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HOST PLANT SELECTION IN *PHYLLONORYCTER* SPECIES LIVING ON WILLOWS AND THEIR HYBRIDS (LEPIDOPTERA: GRACILLARIIDAE)

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Abstract

Own knowledge on host plants and on the breadth of the trophic specialization of central European species of *Phyllonorycter* Hübner, 1822 living on *Salix* spp. obtained over the past 60 years are presented. A total of 8 species were evaluated and divided into four groups after their trophic relationships; monophagous species: *Phyllonorycter quinqueguttella* (Stainton, 1851) on *Salix repens* s. l., and *P. viminetorum* (Stainton, 1854) on *Salix viminalis* (here only provisorly due to the small number of reared specimens); narrowly oligophagous species: *P. dubitella* (Herrich-Schäffer, 1855) and *P. salicicolella* (Sircom, 1848), both on *Salix* species of the section *Capreae*; oligophagous species: *P. hilarella* (Zetterstedt, 1839) and *P. salictella* (Zeller, 1846) on many *Salix* species, each with different trophic preferences; broadly oligophagous species: *Phyllonorycter connexella* (Zeller, 1846) and *P. pastorella* (Zeller, 1846) developing on *Salix* and *Populus* species. The hybrids are also used as host plants, and the laying females positively respond to them as well as to the biological *Salix* species, if at least one of the parental species is the usual host of the relevant *Phyllonorycter* species. The data on host plants reported by other authors are compared.

Keywords: host plants, leaf miners, Lithocolletinae, trophic specialization

INTRODUCTION

Endophagous larvae of mining and gallicolous insects (e.g. some Diptera, Hymenoptera, and Lepidoptera) cannot change the substrate, and the food choice of a laying female is therefore essential which does not strictly apply to exophagous species. The ability of females to recognize specific substances of plant substrates is the result of the long-term evolutionary history and of the relationship between host and guest. Some entomologists of the 20th century have compared this ability of females to experiments called “serodiagnosis” done by the botanist Mez

(1925), in order to create a phylogenetic model of the plant system based on the chemistry of plant tissues. The bionomics of mining insects, including the food choice, were investigated especially by Hering (e.g. 1950, 1957), who inspired a number of contemporary and later entomologists. Povolný (1949, 1967) and Gregor *et al.* (1963) were dealing with the trophic preference in *Phyllonorycter* Hübner, 1822 species living on rosaceous trees, and Gregor (1952) investigated the species of this genus developing on oaks.

This contribution summarizes the results of research on food selection in 8 *Phyllonorycter* species living on willows in central Europe, and its main objective was to evaluate the degree of their host specialization. We also paid special attention to hybrids of willows which have not been systematically investigated as hosts, partly because of their difficult identification. Current and historical knowledge on host plants of these species are summarized by Davis and Deschka (2001) and De Prins and De Prins (2005, 2018), many other authors present records of individual host plants and variously extensive biological data (e.g. Le Marchand, 1936; Kuznetsov, 1981; Emmet *et al.,* 1985; Buszko, 1990; Kuznetsov and Baryshnikova, 1998; Laasonen and Laasonen, 2000; Bengtsson, 2010). Some data on the rearing of *Phyllonorycter* species from the *Salix* hybrids we only found in the paper by Fritz *et al.* (1998). Volf *et al.* (2015) dealt with defensive mechanisms of *Salix* species against herbivores. All these publications offer a comparison with our results.

MATERIALS AND METHODS

The contribution is based on about 1370 adults of *Phyllonorycter* species living on willows reared from mines predominantly of the second (overwintering) generation, intensively collected by the senior author in former Czechoslovakia in 1950–1976, and additionally in the Czech Republic until 2016, both in the wild and in arboreta of the Mendel University, in Brno (SW exposure, 220–250 m a.s.l., N 49°12.8′, E 16°36.85′) and in Křtiny (valley position, 450–460 m a.s.l., N 49°19.1′, E 16°44.65′). The numbers of localities where individual species were collected by F. Gregor are as follows (Czechia/Slovakia): *P. dubitella* 24/4, *P. hilarella* 33/15, *P. quinqueguttella* 1/1, *P. salicicolella* 13/4, *P. salictella* 29/9 (cf. Gregor *et al.,* 2017), *P. connexella* 18/4, *P. pastorella* 5/2. In the arboretum of the Mendel University in Brno, about 450 taxa of willows were concentrated from various parts of the world (Chmelař, 1987) of which about 200 are spontaneous or artificial hybrids and cultivars. This artificial assemblage of species was spontaneously occupied by the species living in the vicinity, namely *Phyllonorycter salictella* and *P. dubitella*, two other species, *P. hilarella* and *P. salicicolella* were introduced by the senior author, but the first one did not survive there. Six of the species evaluated in this paper live permanently in the semi-natural arboretum of Křtiny (except for *P. viminetorum* and *P. quinqueguttella*). The specimens reared by F. Gregor are deposited in the collection of the Moravian Museum in Brno and in his privat collection.

Extensive collection data (about 230 adults of 8 species) were also provided by Aleš Laštůvka from 1970–2016; the localities are accompanied by numbers of faunistic squares, cf. Pruner and Míka (1996) (Tab. I, all leg., det. et coll. A. Laštůvka):

Phyllonorycter dubitella (Herrich-Schäffer, 1855). Czechia, Moravia: Rýmařov (6069), Březinky (6366), Skřípov (6466), Stinava (6567), Prostějov (6568), Brno-Hády (6766), 22♂♂, 14♀♀, ex pupa from *Salix caprea* and *S. aurita*.

Phyllonorycter hilarella (Zetterstedt, 1839). Czechia, Silesia: Rejvíz (5769), Dolní Moravice (6069), Rýmařov (6069), 15♂♂, 12♀♀, always ex pupa from *Salix aurita*.

Phyllonorycter quinqueguttella (Stainton, 1851). Slovakia: Sekule (7368), iii.1986, 8♂♂, 5♀♀, Závod-Abrod (7468), iii.1985, 3♂♂, 4♀♀, Čenkov (8277), iii.1984, 1♂, always ex pupa from *Salix rosmarinifolia*.

Phyllonorycter salicicolella (Sircom, 1848). Czechia, Moravia: Horka nad Moravou (6369), Mušov (7165), 14♂♂, 19♀♀, always ex pupa from *Salix cinerea*.

Phyllonorycter salictella (Zeller, 1846). Czechia, Moravia: Jesenec (6367), Šubířov (6466), Stinava (6567), Němčice nad Hanou (6669), Horka nad Moravou (6369), Morkovice (6769), Ivaň (7065), Mušov (7165), Dolní Věstonice (7165); Slovakia: Sekule (7368); 30♂♂, 25♀♀, ex pupa from *Salix alba, S. melanopsis, S. purpurea, S. rosmarinifolia, S. viminalis*.

Phyllonorycter viminetorum (Stainton, 1854). Czechia, Moravia: Mikulčice (7168), iii.1975, 3♂♂, 4♀♀, ex pupa from *Salix viminalis*.

Phyllonorycter connexella (Zeller, 1846). Czechia, Moravia: Třebíč (6761), Ptáčov (6761), Kladky (6367), Jesenec (6367), Horka nad Moravou (6369), 8♂♂, 6♀♀, ex pupa from *Salix euxina, S. purpurea*.

Phyllonorycter pastorella (Zeller, 1846). Czechia, Moravia: Jesenec (6367), Plumlov (6568), Horka nad Moravou (6369), Prostějov (6568), Chropyně (6670), Pasohlávky (7065), Mušov (7165), Dolní

I: *Numbers of reared adults of all evaluated Phyllonorycter species; N – natural habitats, B – arboretum of Brno, K – arboretum of Křtiny, H – hybrids (predominantly arboretum of Brno), N, B, K, H – F. Gregor leg. et coll., AL – A. Laštůvka leg. et coll.; a – number of host Salix species, b – number of taxonomic Salix sections, c – number of host Salix hybrids*

Phyllonorycter	**Specimens**						**Salix**		
	N	**B**	**K**	**H**	**AL**	**Total**	**a**	**b**	**c**
salictella	192	90	67	189	55	593	31	21	30
hilarella	245	0	31	5	27	308	10	7	4
dubitella	174	72	35	43	36	360	15	6	11
salicicolella	65	7	12	4	33	121	7	3	4
viminetorum	0	0	0	0	7	7	1	1	0
connexella	40	14	5	30	14	103	6	4	7
pastorella	24	0	0	9	36	69	7	6	3
quinqueguttella	15	0	0	1	21	37	1	1	1
Total	755	183	150	281	229	1598			

Věstonice (7165), 16♂♂, 20♀♀, ex pupa from *Salix alba, S. euxina, S. purpurea*.

We understand the categorization and terminology of the trophic specialization as follows. Monophagous species are bound to one (or to a pair of very close host plant species). Narrowly oligophagous species develop on a group of related *Salix* species or they clearly prefer any group. Oligophagous species are known on various *Salix* species which are grouped in more different (and unrelated) sections. The trophic preference of broadly oligophagous species includes two or more host plant genera. This our concept is close to that of Klausnitzer (1983), not of Hering (1951) or Povolný (1956) which are too broad and do not allow resolution up to the level of a host plant species. We use the section name "*Capreae*" instead of "*Vetrix*" for better text clarity. The taxonomic identity of willows was guaranteed by the dendrologist (J. Chmelař), the nomenclature follows Vašut *et al.* (2013) or The Plant List (2013) in some exotic species.

RESULTS

Trophic specialization of evaluated species

Our investigations of central European *Phyllonorycter* species living on willows resulted in the following distribution (Tab. I, II, III):

1) Species monophagous on one or two very close *Salix* species: *Phyllonorycter quinqueguttella,* found only on two very close *Salix* species, *Salix repens, S. rosmarinifolia* (= *S. repens* s. l.) of the section *Incubaceae*, and *Phyllonorycter viminetorum* found on *Salix viminalis* (only provisorly in the second species due to the small number of reared specimens),
2) Species narrowly oligophagous only on several, often close *Salix* species: *Phyllonorycter dubitella* and *P. salicicolella,* both almost exclusively develop on *Salix* species of the section *Capreae*,
3) Species oligophagous on many *Salix* species (each of them with different trophic preferences): *Phyllonorycter hilarella* and *P. salictella;* the first of them develops on all species of the section *Capreae* and other species of the subgenus *Vetrix*; it avoids species of the subgenus *Salix*; the second one mines *Salix* species from various sections of all three subgenera, except for species of the section *Capreae* (in central Europe),
4) Species broadly oligophagous on two plant genera: *Phyllonorycter connexella* and *P. pastorella;* they both mine *Salix* and *Populus*.

This distribution is supported by the numerous material, especially in the case of the pair *salictella/dubitella* with different pattern of the food preference. We reared 341 adults of *P. salictella*, but none *P. dubitella* from six *Salix* species (*S. alba*, *S. daphnoides*, *S. elaeagnos*, *S. myrsinifolia*, *S. purpurea,* and *S. viminalis*), and on the contrary, 262 adults of *P. dubitella*, but none *P. salictella* hatched from three common *Salix* species, all from the section *Capreae* (*S. aurita*, *S. caprea,* and *S. cinerea*). It follows from the above that the species specific pattern of the trophic specialization do not reflect the currently accepted classification of willows. The deviations from this pattern are sporadic and they concern *Salix* species which are unusual or exotic in central Europe, e.g. *Salix appendiculata* (in Czechia only relict occurrence in Šumava Mts.), *S. drummondiana*, and *S. cordata*. The laying females may be desoriented by the unknown *Salix* species.

II: *Numbers of all Phyllonorycter specimens reared both from autochthonous and allochthonous Salix species*

Subgen.	Section	*Salix* spp.	*Phyllonorycter* spp.							
			sal	hil	dub	salcol	vim	con	pas	quin
Salix	*Amygdalinae*	*triandra L.*	2						2	
	Humboldtianae	*nigra Marsh.*	2							
	Longifoliae	*melanopsis Nutt.*	10							
	Magnificae	*magnifica Hemsl.*			1					
	Pentandrae	*pentandra L.*							1	
	Salix	*alba L.*	56					25	19	
		euxina Bel.						33	28	
	Subalbae	*babylonica L.*	7					1	5	
	Tetraspermae	*tetrasperma Roxb.*	1							
Vetrix	*Arbuscella*	*arbusculoides And.*				2				
		drummondiana Barr.			3					
		hegetschweileri Herr.	1							
	Caesiae	*caesia Vill.*	1							
		kochiana Traut.			3					
	Canae	*elaeagnos Scop.*	10							
	Capreae	*aegyptiaca L.*			5					
		appendiculata And.	1		1			1		
		atrocinerea Brot.			6					
		aurita L.		59	7	20				
		caprea L.		116	236	2				
		cinerea L.		55	19	89				
		hookeriana Barratt			1			1		
		muscina Dode			24					
		salviifolia Brot.			1	1				
		silesiaca Willd.		32	8					
		starkeana Willd.				1				
	Cordatae	*cordata Michx.*			1					
		eriocephala Michx.	2						2	
		missouriensis Bebb	2							
	Daphnella	*acutifolia Willd.*	1							
		daphnoides Vill.	16	1						
	Geyerianae	*petiolaris Sm.*	3							
	Hastatae	*hastata L.*		3						
		japonica Thunb.			1					
	Helix	*gilgiana Seemen*	2							
		purpurea L.	215	25				12	3	
	Incubaceae	*repens L.*		1						
		rosmarinifolia L.	4			2				36
	Mexicanae	*lasiolepis Benth.*	1							
	Nigricantes	*apennina (Borgi) Skv.*	3							

Subgen.	Section	*Salix* spp.	*Phyllonorycter* spp.							
			sal	hil	dub	salcol	vim	con	pas	quin
Vetrix	*Nigricantes*	*mielichhoferi Saut.*	1							
		myrsinifolia Salisb.	17	9						
	Variegatae	*variegata Franch*	2							
	Vimen	*gmelinii Pall.*	7							
		turanica Nas.	3							
		udensis Trautv. Mey	1							
		viminalis L.	27	2			7			
Chamaetia	*Glaucae*	*glauca L.*	2							
	Myrtilloides	*alpina Scop.*	2							
		myrtilloides L.	1							
		pedicellaris Pursh.	1							
Specimens totally			404	303	317	117	7	73	60	36

III: *Food preferences of Phyllonorycter on Salix species autochthonous in Czechia (exact numbers see Tab. II)*

			Phyllonorycter spp.							
Salix				*hilarella-group*				*sagitella-group*		
Salix subgenus	*Salix section*	*Salix species*	*salictella*	*hilarella*	*dubitella*	*salicicolella*	*viminetorum*	*connexella*	*pastorella*	*quinqueguttella*
Salix	*Amygdalinae*	*triandra*	o						o	
	Pentandrae	*pentandra*							o	
	Salix	*alba*	■					●	●	
		euxina						●	●	
Vetrix	*Canae*	*elaeagnos*	●							
	Daphnella	*daphnoides*	●	o						
	Hastatae	*hastata*		o						
	Helix	*purpurea*	■	●				●	o	
	Incubaceae	*repens* s.l.	o	o		o				●
	Nigricantes	*myrsinifolia*	●	o						
	Capreae	*appendiculata*	o		o			o		
		aurita		■	o	●				
		caprea		■	■	o				
		cinerea		■	●	■				
		silesiaca		●	o					
	Vimen	*viminalis*	●	o			o			

reared adults: ○ 1–10, ● 11–50, ■ > 50

Comments on individual species

Phyllonorycter dubitella (Herrich-Schäffer, 1855). Species vertically distributed from lowland to submontane areas, with preference of colline locations (e.g. Laštůvka and Laštůvka, 1986), narrowly oligophagous; it clearly prefers species of the section *Capreae*, preferably *S. caprea* (236 reared specimens, i.e. 74.5% of adults reared from biological *Salix* species), including occasionally planted, non-European *Salix muscina*.

Phyllonorycter hilarella (Zetterstedt, 1839). It distinctly prefers cooler mountain locations (e.g. Laštůvka and Laštůvka, 1986). It is oligophagous in the whole subgenus *Vetrix*, with clear preference of the section *Capreae*, we do not have any record from the subgenus *Salix*. It is occasionally quite common on *Salix caprea*, it was very abundant on *S. purpurea* and *S. silesiaca* in Velká Fatra Mts. (Slovakia).

Phyllonorycter quinqueguttella (Stainton, 1851). This species, similarly to its host plants *Salix repens* and *S. rosmarinifolia,* is very local in central Europe and occurs on wet meadows, margins of peat bogs, and on wet sands (Laštůvka and Laštůvka, 1986; Gregor and Laštůvka, 1991). It was reared only from one hybrid, *Salix purpurea* × *rosmarinifolia* (Slovakia occ., Abrod).

Phyllonorycter salicicolella (Sircom, 1848). Locally common from lowlands to middle locations, with distinct preference of *Salix cinerea* and *S. aurita*. The lower number of reared specimens is the result of low population density of this species in both arboreta. It was also reared from *Salix rosmarinifolia* (Laštůvka and Laštůvka, 1986).

Phyllonorycter salictella (Zeller, 1846). Species locally abundant from lowlands to submontane areas (e.g. Laštůvka and Laštůvka, 1986, Gregor *et al.*, 2017), oligophagous, it avoids host species of the section *Capreae* in central Europe, with exception of one our record on *Salix appendiculata*. It numerously exceeded other species in our breeds, especially on hybrids. The most specimens were reared from *Salix purpurea*. The high number of specimens reared from *Salix purpurea* × *viminalis* (47) and *S. americana* × *purpurea* (49) is due to the representation of both preffered parents in these hybrids (Tab. IV).

Phyllonorycter viminetorum (Stainton, 1854). It was recorded only once on *Salix viminalis* in lowland forest habitats in southern Moravia (Laštůvka and Laštůvka, 1986), but *Salix aurita* and *S. caprea* are also given as host plants (e.g. De Prins and De Prins, 2018).

Phyllonorycter connexella (Zeller, 1846) and *P. pastorella* (Zeller, 1846). Species preferring warmer areas (e.g. Laštůvka and Laštůvka, 1986). They are broadly oligophagous on *Salix* and *Populus*, but they avoid *Salix* species of the section *Capreae*. They use host plant species with a smooth underside of leaves.

Hybrids of *Salix* species as hosts

A survey of species and number of specimens reared from hybrids is given in Tab. IV. *Phyllonorycter salictella* hatched from 30 hybrids (189 ex.), 24 of which have a clear share (at least one of the parents) of an obligatory host of this species. *Phyllonorycter dubitella* hatched from 11 hybrids (43 ex.), of which at least one parental species almost always (one exception) belongs in the section *Capreae*. Similarly, *P. hilarella* and *P. salicicolella* were obtained from 4 hybrids, of which always one parental species is the usual host of these species.

There are willows of unclear origin and often difficult to determine among spontaneous hybrids and horticultural cultivars. E.g. the willows labelled as "*S. bicolor* hort." (not *S. bicolor* Ehrh.) in both arboreta could be hybrids between some species of the section *Capreae* and some species from another section, because both *P. dubitella* (9 ex.) and *P. salictella* (5 ex.) hatched from them. The favoured cultivar of unknown origin, *Salix americana* hort., is also a problematic case. Some of the hosts of *Phyllonorycter salictella* must be among the parental species of this cultivar (and none species of the section *Capreae*), because 12 adults of *P. salictella*, but none *P. dubitella* or other species preferring the section *Capreae* hatched from this willow. The complex of hybrids and cultivars known as "*S. dasyclados*" is also a problem (cf., e.g. Chmelař and Meusel, 1976; Vašut *et al.*, 2013). The hybrids under the name "× *dasyclados*" (= *S.* × *dasyclados* Wimm., = *S.* ×*holosericea* Willd.) in the arboretum of Brno come from various European collections, some of them were labelled as "*Aquatica gigantea*". They are, in the prevailing concept, double and triple hybrids of *Salix cinerea* (*caprea*) with *S. viminalis* (reared 6 ex. of *P. salictella* and 8 ex. of *P. dubitella*) (Tab. IV). In the sense of some Russian authors, this taxon is identical with eastern Asiatic *Salix gmelinii* of the section *Vimen* from which 7 ex. of *P. salictella*, but none *P. dubitella* were reared (Tab. II).

The results show that hybrids of willows are not "unreadable" for the laying females. The reared adults document that the laying females do not

IV: *Numbers of Phyllonorycter specimens reared from hybrids and cultivars of Salix species*

×*Salix*		*Phyllonorycter spp.*					
	horticultural name	*sal*	*hil*	*dub*	*salcol*	*con*	*pas*
acutifolia* × *caprea		1					
alba* × *babylonica	×*sepulcralis Simon.*	2				1	
alba* × *euxina	×*rubens Schrank*	7				9	5
???	×*americana hort.*	12					
americana* × *caprea		1		3			
americana* × *purpurea		49					
appendiculata* × *caprea	×*macrophyla Kern.*	2					
appendiculata* × *eleagnos	×*intermedia Host*	1					
appendiculata* × *purpurea	×*austriaca Host*	3					
atrocinerea* × *myrsinifolia		7		4			
aurita* × *myrtilloides	×*onusta Bess.*	1					
aurita* × *silesiaca	×*subaurita And.*			1			
aurita* × *viminalis	×*fruticosa Doll*	1		1			
babylonica* × *euxina	×*blanda And.*						3
???	×*bicolor hort.*	5		9			
caprea* × *cinerea	×*reichardtii A. Kern.*		1				
caprea* × *daphnoides	×*erdingeri Kern.*	1					
caprea* × *elaeagnos	×*seringeana Gaud.*	1	1				
caprea* × *purpurea	×*wimmeriana Gren.*	13		6	1	1	
caprea* × *viminalis	×*smithiana Willd.*	1		7		1	
cinerea* × *myrsinifolia	×*vaudensis Forb.*	2	1				
cinerea* × *purpurea	×*pontederana Willd.*	3			1		
cinerea* × *repens					1		
???	×*dasyclados hort.*	6		8	1		
hastata* × *hegetschweileri		3					
daphnoides* × *dasyclados hort.				1			
daphnoides* × *purpurea	×*calliantha Kern.*					1	
daphnoides* × *triandra						6	
daphnoides* × *viminalis	×*digenea Kern.*	2					
eleagnos* × *silesiaca	×*andreae Wol.*		2				
foetida* × *purpurea		2					
futura* × *integra	×*sirakavensis Kim.*	1					
glauca* × *purpurea							1
hegetschweileri* × *myrsinifolia		3		1			
myrtilloides* × *myrsinifolia		2					
purpurea* × *silesiaca	×*siegertii And.*	5		2			
purpurea* × *udensis		1					
purpurea* × *viminalis	×*rubra Huds.*	47				11	
triandra* × *viminalis	×*mollissima Hoffm.*	4					
Reared adults totally		189	5	43	4	30	9
Attacked hybrids		30	4	11	4	7	3

avoid them and detect with certainty *Salix* species that they have encoded in their trophic pattern. They positively focus on the chemistry (a specific scent signal) of the obligatory host species in a hybrid, and are attracted by it, and the second parental species does not probably act repellently, although the hybrids are both morphologically and molecularly intermediate in various degrees. Our conclusions are consistent with the results of experiments by Fritz *et al.* (1998). These authors evaluated resistance to herbivores in two *Salix* species, namely *Salix sericea* Marshall (with leaves smooth from bellow) and *S. eriocephala* Michx. (leaves densely pubescent), and in their hybrid. The density of *Phyllonorycter salicifoliella* (Chambers, 1871) was also ascertained and the number of reared specimens was almost the same both in the parental *Salix* species and in the hybrid.

Exceptions from species-specific food choices in hybrids are sparce: *Phyllonorycter dubitella* was reared from *S. hegetschweileri* × *myrsinifolia* (1 ex.), where it has no representation of the section *Capreae*, or *P. salictella* (2 ex.) hatched from *S. appendiculata* × *caprea*, where both parental species are from the section *Capreae*.

DISCUSSION

A comparison of our results with the current knowledge of the host specialization in the *Phyllonorycter* species living on willows (cf. Davis and Deschka, 2001; De Prins and De Prins, 2005, 2018) allows us to assess a broader degree of their validity. The numbers of reared adults (Tab. II, IV) only approximate the degree of attractiveness of individual *Salix* species and hybrids. Our material is a result of both targeted and casual investigations, and the numbers of reared adults are greatly affected by occurrence and abundance of *Salix* species. The contemporary species-specific trophic preferences or selections are a result of the long-term evolutionary adaptations to certain *Salix* species. The processes leading to the stenophagy of *Phyllonorycter* on willows could take place in various ways in two different *Phyllonorycter* species-groups. The *hilarella*-group (identical with the *hilarella*-subgroup by Davis and Deschka, 2001) contains *P. dubitella, P. hilarella, P. salicicolella, P. salictella,* and *P. viminetorum* in central Europe. It is obvious a clear specialization of three *Phyllonorycter* species of this group on the willow section *Capreae* (*P. dubitella, P. salicicolella, P. hilarella*) and narrow specialization of *P. viminetorum* on *Salix viminalis*. On the contrary, *P. salictella* uses many *Salix* species from other sections, but it avoids species of the section *Capreae* in central Europe. The remaining three species (belonging to the second group called here as *sagitella*-group), i.e. *P. connexella*, *P. pastorella*, and *P. quinqueguttella*, belong among species predominantly and probably primarily bound to *Populus* species, and a (multiple) transition from *Populus* to *Salix* species is possible, with an extreme trophic specialization of *P. quinqueguttella.*

The food selection patterns found for central Europe do not have to be valid throughout the whole ranges. Any regional differences may be due to a different species spectrum of potential hosts. Our results are more or less consistent with published data on broadly oligophagous species *Phyllonorycter connexella* and *P. pastorella* which we mostly reared from *Salix alba*, *S. euxina*, *S. babylonica, S. purpurea,* and their hybrids. Contrary to the published data (De Prins and De Prins, 2005, 2018), we did not find *P. connexella* on *Salix pentandra* and *S. viminalis*, and *P. pastorella* on *Salix caprea* and *S. viminalis*. The lower number of reared adults of *P. pastorella* is due to the fact that adults owerwinter and they were often hatched at the time of mines collection. In principle, our results correspond to general knowledge in two narrow trophic specialists, *P. viminetorum* and *P. quinqueguttella.* We did not find *P. viminetorum* on other *Salix* species than *S. viminalis* which may be due to the scarcity of this *Phyllonorycter* species in Czechia. The acquired knowledge on the trophic relations of *P. dubitella* and *P. salicicolella* is also obviously generally valid, both clearly prefer willows of the section *Capreae*. Both, our and published findings on *Salix* species from other sections are sporadic, namely *Salix alba* and *S. euxina* (cf. Davis and Deschka, 2001) for *P. dubitella,* and *Salix euxina*, *S. pentandra*, *S. purpurea*, *S. viminalis*, etc. for *P. salicicolella* (De Prins and De Prins, 2018). Similarly, *P. hilarella* clearly prefers willows of the section *Capreae*, but we also recorded it numerously on some species from other sections of the subgenus *Vetrix*, quite exceptionally, *Salix pentandra* and *S. euxina* are also listed as host plants (Svensson, 1966; Davis and Deschka, 2001). Somewhat greater discrepancies between our results and published data are evident in *P. salictella,* if we take into account not only central European records. While in central Europe the species of the section *Capreae* are quite exceptional host plants, they are common hosts in some parts of southwestern and western Europe, and in Scandinavia (cf. Davis and Deschka, 2001; Corley, 2015; De Prins and De Prins, 2018).

V: *Food specialization of Phyllonorycter species living on Salix spp. (own and published data) compared with leaf gallicolous Euura s. l. species (Hymenoptera) (data after Baudyš, 1953, Beneš, 2015, modified after Liston et al., 2017); mountain willows of the section Chamaetia are not included.*

	Phyllonorycter								***Euura***																						
Salix spp.	***salictella***	***hilarella***	***dubitella***	***salicicolella***	***viminetorum***	***connexella***	***pastorella***	***quinqueguttella***	***acutifoliae***	***anglica***	***brevicornis***	***bridgmanii***	***destricta***	***collactanea***	***cyrnea***	***kriechbaumeri***	***leucapsis***	***leucosticta***	***oblita***	***peduncluli***	***piliserra***	***plicadaphnoides***	***polita***	***proxima***	***prussica***	***purpureae***	***scotaspis***	***triandrae***	***vesicator***	***viminalis***	***virilis***
Subgenus Salix																															
Sect. Amygdalinae																															
triandra	•						•												•								•				
Sect. Pentandrae																															
pentandra	•					•	•						•																		
Sect. Salix																															
alba	•					•	•												•					•							
euxina	•					•	•												•					•							
Subgenus Vetrix																															
Sect. Canae																															
eleagnos	•															•															
Sect. Capreae																															
aurita		•	•	•							•	•			•		•	•		•											
caprea		•	•	•	•	•	•					•			•			•		•											
cinerea		•	•	•							•	•					•	•							•						
silesiaca		•	•									•								•											
Sect. Daphnella																															
daphnoides	•	•				•			•													•									
Sect. Hastatae																															
hastata		•										•																			
Sect. Helix																															
purpurea	•	•				•	•																•			•			•	•	•
Sect. Incubaceae																															
repens	•	•				•		•						•																	
rosmarinifolia	•			•				•						•																	
Sect. Nigricantes																															
myrsinifolia	•	•																													
Sect Vimen																															
viminalis	•	•		•	•	•	•			•											•					•					
Hosts totally	*11*	*10*	*4*	*5*	*2*	*8*	*7*	*2*	*1*	*1*	*2*	*5*	*1*	*2*	*2*	*1*	*2*	*3*	*3*	*3*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
Number of sections	*9*	*7*	*1*	*3*	*2*	*7*	*6*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*

The species of the section *Capreae* are reported among host plants also in Great Britain, besides, the species was (is) traditionally mentioned under the name *P. viminiella* (Sircom, 1848) there.

It is interesting to compare the food preferences of *Phyllonorycter* with leaf gallicolous species of *Euura* Newman, 1837 (Hymenoptera) (Tab. V), both with the endogenous way of life of their praeimaginal stages (data after Beneš, 2015; modified after Liston *et al.*, 2017). Similar patterns of the food selection of these species have already been observed by Baudyš (1948, 1953). The preference (or even exclusivity) of the section *Capreae* is distinct in both genera: 3 *Phyllonorycter* (38%) and 7 *Euura* s. l. species (30%). Otherwise, the *Euura* s. l. species are much more specialized. About half of *Phyllonorycter* species use willows of six and more sections, and only 2 species (25%) are bound to one section. On the contrary, the vast majority of *Euura* s. l. species use the willows of one section (91%) of which even 14 are strictly monophagous on a single species, the most on *Salix purpurea* (5) and *S. viminalis* (3). Only 2 species develop on willows of two sections. The exclusiveness of the section *Incubaceae* (*Salix repens* and *S. rosmarinifolia*) with two food specialists (*Phyllonorycter quinqueguttella* and *Euura collactanea*) is also interesting.

CONCLUSIONS

The *Phyllonorycter* species living on willows (*Salix* spp.) show various breadth of food specialization from the broadly oligophagous (*P. connexella* and *P. pastorella*) to the nearly strictly monophagous species (*P. quinqueguttella*) which is consistent with the hypothesis of gradual trophic specialization (stenophagy) leading up to the monophagy in the mining Lepidoptera. The processes leading to the stenophagy on willows could take place in various ways in two different *Phyllonorycter* species-groups. In the first group of five species (*P. dubitella, P. hilarella, P. salicicolella, P. salictella*, and *P. viminetorum*), it is obvious a clear specialization of three species on the section *Capreae* (*P. dubitella, P. salicicolella, P. hilarella*), and on the contrary, use of many *Salix* species from other sections in *P. salictella* which avoids species of the section *Capreae* in central Europe. The remaining three species, i.e. *P. connexella*, *P. pastorella*, and *P. quinqueguttella*, probably primarily belong among *Populus* feeding species, and a (multiple) transition from *Populus* to *Salix* species is possible, with an extreme trophic specialization in *P. quinqueguttella.* Similar food selection pattern can also be observed in other insect groups, e.g. gallicolous Hymenoptera. In the interspecific hybrids of willows, the laying females clearly detect the *Salix* species encoded in their trophic pattern, i. e. the hybrids are also used as host plants, if at least one of the parental species is the regular host of the relevant *Phyllonorycter* species.

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REFERENCES

BAUDYŠ, E. 1948. The relationship of the gall-forming insects and various species of willows [in Czech: Vztah hálkotvorců k různým druhům vrb]. *Folia entomologica*, 11: 82–86.

BAUDYŠ, E. 1953. The zoocecidia of basket willows in Moravia [in Czech: Příspěvek k rozšíření zoocecidií vrb na Moravě]. *Acta Universitatis Agriculturae et Silviculturae A*, 1: 1–28

BENEŠ, K. 2015. Czech species of the gall-making sawflies of the genera Phyllocolpa, Tubpontania and Pontania (Hymenoptera, Nematinae). *Acta Musei Moraviae, Scientiae biologicae,* 100: 137–156.

BENGTSSON, B. A. 2010. Notes on some Nordic species of Phyllonorycter Hübner, 1822 (Lepidoptera, Gracillariidae). *Entomologisk Tidskrift,* 131: 195–204.

BUSZKO, J. 1990. Studies on the mining Lepidoptera of Poland. X. Mining Lepidoptera of Toruń and surrounding areas. *Acta Zoologica Cracoviensia,* 33(17): 367–452.

CHMELAŘ, J. 1987. *Salicetum. List of Plants. The Botanical Gardens – Arboretum.* Brno: Agricultural University.

CHMELAŘ, J. and MEUSEL, W. 1976. *Die Weiden Europas. Die Gattung Salix*. Die Neue Brehm-Bücherei 494. Wittenberg-Lutherstadt: A. Ziemsen-Verlag.

CORLEY, M. F. V. 2015. *Lepidoptera of Continental Portugal. A fully revised list*. Faringdon.

DAVIS, D. R. and DESCHKA, G. 2001. Biology and systematics of the North American Phyllonorycter leafminers on Salicaceae, with a synoptic catalog of the Palearctic species (Lepidoptera: Gracillariidae). *Smithsonian Contributions to Zoology*, 614: 1–89.

DE PRINS, J. and DE PRINS, W. 2005. *World catalogue of Insects. Vol. 6. Gracillariidae (Lepidoptera)*. Stenstrup: Apollo Books.

DE PRINS, J. and DE PRINS, W. 2018. *Global Taxonomic Database of Gracillariidae (Lepidoptera)*. [Online]. Available at: http://www.gracillariidae.net [Accessed: 2018, October 28].

EMMET, A. M., WATKINSON, I. A. and WILSON, M. R. 1985. Gracillariidae. In: HEATH, J. AND EMMET, A. M. (Eds.). *The moths and butterflies of Great Britain and Ireland*. Colchester: Harley Books, pp. 244–363.

FRITZ, R. S., ROCHE, B. M. and BRUNSFELD, S. J. 1998. Genetic variation in resistance of hybrid willows to herbivores. *Oikos*, 83: 117–128.

GREGOR, F. 1952. The mining moths of the genus Lithocolletis on oaks in the Czechoslovak Republic [in Czech: Moli rodu Lithocolletis Hb. na dubech v ČSR]. *Zoologické Entomologické Listy*, 1(15): 24–56.

GREGOR, F. and LAŠTŮVKA, A. 1991. Faunistic records from Czechoslovakia. Lepidoptera, Gracillariidae. *Acta Entomologica Bohemoslovaca*, 88: 222.

GREGOR, F., LAŠTŮVKA, Z. and ŠEFROVÁ, H. 2017. Altitudinal variability in wing pattern of Phyllonorycter salictella (Zeller, 1846) (Lepidoptera: Lithocolletinae). *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis*, 65(3): 833–838.

GREGOR, F., POVOLNÝ, D. and ŘEZÁČ, M. 1963. Systematic oligophagy of the Central-European species of the genus Lithocolletis Hbn. and Argyresthia Hbn. (Lep.) on Prunoideae. *Acta Societatis Entomologicae* Čechosloveniae, 60: 81–93.

HERING, E. M. 1950. Die Oligophagie phytophager Insekten als Hinweis auf eine Verwandtschaft der Rosaceen mit den Familien Amentofera. In: *Proceedings of the VIII. International Congress of Entomology in Stockholm, 1948*. Stockholm: Axel B. Elfstroms Boktryckeri, pp. 74–79.

HERING, E. M. 1951. *Biology of the Leaf Miners*. The Hague: W. Junk.

HERING, E. M. 1957. *Bestimmungstabellen der Blattminen von Europa einschließlich des Mittelmeerbeckens und der Kanarischen Inseln*. The Hague: W. Junk.

KLAUSNITZER, B. 1983. Bemerkungen über die Ursachen und die Entstehung der Monophagie bei Insekten. In: *Verhandlungen des zehnten Internationalen Symposiums über Entomofaunistik Mitteleuropas (S.I.E.E.C.).* 15–20 August 1983, Budapest, pp. 5–12.

KUZNETZOV, V. I. 1981. Fam. Gracillariidae (Lithocolletidae) – moli-pestryanki. In: MEDVEDEV G. S. (Ed.). *A guide to the insects of the European part of the USSR. Vol. IV. Lepidoptera. Part 2*. Leningrad: Nauka, pp. 149–311.

KUZNETZOV, V. I. and BARYSHNIKOVA, S. V. 1998. Brief catalogue of the mining moths of the fam. Gracillariidae (Lepidoptera) of Russia and adjacent countries. *Trudy Zoologicheskogo Instituta, Rossijskaya Akademia Nauk*, 274: 1–60.

LAASONEN, E. M. and LAASONEN, L. 2000. Habitual differences of Phyllonorycter salictella (Zeller, 1846) and P. heringiella (Gronlien, 1932) (Lepidotera: Gracillariidae) in two Finnish materials, a problem pair. *Entomologica Fennica*, 11: 175–181.

LAŠTŮVKA, A. and LAŠTŮVKA, Z. 1986. Contribution to the faunistics of Phyllonorycter species in Czechoslovakia (Lepidoptera, Gracillariidae) [in Czech: Příspěvek k faunistice zástupců rodu Phyllonorycter Hübner, 1822 v Československu (Lepidoptera, Gracillariidae)]. *Zprávy Československé Společnosti Entomologické ČSAV*, 22: 15–20 (in Czech).

LE MARCHAND, S. 1936. Clé ou table analytique pour la détermination des espèces françaises de Lithocolletis (Famille des Gracilariidae). *L´Amateur de Papillons*, 8: 83–118.

Liston, A. D., Heibo, E., Prous, M., VÅrdal, H., Nyman, T. and VIKBERG, V., 2017. North European gall-inducing Euura sawflies (Hymenoptera, Tenthredinidae, Nematinae). *Zootaxa*, 4302: 1–115.

MEZ, C. C. 1925. *Drei Vorträge über die Stammesgeschichte der Pflanzenwelt mit 1 Stammbaum des Pflanzenreichs.* Freising-München: Datterer & Cie.

POVOLNÝ, D. 1949. Podkopěnkoví moli rodu Lithocolletis Hb. na ovocných stromech. (The members of genus Lithocolletis Hb. mining Prunoidea and Pomoidea). *Acta Universitatis Agriculturae et Silviculturae, Brno,* C45: 57.

POVOLNÝ, D. 1956. Stenophagy and systematic oligophagy of the mining insects and its relation to some questions of the origin of species [in Czech: Stenofágie a systematická oligofágie minujícího hmyzu a její

vztah k některým otázkám vzniku druhu]. *Acta Universitatis Agriculturae et Silviculturae (Brno)*, 4: 291–302.

POVOLNÝ, D. 1967. Kritisches über die mitteleuropäischen Pomoideae-Minierer aus der Gattung Lithocolletis (Lepidoptera, Lithocolletidae). *Acta Universitatis Agricriculturae Brno, Facultas Agronomica*, 15: 587–594.

PRUNER, L. and MÍKA, P. 1996. List of settlements in the Czech Republic with associated map field codes for faunistic grid mapping system [in Czech: Seznam obcí a jejich částí v České republice s čísly mapových polí pro síťové mapování fauny]. *Klapalekiana* 32(Suppl.): 1–115.

SVENSSON, I. 1966. New and confused species of Microlepidoptera. *Opuscula Entomologica,* 31: 183–202.

THE PLANT LIST 2013. *The plant list. A working list of all plant species*. Version 1.1. [Online]. Available at http://www.theplantlist.org/ [Accessed: 2018, October 28].

VAŠUT, R. J., SOCHOR, M. and HRONEŠ, M. 2013. *Willows of the Czech Republic* [in Czech: *Vrby* České *republiky*]. Olomouc: Univerzita Palackého.

VOLF, M., HRCEK, J., JULKUNEN-TIITTO, R. and NOVOTNY, V. 2015. To each its own: differential response of specialist and generalist herbivores to plant defence in willows. *Journal of Animal Ecology*, 84: 1123–1132.

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