosis (Figs 7, 12, 17, 22). Ground colour of the upperside deep yellow or orange, scattered with dark vertical lines; the dark terminal fascia (when present) is generally wide; however, the upperside is often identical to that of the previous subspecies and the differentiation from it is possible only by examining the underside. On the underside fore- and hindwing with identical colour and pattern: ground colour orange-yellow or orange scattered with dark vertical stripes (a little more dense on the hindwings); hindwing without a trace of whitish radiating streaks (sometimes a streak of a slightly lighter yellow, for example in specimens from Poland and Slovakia).

On the upperside, the dark terminal fascia is variable: according to Povolný and Moucha (1957) in Slovakia most of the individuals from the Ore Mountains have this fascia less developed than those from Vihorlat Mountains and in the first locality it is absent in a high percentage of females (but also males). In Poland (Blaik 2003) this fascia is wide and always present in the males (more or less distinct), almost always indistinct or absent in the females; specimens were collected in a locality with a large area of the forewing upperside without dark markings.

In the female genitalia signum large (1.2–1.4 mm). Bullae tympani without roundish lobe.

Distribution. North-eastern and south-eastern Germany (cf. Skou and Sihvonen 2015: map on page 99), Austria (Huemer 2013: Lower Austria), southern Poland, Czech Republic, Slovakia, north-eastern Hungary. For Romania, see the previous subspecies. Viidalepp (1996) attributes to *roraria* s. str. the populations from Ukraine, south-eastern Russia and southern Urals.

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Appendix I

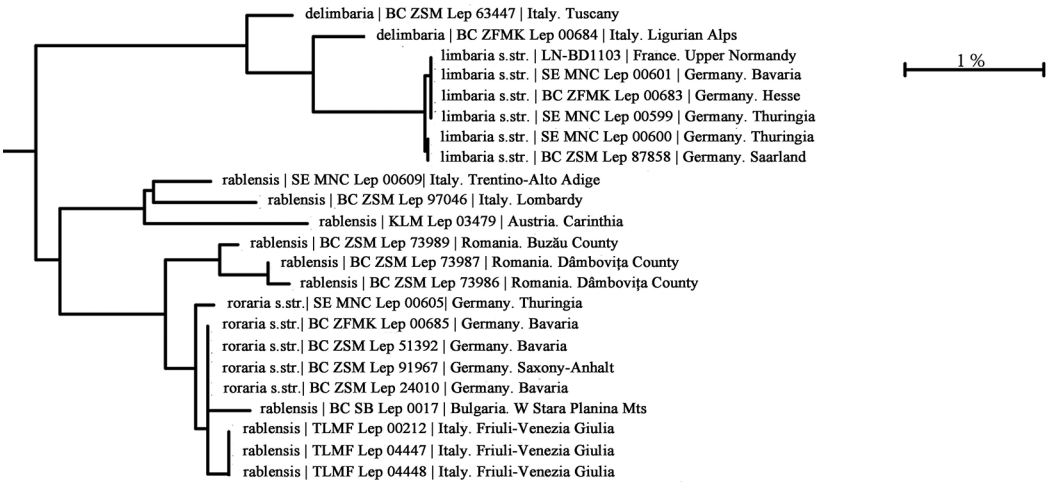


Figure A1. Neighbour joining tree (Kimura 2-parameter distance model for COI-5P marker, data from BOLD data systems) for 23 European specimens. Terminals with taxon, specimen ID and geography.