

PHYLLONORYCTER CERRIS (GREGOR), TAXONOMY, BIOLOGY AND DISTRIBUTION (LEPIDOPTERA: GRACILLARIIDAE)

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Abstract

Species independence of *Phyllonorycter cerris* (Gregor, 1952) is evidenced by differences in coloration, results of molecular analysis, and trophic specialization. The differences between *P. cerris* and *P. quercifoliella* (Zeller, 1839) lie in the basic appearance of the forewings, and in the location and shape of some strigulae. The genetic distance (COI) between *Phyllonorycter cerris* and *P. quercifoliella* is 2.5%. The larva of *Phyllonorycter cerris* mines only *Quercus cerris* L. in central Europe, *P. quercifoliella* mines oligophagously *Quercus* spp. of the section *Robur* Reich. *Phyllonorycter cerris* is redescribed, data on biology, population densities, and distribution are added. Occurrence in Czechia is analysed in detail, the first precise faunistic data from Bohemia are given.

Keywords: *Phyllonorycter*, *Quercus cerris*, monophagy, taxonomy, biology, ecology, distribution

INTRODUCTION

About 30 *Phyllonorycter* Hübner, 1822 species live on *Quercus* spp. in Europe (De Prins and De Prins, 2022), new species have been also found recently (Laštůvka and Laštůvka, 2007). Almost 70 years ago, *Lithocolletis quercifoliella* ssp. *cerris* Gregor, 1952 was described, but its first depiction dates back to 1948 (Povolný and Gregor, 1948, as *P. quercifoliella*). This taxon was later considered a form (e.g. Hrubý, 1964; Laštůvka and Laštůvka, 1986) or subspecies (De Prins and De Prins, 2005, 2022) of *P. quercifoliella* (Zeller, 1839), or it was not distinguished from this species. Laštůvka *et al.* (2018) and Lopez-Vaamonde *et al.* (2021) present it as a separate species. It is close to *Phyllonorycter extincta* Deschka, 1974 morphologically, and they form together with *P. mirbeckifoliae* Deschka, 1974 and *P. quercifoliella* a monophyletic group of very close taxa.

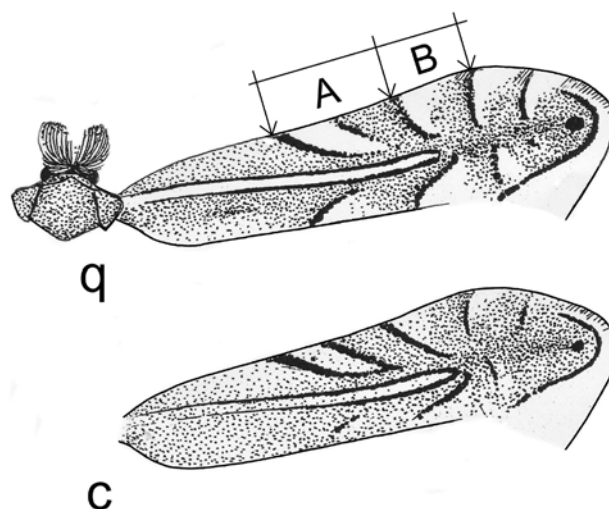
New systematic investigations and analyses by the first author, carried out since 1999, brought evidence, that “ssp. *cerris*” is a separate species. This

contribution brings redescription of this species, and results of morphological (morphometric), molecular, biological (laboratory breedings), ecological, and distributional analyses.

MATERIALS AND METHODS

The work is based on extensive material of cca 1050 adults of *Phyllonorycter cerris*, reared from mines collected on *Quercus cerris* at 42 localities in former Czechoslovakia (1942–1952) and in Czechia (1992–2018) (Tab. IV). The mines were partly collected in October and early November, but most of them on dry leaves during the winter (“winter test”). Comparative material of 300 *P. quercifoliella* adults was collected on autochthonous *Quercus* species mostly around the city of Brno (Medlánky, Soběšice, Útěchov, and other, all faunistic square 6765).

Occurrence data on *Quercus cerris* in Czechia were drawn from databases of the Institute “ÚHÚL” in Brno, from the publication by Slavík (1990), and from Mr. R. Stejskal (National Park



1: Forewings of *Phyllonorycter quercifoliella* (q) and *P. cerris* (c); A/B – costal index (figures after Povolný and Gregor, 1948 and Gregor, 1952, modified)

of Podyjí, Znojmo). Occurrence (presence) of other monophagous Lepidoptera, Diptera, and Hymenoptera was also registered on leaves of *Quercus cerris* since 2000.

Differential diagnosis is based primarily on a measurable feature on the forewing, called here “costal index”. The costal index (CI) was calculated according to the formula $CI = A/B$, where A is the distance between dark proximal edges of the first and second costal strigula, and B is the distance between edges of the second and third strigula (Fig. 1). So that the costal index means the measurement method as well as a numerical value obtained by this method. This character was measured in 256 adults of *P. cerris*, in 175 adults of *P. quercifoliella* (used adults with preserved patterns on both forewings), and in 71 adults of both taxa from experimental breedings.

DNA was extracted and barcodes were sequenced at the Canadian Centre for DNA Barcoding (CCDB, Guelph). We used barcode data (COI) for 49 specimens of *Phyllonorycter quercifoliella* and for 8 specimens of *P. cerris* (full-length DNA barcodes of 658 bp in all cases). Barcode data were analysed using the analytical tools of the Barcode of Life Data Systems (BOLD; www.boldsystems.org; Ratnasingham and Hebert, 2007) to compute mean and maximum intraspecific variation as well as mean and minimum distances between species. Besides the distance analyses computed on BOLD, the COI sequences were also analysed using neighbor-joining and maximum-parsimony approaches in PAUP * 4.0b8a (Swofford, 2002). All genetic distances were calculated using Kimura's 2 parameter model (K2P). The level of support for individual nodes was evaluated by nonparametric bootstrapping with 1000 replicates MP analyses.

Some questions of this work were solved by the study of mines on dry leaves of *Quercus cerris* (“winter test”) both fallen to the ground, and collected on unfallen bushes and lower branches of trees. This study brought data on the distribution of *Phyllonorycter cerris* in Czechia, on its population dynamics, and on the absolute population abundance. The population abundance of *P. cerris* was analysed on an isolated, about 200 years old tree of *Quercus cerris*, trunk circumference 235 cm, in the locality of Černá Hora, Zámek, at the southeastern edge of the forest growth of the *Carpineto-Quercetum* association, 49.4157333 N, 16.5775583 E.

The trophic specialization of *Phyllonorycter cerris* and *P. quercifoliella* was evaluated on seedlings of *Quercus cerris* and *Q. petraea* in isolators, especially whether or to what extent the taxa can receive the host plant on which their females do not lay eggs in nature, and whether they are able to complete development. We have established a total of 8 experimental breeds, 4 with mines of *Phyllonorycter quercifoliella* on leaves of *Quercus petraea* inserted into isolators with *Q. cerris*, and 4 vice versa (overview of combinations see Tab. II). If the larvae developed until pupation, the leaves were cut off, and pupae were individually reared until adults.

RESULTS

Phyllonorycter cerris (Gregor, 1952)

Lith. quercifoliella ssp. *Cerris*, 1952; *Zoologické Entomologické listy*, 1: 42

Type material. Syntypes, 1♂, 1♀, Slovakia, Kováčovské kopce Hills, ex l. iii.1950, larvae x.1949, lgt. F. Gregor (not found, probably lost).

Studied material. About 1050 adults from various parts of Czechia (both from Bohemia and Moravia)

and Slovakia, lgt. et coll. F. Gregor (Tab. IV); 8♂♂, Bohemia, Český kras Karst area, Srbsko, Císařská rokle (6050), mines 12.x.1997, ex l. i.1998, lgt. et coll. J. Vávra.

Differential Diagnosis (Tab. I)

Similar to *Phyllonorycter quercifoliella*. Compared to this species, the forewing strigulae are pale ochreous, less distinct (silvery white, contrasting in *P. quercifoliella*); their dark borders are more distinct only in the central part of the wing. This difference is characteristic and stable, but it is well observable at a certain point of view and in a good light. The most decisive differential character is the “costal index”. The values of the costal index are 0.85–1.45 for *P. cerris* and 1.23–1.98 for *P. quercifoliella* (see methods and a separate paragraph after redescription, Figs 1, 5, 8). The second costal strigula (its black border respectively) of *P. cerris* is adjacent

to the wing edge at an angle of 30–70°, and the first two strigulae are nearly parallel (the angle of the second strigula is 60–90° in *P. quercifoliella*, and the space between the first and second strigula is more or less triangular) (Fig. 2). The first costal strigula with unbroken dark border on both sides (slightly interrupted at the top in *P. quercifoliella*). The fourth costal strigula reduced (all 4 costal strigulae distinct white in *P. quercifoliella*). The dorsal strigulae reduced, the second one very oblique (3 distinct white dorsal strigulae in *P. quercifoliella*). The basal streak and its dark border slightly enlarged distally (evenly wide in *P. quercifoliella*). There are no individuals in the extensive study material, who would have an intermediate position in the whole complex of characters between *P. cerris* and *P. quercifoliella*. In any case, the whole complex of diagnostic characters must always be considered.

I: Differential characters of *Phyllonorycter cerris* and *P. quercifoliella*

Diagnostic character	<i>P. quercifoliella</i>	<i>P. cerris</i>
1. Host plant	<i>Quercus</i> , sect. <i>Robur</i>	<i>Quercus</i> , sect. <i>Cerris</i>
2. Dark border of the 2 nd dorsal strigula	angle 60–90° to the wing edge	angle 30–70° to the wing edge
3. Costal index	1.23–1.98	0.85–1.45
4. Dark border of the 1 st costal strigula	interrupted at the top	unbroken
5. Costal strigulae 3 and 4	distinct, white	more or less reduced
6. Dorsal strigulae	distinct, white	reduced, 2 nd very oblique
7. Basal streak	silvery white, contrasting, evenly wide	pale ochreous, less shiny, enlarged distally



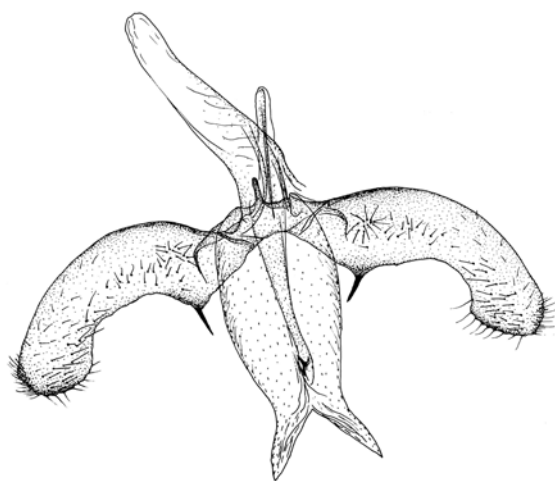
2: Adults of *Phyllonorycter cerris* (above) and *P. quercifoliella*
Source: Orig. A. Laštůvka

Redescription

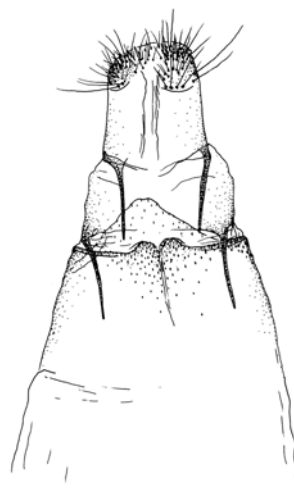
Adult (Fig. 2). Wingspan 7–9 mm; head tuft pale orange-brown to fuscous, some scales darker; labial palpus white; antenna whitish grey; thorax orange-brown without white medial line; forewing pale ochreous to pale brown, with four costal (the fourth of them strongly reduced) and three dorsal strigulae, lined in black inward; the basal streak and strigulae somewhat paler than the forewing ground color, all drawings generally less distinct, and a little shiny; the brownish black drawings widest in the middle of the wing, basally, dorsally and apically reduced; the first costal strigula bordered continuously on both sides, nearly parallel with the second one; the basal streak and its dark border slightly enlarged distally, pointed; the second dorsal strigula oblique, the third one very small and less distinct; apex with a small dot of black scales; fringe line distinct, sharp, from the fourth costal nearly to the second dorsal strigula; cilia whitish grey; hindwing grey, with long whitish grey scales; legs yellowish white; abdomen fuscous, caudal tuft whitish. The larger specimens show more distinct forewing drawings, smaller moths are lighter, with less pronounced drawings.

Male genitalia (Fig. 3). Symmetrical; tegumen and uncus broad, simple; valva distinctly bent ventrally, with rigid hairs in a belt in central part and distally, with a short filament basally, and a distinct lobe with a large thorn on ventral edge; vinculum short, saccus narrow, medium length; 8th sternit large, bilobed distally; phallus long, straight, with a hook-shaped projection on its end.

Female genitalia (Fig. 4). Papillae anales short and relatively broad, with dense middle long hairs; both apophyses short; lamella antevaginalis broad, with two broad lobes distally; 8th segment with narrow sclerotized border distally; ductus bursae fibrous; corpus bursae with distinct “wing-shaped” signum. Clear morphological differences in genitalia of all taxa of the *P. quercifoliella*-group were not found.



3: Male genitalia of *Phyllonorycter cerris*
Source: Orig. A. Laštůvka



4: Female genitalia of *Phyllonorycter cerris*
Source: Orig. A. Laštůvka

The “Costal Index”

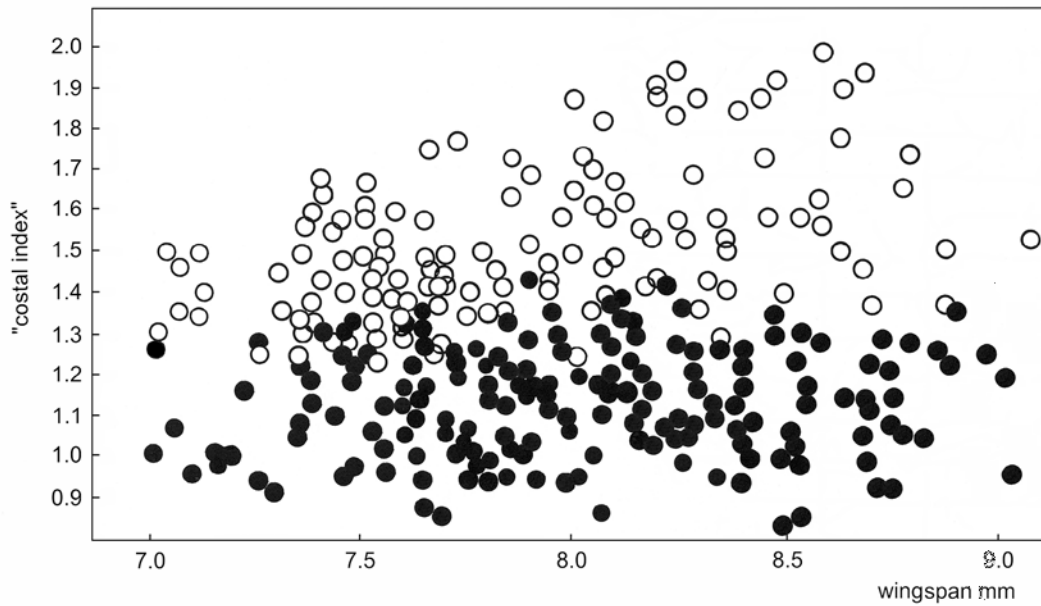
The most decisive differential character is measurable and here presented as so-called “costal index” (for the calculation see methods). The values of the costal index are 0.85–1.45 for *P. cerris* and 1.23–1.98 for *P. quercifoliella* (Figs 1, 5, 8). The values of both taxa slightly overlap which is also evident from the graphs (Figs 5, 8), but otherwise these adults did not show a transient appearance. These values are independent of adult size in *P. cerris*, but they slightly increase in large adults of *P. quercifoliella*.

Barcoding Results

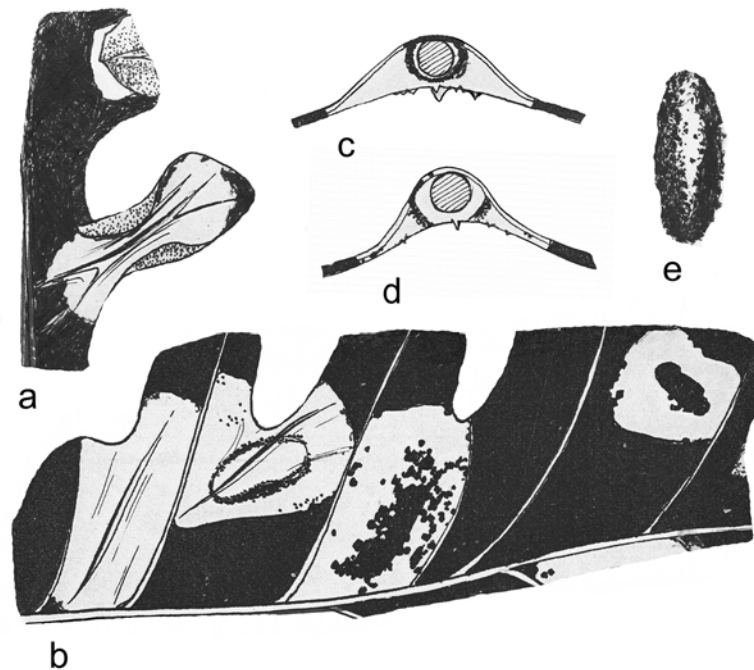
The intraspecific genetic variation among specimens of the same species is generally low, max 0.8% in *P. quercifoliella* and 1.07% in *P. cerris*. The p-distance between *Phyllonorycter cerris* and its nearest neighbour is 2.5%, so that the results support the distinction of *P. cerris* as a separate species.

Development and Mine

The species develops two generations annually in central Europe, adults are on the wing from the end of April to June, and again from July to the beginning of September, mines with larvae from May to July and from September to November. In central Europe, the larva mines obligatorily on leaves of *Quercus cerris* L., we also found it on allochthonous *Q. libani* Ol. in ornamental greenery. The development on other *Quercus* species is quite exceptional. The lower mine is oval or partially irregular, 11–22 mm long. It may be placed anywhere on the leaf, often between two veins, sometimes on the edge and causes a fold. An isle of the upper leaf parenchyma remains unconsumed in the middle of the mine, at the bottom, the mine is characterized by one significant central fold. The pupa is placed in a solid silk cocoon, which



5: Values of the costal index of *Phyllonorycter cerris* (●) and *P. quercifoliella* (○) (calculation see methods and Fig. 1, material data see Tab. IV)



6: Mines of *Phyllonorycter cerris*; a – summer mine, b – four winter mines in different perspectives, c – summer mine, cross section, d – winter mine, cross section, e – an abnormal summer cocoon (after Gregor, 1952, modified)

is completely covered with droppings in the summer generation, and is attached to the isle of unconsumed parenchyma on the upper side of the mine. In the winter generation, the cocoon is

attached both to the upper and lower surface of the mine, and is covered with droppings only on the sides and at the end (Figs 6, 7). Mines of *P. cerris* and *P. quercifoliella* do not differ from each other.



7: Mines of the new generation of *Phyllonorycter quercifoliella* on leaves of *Quercus cerris* in the isolator (breeding 6, cf. Tab. II)
Source: Photo F. Gregor

Trophic Specialization Test

Experimental breeding of *Phyllonorycter cerris* and *P. quercifoliella* on “incorrect” host plants was to verify the degree of the monophagous binding of *P. cerris*. Five of the eight breeds were successful. The experiment was indicative, did not allow to monitor behavior of adults in isolators and numbers of eggs laid, but it brought two clear results (Tab. II, Fig. 8).

1. Specific coloration of *P. cerris* is preserved in the offspring on the incorrect host, i.e. it is not caused by food (it is not a trophic form).
2. The larvae of both taxa accepted those *Quercus* species on which their females (probably) do not lay eggs in nature.

The first result was predictable, the second somewhat surprising, but explainable. Laying females could be confused by the odorous trace of the leaves of the correct host plant that were inserted into the isolators. Fresh or only slightly

withered leaves with mines were placed in isolators with successful breedings (4–8), but the leaves from the refrigerator, where they could lose their odor attractiveness during the winter, were placed in isolators with unsuccessful breedings (1–3). Therefore, these breedings could be unsuccessful.

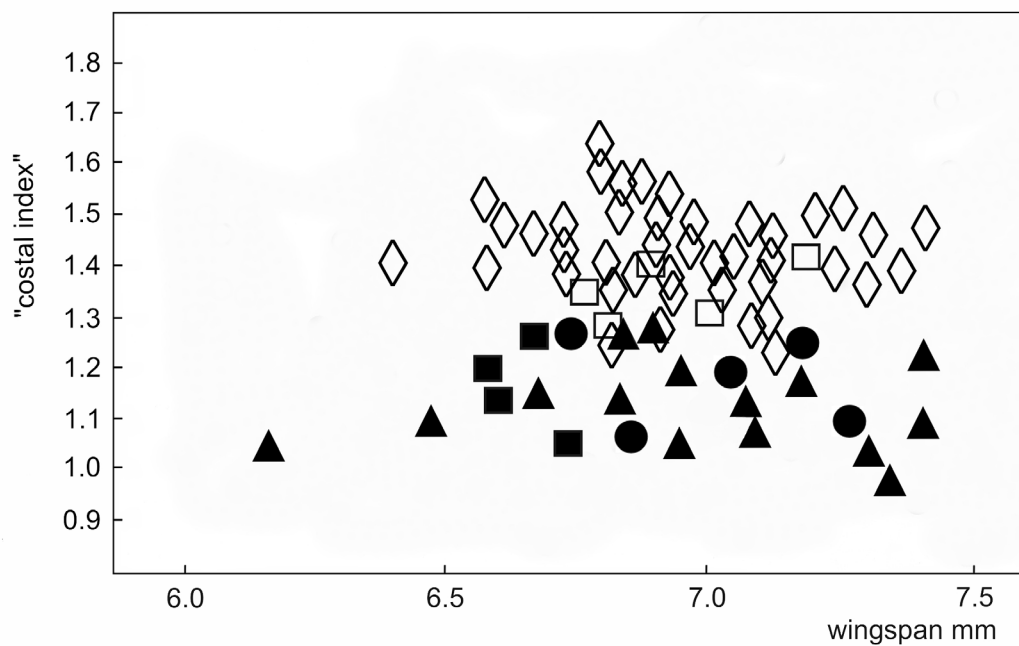
The result of unnatural breeding conditions in the isolators was a smaller size of reared adults and a less pronounced coloration of the forewings. The larvae pupated both in normal summer cocoons (totally covered with droppings) and in partially uncovered.

Dispersion

Regular winter tests of *Phyllonorycter cerris* mines in the locality of Brno-Medlánky/Řečkovice made it possible to determine, how this taxon spreads to the surroundings from its permanent population. The passive spread of pupae in dry leaves and of adults depends on the strength and direction of the wind

II: Combinations of *Phyllonorycter cerris* and *P. quercifoliella* on seedlings of *Quercus cerris* and *Q. petraea* in the experimental breeding and its results; breeding 8 served as a control

Number of breeding	1	2	3	4	5	6	7	8
Symbol of the costal index in the Fig. 8				■	□	◇	▲	●
Parents from <i>Quercus</i>	<i>Q. cerris</i>	<i>Q. petraea</i>	<i>Q. petraea</i>	<i>Q. cerris</i>	<i>Q. petraea</i>	<i>Q. petraea</i>	<i>Q. cerris</i>	<i>Q. cerris</i>
Plant in isolator	<i>Q. petraea</i>	<i>Q. cerris</i>	<i>Q. cerris</i>	<i>Q. petraea</i>	<i>Q. cerris</i>	<i>Q. cerris</i>	<i>Q. petraea</i>	<i>Q. cerris</i>
Leaves inserted	iv.2011	iii.2009	iv.2009	vi.200	vi.2010	iv.2011	vi.2011	vii.2011
Inserted mines	60	40	30	30	70	75	35	33
New mines	0	0	0	4	5	50	15	5
Adults emerged	0	0	0	4	5	42	15	5



8: Values of the costal index in the adults from the experimental breeding; symbols see Tab. II

as well as on terrain obstacles. We also observed *Phyllonorycter abrasella*, which accompanies *P. cerris* in all localities of autochthonous occurrence of *Quercus cerris* in southern Moravia. Both species spread most easily through field (from A to C), little through the forest (from A to B), and at least to a distant point D, moreover through a forest barrier (Tab. III, Fig. 9). These results show that the spread of *Phyllonorycter cerris* to the vicinity of the basic population is limited, and its dispersion potential is minimal over longer distances.

Absolute Abundance

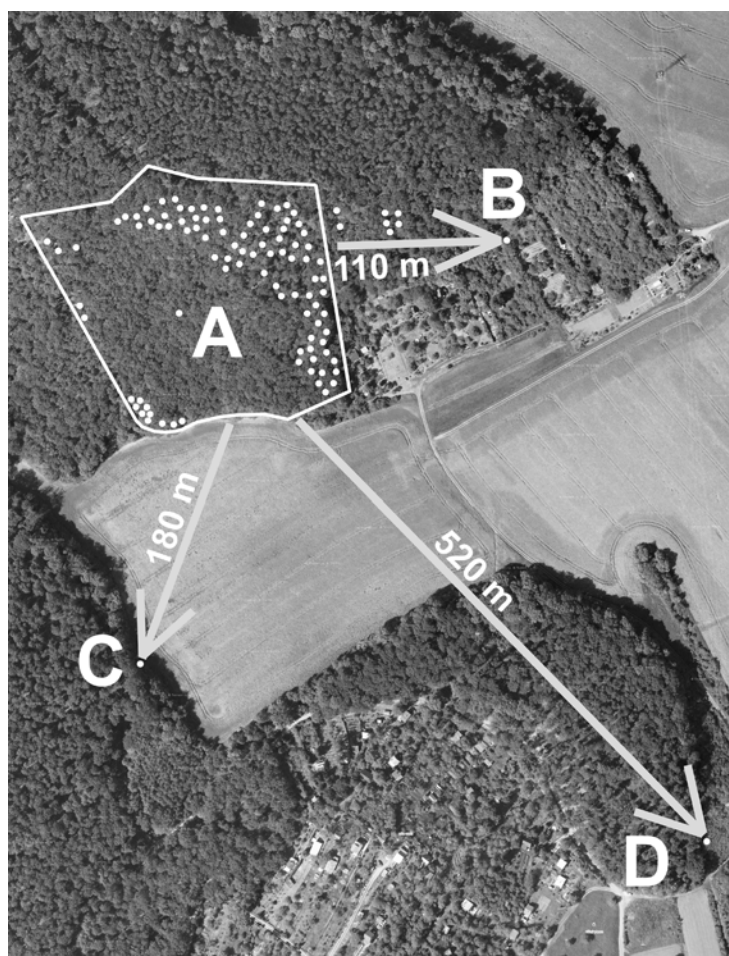
Assuming that *Phyllonorycter cerris* adults do not actively spread to a greater distance from the host plant, the question arises as to what population density allows this species to persist on isolated (park) solitaires for decades without reproductive contact with other populations. Such parameters are met by the old tree of *Quercus cerris*, growing near the castle in the town of Černá Hora. The

basic information, i.e. the total number of leaves of this tree, we derived with probes of fallen leaves measuring 1×1 m, on the one hand by 10 probes under the tree crown, on the other hand 15 probes around the tree, to 200 thousand leaves in 2015 (which was a favourable year for the *P. cerris* population). In 2013–2020, we obtained the following fluctuation series of mine numbers per 1000 leaves by 128 winter tests: 4, 3, 19, 16, 12, 0.5, 12, and 14. In the critical season 2017/2018, the number of mines on the whole tree dropped to 100, which is probably a value close to the subsistence minimum of the entire population.

During the winter 2018/2019, we registered two cases of extreme spatial disproportion of *Phyllonorycter cerris* mines, when their abundance at the edge of the stand was many times (seven or fifteen times) higher than on the nearest (approximately 5 m) trees of the forest interior. It was seven times more (calculated to 1000 leaves, 791:126) at the Medlánky locality (southern

III: Number of *Phyllonorycter cerris* and *P. abrasella* mines at four study localities; average values for 5 years given, conversion to 1000 leaves; dispersion distances see Fig. 9

Site	Distance from A [m]	<i>P. cerris</i>	<i>P. abrasella</i>	Both spp.
A	-	56	40	96
B	110	7	11	18
C	180	20	31	51
D	520	0	1	1



9: Dispersion of *Phyllonorycter cerris* to the vicinity of the permanent population; A – basic *Quercus cerris* stand, ○ – schematic layout of *Q. cerris* trees; B – eastern border of the stand; solitary tree, trunk circumference 130 cm, forest clearing, C – *Q. cerris* trees of height 7 and 9 m, D – shaded tree, height 4 m

exposition, young trees), and fifteen times (1691:114) at the Útěchov locality (northern exposition, branches of the marginal tree). The described situation may be due to the soil moisture deficit after a previous longer period with a lack of atmospheric precipitation. The branches of these trees sprouted secondarily and their young leaves probably had a higher odor attractiveness for laying females.

Occurrence in Czechia

The first author analysed the distribution of *Phyllonorycter cerris* in Czechia in detail with regard to autochthonous and allochthonous occurrence of the host plant (Tab. IV, Fig. 10). We also include *Phyllonorycter abrasella* and *P. ilicifoliella* in the map and in the list of localities which regularly accompany *Phyllonorycter cerris* in southern Moravia, but usually were not found outside this area.

1. Southern Moravian area of autochthonous occurrence of *Quercus cerris*

In the lower Dyje and Morava rivers regions, there is undoubtedly a permanent reproductive

contact between populations of *Phyllonorycter cerris*. Outside this planar area of continuous oak forests, there are individual populations of *P. cerris* in natural stands of *Quercus cerris* in the Pálava Hills, in the Podyjí National Park, in the Znojmo region, and near towns of Brno and Moravský Krumlov. Secondary occurrence sites of *P. cerris* with small and usually isolated populations are in windbreaks, park trees, or wooded clearings.

2. Localities of secondary occurrence of *Phyllonorycter cerris* in Czechia

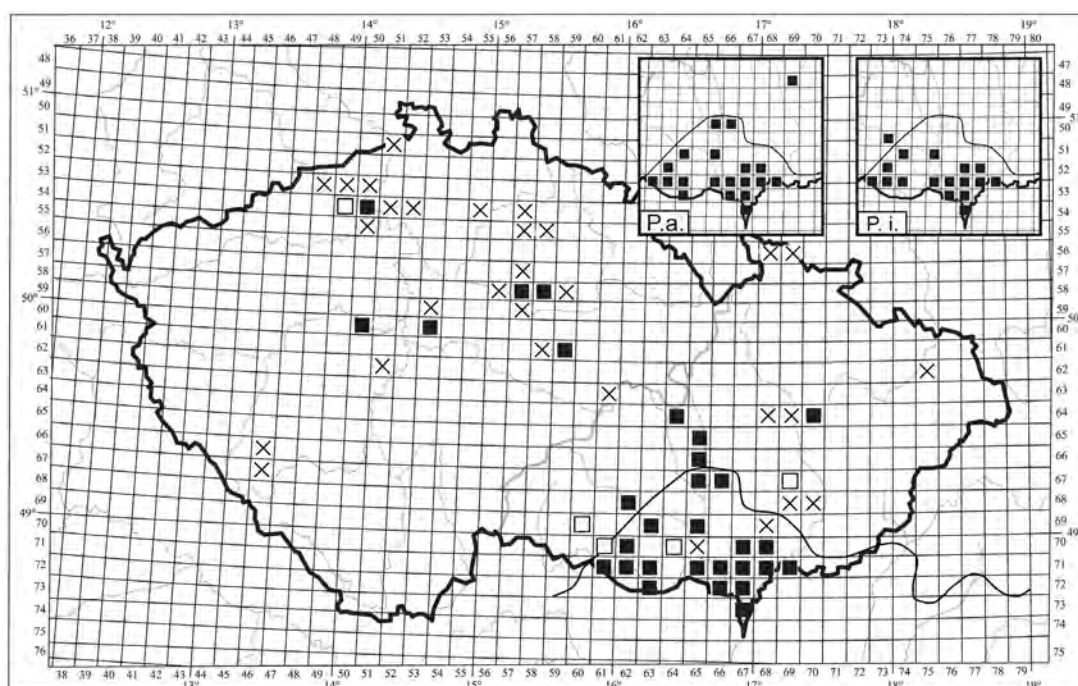
About two centuries ago, *Quercus cerris* was planted as a farm or ornamental tree with material of southern Moravian provenance, from where *Phyllonorycter cerris* pupae with nursery seedlings could be introduced into remote regions in Bohemia and Moravia and establish populations outside the autochthonous *Quercus cerris* area.

Distribution

Phyllonorycter cerris probably copies the distributional range of *Quercus cerris* (and possibly other species of the section *Cerris* Oerst)

IV: Finding data of *Phyllonorycter cerris* in Czechia; (S) after the locality name – secondary occurrence of *Phyllonorycter cerris* and *Quercus cerris*; M – only a mine of *P. cerris*, adult not reared; a, i – syntopic occurrence of *P. abrasella* or *P. ilicifoliella* with *P. cerris*; JV – collected by J. Vávra

Moravia, inside the range of <i>Q. cerris</i>	Square	Note	Date
Brno-Medlánky, Řečkovice	6765	a	2001–2020
Brno-Nejedlého str.	6765		2001–2020
Brno-Černá Pole, arboretum	6765		2007–2014
Brno-Hády	6766	a	1944–1950, 2007–2015
Polánka	6963	i	2002–2011
Moravský Krumlov	6963	ai	10.x.1948, 2002–2011
Pohořelice (S)	6965	ai	10.iv.2013, 23.iii.2019
Trnové Pole, větrolam (S)	7064	M	27.ix.2011
Kobylí (S)	7067	a	2003, 2005, 2007
Podmolí – Kozí hřbet	7161	ai	1.iv.2003, 6.xi.2003
NP Podyjí – Šobes	7161	ai	2.x.2002, 23.x.2006
Havraníky	7162	ai	13.x.2005
Těšetice	7162	ai	19.vii.2005, 16.xi.2007
Nesachleby	7162	ai	21.iii.2002, 13.xi.2002
Božice – Karlov	7163	ai	29.x.2002, 16.xi.2006
Děvín	7165	a	2002–2005
Mikulov – Sv. Kopeček	7165	i	13.xi.2008, 15.xi.2010
Milovice	7166	ai	5.x.2009, 26.vi.2012
Starý Poddvorov	7167	ai	2.x.2008
Mutěnice – Zbrod	7168	ai	3.ix.2007, 21.x.2008
Rohatec – Sobonky	7169	ai	1.iii.2012
Valtrovice větrolam (S)	7263	a	28.x.2011
Valtice – Rendez-vous	7267	ai	28.ix.2005
Lednice	7266	ai	1948–1950
Charvátská Nová Ves	7267	ai	2005, 2006, 2010
Valtice – Boří Dvůr	7267	ai	21.iv.2003
Hlohovec	7267	ai	28.vii.2010
Břeclav – Boří les	7267	ai	1953
Moravia, out of range of <i>Q. cerris</i>			
Rozseč 630 m	6464		5.iv.2011, 29.x.2011
Krčman	6470	a	1951, 2007–2012
Černá Hora, zámek	6565		2013–2020
Útěchov, U buku	6765		2002–2020
Morkovice	6769	M	16.iv.2011
Náměšť n. O.	6862	i	2002–2009
Nové Syrovice	6960	M	12.i.2012
Vranovská Ves	7061	M	12.i.2012
Bohemia, out of range of <i>Q. cerris</i>			
Libá Hora Hill 686 m	5449	M	20.vii.1952
Dubice	5449/50		v.1952
Žehuňská obora, Choťovice	5857		25.xi.2009
Žehuňská obora, Bludy	5858		8.vii.2012
Český kras, Císařská rokle	6050	JV	12.x.1997 (ex p. i.1998)
Průhonice, Park	6053		1948
Třemošnice	6159		1.vi.2011



10: Records of *Phyllonorycter cerris* in Czechia documented by reared adults ■; only mine with pupa or with a cocoon ◻ (see Tab. IV); occurrence localities of *Quercus cerris* (after Slavík, 1990) without *P. cerris* ×; the solid wavy line – a border of autochthonous occurrence of *Quercus cerris*; records of two additional species are given in the right upper corner, P.a. – *Phyllonorycter abrasella*, P.i. – *P. ilicifoliella*

further southeast. It was so far recorded in SE parts of Czechia, in southern Slovakia (Gregor, 1952), eastern Austria, Hungary, and Montenegro (unpublished records of authors).

DISCUSSION

The results of this work show that *Phyllonorycter cerris* is a separate species, not a subspecies. There is clearly a trophic and reproductive barrier between *P. cerris* and *P. quercifoliella*, and the current sympatric distribution and often even syntopic occurrence of both taxa further demonstrate their independence. Deschka (1974) described *Phyllonorycter mirbeckifoliae* and *P. quercifoliella* ssp. *extincta* from Tunisia. The second of the taxa is later listed as a separate species (De Prins and De Prins, 2005, 2022). *Phyllonorycter extincta* and *P. cerris* are very similar, with *P. cerris* being habitually intermediate between *P. extincta* and *P. quercifoliella*. Another, yet undescribed taxon, very close to *P. cerris* in the forewing drawings is known from Spain (collected by A. and Z. Laštůvka). Deschka (1974) believes that this entire monophyletic group originates in North Africa. But another option is also offered. The oligophagous and widespread *Phyllonorycter quercifoliella* could diverge in more areas, e.g. in the Iberian Peninsula, in North Africa and in the southeastern Europe or southwestern Asia. *Phyllonorycter cerris* could separate within the *Quercus* spp. of the section *Cerris* Oerst. in the eastern Mediterranean.

Current secondary occurrence of *Phyllonorycter cerris* in Czechia is of anthropogenic origin, not a result of spontaneous spread, because the dispersion potential of this species is according to our observations probably very low. Small populations of *P. cerris* then persists on solitary trees for a long time, even when the abundance decreases to values close to the subsistence minimum.

Our experimental breeding performed to verify the trophic specialization of *P. cerris* and *P. quercifoliella* shows that laying females may be wrong under artificial conditions. If it was experimentally confirmed that the wider trophic range of mining larvae compared to laying females is a rule (atavism?), it would support the theory of so-called stenophagy in Hering's conception of the gradual narrowing of the trophic specialization of miners, leading to monophagy (e.g. Hering, 1950; Povolný, 1956). The mistakes of laying females in mining Lepidoptera are probably sporadic, with unsuccessful continuation. *Cameraria ohridella* Deschka and Dimić, 1986 on *Acer* spp. can be an example of the successful development (e.g. Gregor *et al.*, 1998). Similar cases do not usually result to a change of the host plant. However, such deviations may have been part of the evolutionary process of some taxa. The larvae of permanently mining species cannot change their host plant during development. On the other hand, "exobiotic" mining species such as Coleophoridae leave mines and form new ones on other leaves or even on other plants. A peculiar example is the finding of

a case and mines of *Coleophora ochripennella* Zeller, 1849 on *Cannabis sativa* L. to which the larva moved from *Ballota nigra* L., one of its obligatory host plants. Both plants (from different families) grew in close contact and the larval case was formed from fragments of leaves from both plants (southern Moravia, Pohořelice, 1998, observed by the first author).

In addition to *Phyllonorycter cerris*, several other small moths mine monophagously on *Quercus cerris*. In the area of autochthonous occurrence of *Q. cerris* in southern Moravia, these are, e.g., *Phyllonorycter abrasella*, *P. ilicifoliella* (Gracillariidae), *Stigmella zangheri* (Klimesch, 1951), *Ectoedemia liechtensteini* (Zimmermann, 1944), and *E. cerris* (Zimmermann, 1944) (Nepticulidae). Not

only mining, but also some gall-forming species are monophagously bound to *Quercus cerris*. These are mainly *Dryomia circinans* (Giraud, 1861), *Janetia cerris* (Kollar, 1850), *J. szepligetii* (Kiefer, 1896) and *J. nervicola* (Kiefer, 1909) (Cecidomyiidae) (Skuhrový and Skuhrová, 1971), and *Andricus multiplicatus* (Giraud, 1859) (Cynipidae). In the same area, but in artificially established, isolated *Quercus cerris* cultures, the species spectrum of specialists is significantly poorer. An example is the Pohořelice-Smolín locality, a *Quercus cerris* culture founded on non-forest land (sand pit) in 2009. Only mines of *P. abrasella* and *P. cerris* were abundant, number of galls negligible, and species of the family Nepticulidae were not found.

CONCLUSION

An extensive study of the morphology and biology of the taxon *Lithocolletis quercifoliella* ssp. *cerris* Gregor, 1952 (= *Phyllonorycter cerris*) proved its species independence. The species is redescribed, with differential diagnosis and barcoding results (the p-distance between *Phyllonorycter cerris* and its nearest neighbour *P. quercifoliella* is 2.5%). The larva of *Phyllonorycter cerris* mines only *Quercus cerris* in central Europe, *P. quercifoliella* mines oligophagously *Quercus* spp. of the section *Robur* Reich. The larvae of both taxa accepted “incorrect” *Quercus* species on which their females (probably) do not lay eggs in nature, the specific coloration is preserved in the offspring in both taxa (it is not caused by food and therefore *P. cerris* is not a trophic form). Results of research on adults dispersion, population densities and distribution are added. Records of this species in Czechia are analysed with respect to autochthonous and allochthonous occurrence of *Quercus cerris*.

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