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Спорові рослини та гриби

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SPECIES DIFFERENTIATION IN THE *MAGNICELLULATAE* COMPLEX (*PODOSPHAERA, ERYSIPHALES*) WITHIN THE SPECIMENS COLLECTED IN UKRAINE

Key words: taxonomy, powdery mildew fungi, Sphaerotheca, Podosphaera fusca, *Europe*

Introduction

The genera *Sphaerotheca* Lév. and *Podosphaera* Kunze were merged under the priority name *Podosphaera* (Braun, Takamatsu, 2000) following molecular data (Saenz, Taylor, 1999; Takamatsu et al., 2000). The formerly recognized genus *Sphaerotheca* included species with a single ascus per chasmothecium devoid of virgate appendages typical of *Podosphaera* s. str. Prior to this, Blumer (1933, 1967) and Golovin (Головин, 1958) subdivided *Sphaerotheca* into sections. However, the proposed taxa did not conform to the ICBN and therefore have not been accepted. Subsequently, Braun (1978), based upon Blumer's and Golovin's proposals, separated within the genus two sections, *Sphaerotheca* and *Magnicellulatae* U. Braun. The latter comprises species with clearly visible large peridial cells (over 30 μm in diam.). With the genus *Sphaerotheca* included into *Podosphaera,* this section is regarded as a subsection within the section *Sphaerotheca* (Lév.) U. Braun et N. Shishkoff in *Podosphaera* s. l. (Braun, Takamatsu, 2000). Some species of this subsection, viz. *P. balsaminae* (Wallr.) U. Braun et S. Takam., *P. delphinii* (P. Karst.) U. Braun et S. Takam., *P. fuliginea* (Schltdl.) U. Braun et S. Takam., *P. fusca* (Fr.) U. Braun et Shishkoff, *P. helianthemi*

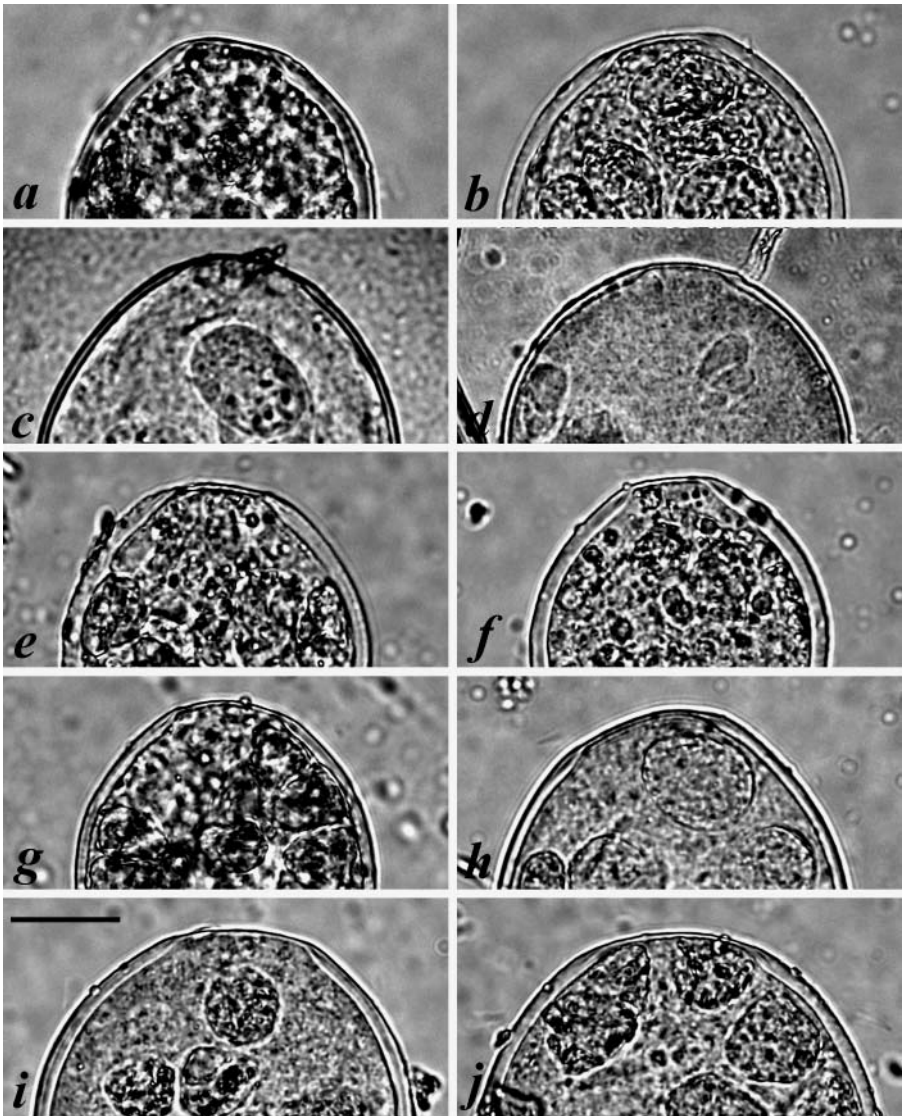

Fig. 1. Apical parts of the asci with oculi: *a — Podosphaera balsaminae*, *b — P. delphinii*, *c— P. fuliginea*, *d — P. fusca* from *Doronicum austriacum*, *e — P. helianthemi*, *f—h — Podosphaera* spp. from *Melampyrum arvense*, *M. nemorosum* and *M. pratense*, *i—j — P. xanthii* from *Physalis alkekengi* and *Verbena hybrida*, respectively. Bar for all images is 20 μm

(L. Junell) U. Braun et S. Takam. and *P. plantaginis* (Castagne) U. Braun et S. Takam., are known to occur in Ukraine (Гелюта, 1989). Among them, *P. fusca* is a polyphagous species parasitizing *Asteraceae, Bignoniaceae, Campanulaceae, Cucurbitaceae, Lamiaceae, Polemoniaceae, Scrophulariaceae* s. l. (incl. *Orobanchaceae*), *Solanaceae*, *Valerianaceae*, and *Verbenaceae* (Braun, 1987; Braun et al., 2001). However, in Ukraine it was recorded only on host plants belonging to *Asteraceae, Cucurbitaceae, Orobanchaceae*, *Scrophulariaceae* s. str., *Solanaceae*, and *Verbenaceae* (Гелюта, 1989).

Molecular phylogenetic analyses (Hirata et al., 2000; Ito, Takamatsu, 2010; Takamatsu et al., 2010) demonstrated that *P. fusca* is indeed a large complex with numerous haplotypes forming three groups. On the basis of some morphological and biological characteristics corresponding to the molecular phylogenetic data, *P. fusca* s. l. was split by Braun et al. (2001) into two still compound species, *P. fusca* s. str. (Groups 1—2) and *P. xanthii* (Castagne) U. Braun et Shishkoff (Group 3). The main distinguishing character for these species is the size of the ascus oculus, a thin-walled apical portion of the ascus (Fig. 1). In addition, size of chasmothecia is taken into account. Since in the recent molecular research mostly East Asian collections were used for sequencing (except for a few specimens from Europe), we suggest that further phylogenetic analyses as well as morphological identification for both complexes, *P. fusca* s. str. and *P. xanthii*, are required including European collections, in particular specimens from Ukraine.

Materials and Methods

All studied materials are located in the Mycological Herbarium of the M.G. Kholodny Institute of Botany (*KW*). About 600 specimens of *P. fusca* s. l. collected from 49 host species of 34 genera belonging to *Asteraceae, Cucurbitaceae, Orobanchaceae*, *Scrophulariaceae*, *Solanaceae*, and *Verbenaceae* were critically examined[1]. Additionally, over hundred specimens of other species from the subsection *Magnicellulatae* (U. Braun) U. Braun et N. Shishkoff were studied. They are as follows: *P. balsaminae, P. delphinii*, *P. fuliginea, P. helianthemi*, and *P. plantaginis*. To delimit *P. fusca* s. str. and *P. xanthii*, according to Braun et al. (2001), the following features were used: *P. fusca* s. str. characterized by having relatively small chasmothecia (55—90 μm diam., mostly < 85 μm) and oculi (8—15 μm diam., average 12 μm); *P. xanthii* — by having large chasmothecia (75—100 μm diam., usually > 85 μm) and large oculi (15—30 μm diam., average 20 μm).

For microscope slides we removed mature chasmothecia from the specimen surface under a dissecting microscope, placed them using a preparation needle in a drop of distilled water, and added a coverslip. After measuring chasmothecia in a few minutes, we pressed gently the coverslip. Release of the asci was observed under standard light microscopy using small magnification; if necessary, the procedure was repeated. Measurements and photographs were taken under the *Primo Star* (Carl Zeiss) microscope, a digital camera *Canon A 300*, and software *AxioVision 4.7*.

The taxonomy and nomenclature of the host plants mainly follow «Vascular plants of Ukraine. A nomenclatural checklist» (Mosyakin, Fedoronchuk, 1999).

Results

We studied all species of the subsection *Magnicellulatae* registered in Ukraine, viz *P. balsaminae*, *P. delphinii*, *P. fuliginea*, *P. fusca* s. l., *P. helianthemi*, and *P. plantaginis*.

Podosphaera balsaminae (Fig. 1, *a*) is a quite rare species in Ukraine. According to literature data and our previous observations, it was found only on *Impatiens noli-tangere* L. in Western, Central and Left-Bank Polissya, in the Carpathian, Precarpathian

[1] For most specimens, only oculus size was measured.

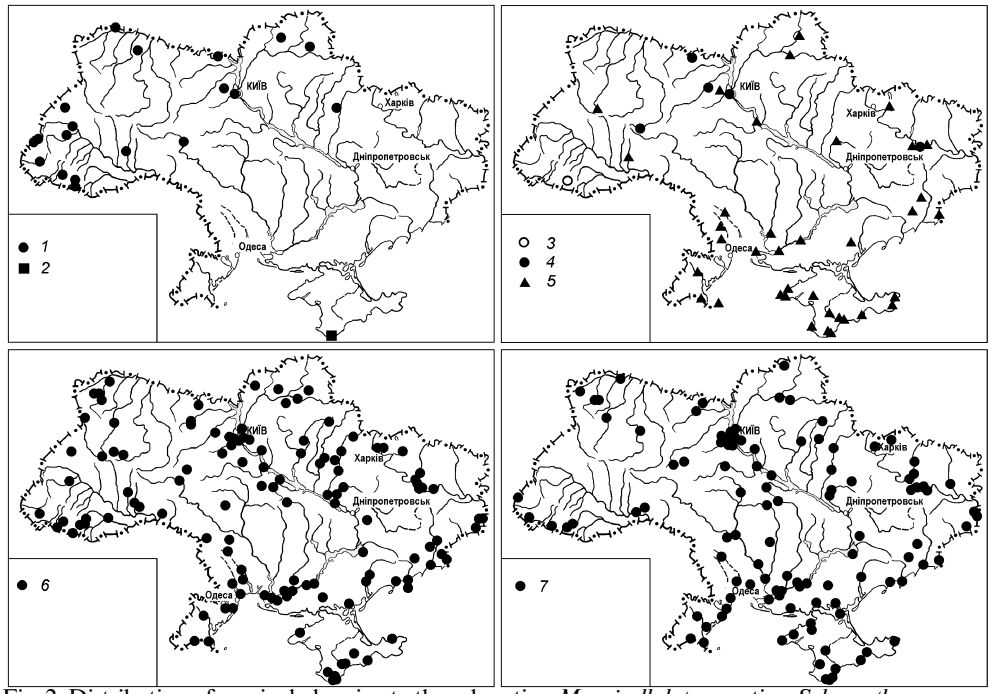

Fig. 2. Distribution of species belonging to the subsection *Magnicellulatae*, section *Sphaerotheca*, genus *Podosphaera* s. l. in Ukraine: *1 — P. balsaminae*, *2 — P. helianthemi*, *3 — P. delphinii*, *4 — P. fuliginea*, *5 — P. plantaginis*, *6 — P. fusca* and *7 — P. xanthii*

and Roztochia forests, Western, Left-Bank and Right-Bank Forest-Steppe (Целле, 1925; Лавітська, 1939, 1949; Гелюта, 1989; Коломієць, 1996) (Fig. 2, *1*). Thus, the fungus occurs mainly in forest regions of Ukraine, correspondingly to its host plant distribution. The examined specimens of *P. balsaminae* have large chasmothecia (85—110 μm diam) and asci with relatively small oculi (10—17 μm wide). Our examination results are consistent with those of Braun et al. (2001), and therefore we conclude that our collections belong to *P. balsaminae*.

Podosphaera delphinii (Fig. 1, *b*) is known in Ukraine from two localities, in the Carpathians and Male Polissya (Марченко, 1974; Гелюта, 1989) (Fig. 2, *3*). We studied specimens collected by Marchenko on *Trollius europaeus* L. near Kvasy village, Rakhiv District, Zakarpatska Region. Measurements for chasmothecia (69—91 μm, mostly <85 μm) and ascus oculi (12—16 μm) are close to those of *P. fusca* s. str. It should be noted that Braun et al. (2001) reported on *Trollius* another species, *P. astragali* (L. Junell) U. Braun et S. Takam., with chasmothecia measured 55—90 μm and oculi 10 μm in average, which does not completely correspond to our data. Unfortunately, samples of *P. delphinii* were not used for sequencing in the molecular phylogenetic analysis conducted by Japanese mycologists (Hirata et al., 2000; Ito, Takamatsu, 2010).

Podosphaera fuliginea (Fig. 1, *c*) is a rare species in Ukraine. It was recorded on *Veronica incana* L., *V. longifolia* L. and *V. spicata* L. in the Right-Bank Polissya, in the Right-Bank and Kharkiv Forest-Steppe and Donetsk Grass-Meadow Steppe (Потебня,

1916; Целле, 1925; Лавітська, 1949; Лавітська, Морочковська, 1974; Гелюта, 1989) (Fig. 2, *4*). Distribution of this species in Ukraine is apparently restricted to the north of the country. The fungus has small chasmothecia (60—83 μm diam) which corresponds with *P. fusca* s. str. Examination of the Ukrainian specimens shows as big oculi (16—24 μm) as those in *P. xanthii*; however, our collections differ by slightly longer and well-developed ascospores. Moreover, as it was demonstrated by molecular research (Hirata et al., 2000; Ito, Takamatsu, 2010), this fungus forms a unique clade basal in the subsection *Magnicellulatae* and therefore is regarded as a separate species. It should be noted that in Ukraine other species of genus *Veronica* L. (*V. chamaedrys* L., *V. filiformis* Smith and *V. gentianoides* Vahl.) are also infected by powdery mildew fungi. However, for them only anamorphs of unclear taxonomic position were found.

Podosphaera helianthemi, as well as *P. delphinii*, is extremely rare in Ukraine. It was reported only twice, on *Helianthemum grandiflorum* (*Cistaceae*) in the Mountain Crimea (Гелюта, 1989) and on *H. canum* (L.) Hornem. (Морочковський та ін., 1969) (Fig. 2, *2*). For the latter reference, the exact locality is unknown and herbarium material does not exist. In the Crimean specimens, chasmothecia are small (78—88 μm diam), and asci are with relatively small oculi (11—19, average 15 μm; Fig. 1, *e*). Thus, *P. helianthemi* is presumably close to *P. fusca*; however, it was not included into the mentioned molecular phylogenetic studies (Hirata et al., 2000; Ito, Takamatsu, 2010).

Another species of the subsection, *P. plantaginis*, is quite widespread in Ukraine. The fungus was recorded on *Plantago lanceolata* L., *P. media* L., and *P. urvillei* Opiz in many regions, although it seems to be rather rare in the north of the country (Fig. 2, *5*). All examined specimens have mostly small oculi (mean dimensions varying within 12,0—15,5 μm), and therefore the fungus is close to *P. fusca* s. str. However, like the previous species, *P. plantaginis* was not sampled for the sequencing.

As mentioned above, the large complex *P. fusca* s. l. was further divided into two rather complex species, *P. fusca* s. str. and *P. xanthii* (Braun et al., 2001). Having examined numerous specimens of *P. fusca* s. l. from different areas in Ukraine, we found that morphologically they also fall into two groups corresponding to *P. fusca* s. str. (small ascomata, asci with small oculi; Fig. 1, *d*) and *P. xanthii* (large ascomata, asci with large oculi; Fig. 1, *i—j*) (Table 1). The only exception are fungi parasitizing *Melampyrum* L. (*Orobanchaceae*) (Fig. 1, *f—h*) which do not split to these groups. As it is seen in the table, *P. fusca* s. str. infects species of the genera *Conyza* L., *Crepis* L., *Doronicum* L., *Erigeron* L., *Euphrasia* L., *Hieracium* L., *Lapsana* L., *Leontodon* L., *Lepidotheca* Nutt., *Macrosyringion* Rothm., *Odontites* Ludw., *Phalacroloma* Cass., *Rhinanthus* L., *Scrophularia* L., and *Taraxacum* Weber, while *P. xanthii* occurs on *Adenostyles* Cass., *Arnica* L., *Bidens* L., *Calendula* L., *Coreopsis* L., *Cosmos* Cav., *Cucurbita* L., *Dahlia* Cav., *Dimorphotheca* Moench, *Gazania* Gaertn., *Helianthus* L., *Lagenaria* Ser., *Petunia* Juss., *Physalis* L., *Pulicaria* Gaertn., *Senecio* L., *Verbena* L. and *Xanthium* L. Thus, in Ukraine the former species is recorded on representatives of *Asteraceae*, *Orobanchaceae* and *Scrophulariaceae*, the latter has a wider host range parasitizing members of *Asteraceae*, *Cucurbitaceae*, *Solanaceae* and *Verbenaceae*. Moreover, there is an obligate relationship between each species, *P. fusca* s. str. and *P. xanthii* respectively, and certain genera of these families.

Table 1. **Host specifity of *Podosphaera fusca* s. str. and *P. xanthii* within Ukraine**

Families and species of host plants	*Podosphaera fusca* s. str.	*Podosphaera xanthii*	Regions
ASTERACEAE	+	+	
Adenostyles alliariae (Gouan) A. Kern.		+	IFr, Zak
Arnica montana L.		+	IFr, Zak
Bidens cernua L.		+	Chernih, Dnipr, Khark, Khers, Kyiv, Kyiv city, Polt, Vol, Zap
Bidens tripartita L.		+	Cherk, Chernih, Dnipr, Don, Khark, Khers, Kir, Kyiv, Kyiv city, Myk, Polt, Sum, Vol, Zak, Zap, Zhyt
Calendula officinalis L.		+	ARC, Cherk, Chernih, Don, Khark, Khm, Kyiv, Kyiv city, Od, Polt, Rivn, Sum, Vinn, Zak, Zap, Zhyt
Conyza canadensis (L.) Cronq.	+		Cherk, Don, Khark, Khers, Kyiv, Kyiv city, Kir, Lv, Myk, Od, Polt, Sum, Vol, Zak, Zap, Zhyt
Coreopsis grandiflora Hogg ex Sweet		+	Khm, Kyiv
Cosmos bipinnatus Cav.		+	ARC, Cherk, IFr, Khers, Kyiv, Kyiv city, Lv, Od
Crepis paludosa (L.) Moench	+		Vol, Zak
Crepis tectorum L.	+		Kyiv city
Dahlia sp.		+	ARC, Kyiv city
Dimorphotheca sp.		+	Kyiv city
Doronicum austriacum Jacq.	+		IFr
Erigeron acris L.	+		Od
Gazania sp.		+	Od
Hieracium sp.	+		Zak
Helianthus annuus L.		+	Vol
Lapsana communis L.	+		ARC, Cherk, Don, Khark, Khm, Kyiv city, Luh, Lv, Vol, Zak
Leontodon autumnalis L.	+		Dnipr, Rivn, Zak
Lepidotheca suaveolens (Pursh) Nutt.	+		Cherk, Kyiv, Kyiv city, Vol, Zak
Phalacroloma annuum (L.) Dumort.	+		Kyiv city
Pulicaria uliginosa Steven		+	Khers
Senecio borysthenicus (DC.) Andrz. ex Czern.		+	Khers
Senecio jacobaea L.		+	ARC, Chernih, Don, Kyiv
Taraxacum erythrospermum Andrz.	+		Khers, Zap

End of Tabl. 1

Families and species of host plants	*Podosphaera fusca* s. str.	*Podosphaera xanthii*	Regions
Taraxacum officinale Wigg.	+		ARC, Cherk, Chernih, Dnipr, Don, IFr, Khark, Khers, Khm, Kyiv, Kyiv city, Luh, Lv, Myk, Od, Polt, Sum, Tern, Vinn, Vol, Zak, Zap, Zhyt
Taraxacum serotinum (Waldst. et Kit.) Poir.	+		Don, Khark
Taraxacum spp.	+		ARC, Dnipr, Don, Khers, Myk, Od, Polt, Zap
Xanthium albinum (Widder) H. Scholz		+	Don, Khark, Khers, Luh, Myk, Od, Zak, Zap
Xanthium pensylvanicum Wallr.		+	ARC, Don, Khers, Od
Xanthium spinosum L.		+	ARC, Cherk, Don, Dnipr, Khark, Khers, Kyiv city, Myk, Od
Xanthium spp.		+	ARC, Cherk, Chernih, Don, Dnipr, Khark, Khers, Kir, Kyiv, Kyiv city, Luh, Myk, Polt, Zak, Zap
CUCURBITACEAE		+	
Cucurbita pepo L.		+	ARC, Khers, Kir, Kyiv, Kyiv city, Lv, Myk, Od, Zak, Zap
Lagenaria siceraria (Molina) Standl.		+	Kyiv city
SCROPHULARIACEAE	+		
Scrophularia bicolor Smith	+		ARC
Scrophularia cretacea Fisch. ex Spreng.	+		Luh
SOLANACEAE		+	
Petunia × *atkinsiana* D. Don ex Loudon		+	Vol
Physalis alkekengi L.		+	Cherk, Don, Khm, Kyiv city, Myk
VERBENACEAE		+	
Verbena hybrida Hort. ex Vilm.		+	ARC, Cherk, Khm, Kyiv city, Zak, Zhyt

N o t e. In the tables the following abbreviations for the administrative units are used: ARC — Autonomous Republic of Crimea; Vinn — Vinnytsia, Vol — Volynska, Dnipr — Dnipropetrovsk, Don — Donetsk, Zhyt — Zhytomyr, Zak — Zakarpatska, Zap — Zaporizhya, IFr — Ivano-Frankivsk, Kyiv — Kyiv, Kir — Kirovohrad, Luh — Luhansk, Lv — Lviv, Myk — Mykolaiv, Od — Odesa, Polt — Poltava, Rivn — Rivne, Sum — Sumy, Tern — Ternopil, Khark — Kharkiv, Khers — Kherson, Khm — Khmelnytskyi, Cherk — Cherkasy, and Chernih — Chernihiv Regions.

Due to close relationship between the fungal species in the subsection *Magnicellulatae* and their host plants, it seems interesting to compare these observations with the mentioned molecular phylogenetic data (Hirata et al., 2000; Ito, Takamatsu,

2010) and their taxonomic interpretations (Braun et al., 2001). The phylogenetic tree provided by Ito et Takamatsu (2010) showed that fungi parasitizing members of the genera[2] *Conyza*, *Leontodon*, *Matricaria* (incl. *Lepidotheca*), and *Taraxacum* fall into Groups 1—2 (corresponding to *P. fusca* s. str. — small oculi) while haplotypes on *Bidens*, *Calendula*, *Coreopsis*, *Cosmos*, *Cucurbita*, *Helianthus*, *Physalis*, and *Verbena* are included into big Group 3 (*P. xanthii* — large oculi). Thus, at the generic level the results of both studies are consistent. Apparently, the affinities revealed for collections from East Asia are confirmed for the material collected in Europe.

Most interesting are relationships of *P. fusca* s. str. and *P. xanthii*, respectively, with various taxa within *Asteraceae* which occupies the top position in vascular plant evolution, being at the same time the major host family for powdery mildew fungi. It is clear from Table 2 that in Ukraine both species are recorded only on two subfamilies, *Asteroideae* and *Cichorioideae*. Members of the other two, less advanced subfamilies *Mutisioideae* and *Carduoideae*, are not infected by these fungi. Although taxa of *Carduoideae* are very common in Ukraine, its representatives are attacked by other powdery mildews, namely species of *Golovinomyces* (U. Braun) Heluta, *Leveillula* G. Arnaud and, more rarely, *Erysiphe* R. Hedw. ex DC. On plants of the subfamily *Cichorioideae*, excepting *Gazania* sp. introduced from South Africa, only *P. fusca* s. str. is known to occur, while *Asteroideae* includes hosts for both species of fungi. However, there is strict association between the fungi and host tribes within *Asteroideae*, except for *Senecioneae* (we have recorded one specimen of *P. fusca* s. str. on *Doronicum austriacum* Jacq.).

Thus, morphological species of the *P. fusca* s. l. complex are specialized to host genera, and furthemore, to the tribes within *Asteraceae*. Similar specialization was reported for other fungi parasitizing this family, for *Neoerysiphe* U. Braun (Takamatsu et al., 2008; Heluta et al., 2010) and partly *Golovinomyces* (Matsuda, Takamatsu, 2003).

A more complicated situation is with fungi infecting *Orobanchaceae*[3], for example, the genus *Melampyrum*. Based on the diameter of the oculus, we revealed a consecutive row of the haplotypes with no hiatus between *P. fusca* s. str. and *P. xanthii* (Table 3). Due to small oculi (8—15 μm), Braun et al. (2001) included collections on *Melampyrum* spp. in *P. fusca* s. str. A single specimen of the fungus on *M. nemorosum* L. used in molecular phylogenetic analyses (Hirata et al., 2000; Ito, Takamatsu, 2010) is comprised in Group 1 and could indeed represent this species. Our collections from *M. argyrocomum* Fisch. ex Koso-Pol., *M. arvense* L., and *M. cristatum* L. have small oculi, 5—13,5 μm. They also may belong to *P. fusca* s. str. However, specimens on *M. laciniatum* Koshevn. et Zinger, *M. nemorosum*, and *M. pratense* L. show oculi measuring 8,5—23 μm, on average varying within 13,5—20 μm. Thus, there is a transition between *P. fusca* s. str. and *P. xanthii* through a series of intermediate taxa. In order to explain this phenomenon, we can propose the following hypothesis. Apparently, the asci with large oculi, which are more advanced in evolutionary development, may have occurred multiple times in different phylogenetic lineages. This is consistent with the fact that in the mentioned phylogenetic tree (Ito, Takamatsu, 2010) all

[2] Only genera common for both studies are analyzed.

[3] Former *Scrophulariaceae* are divided into families according to Olmstead et al. (2001).

haplotypes having asci with small oculi (i.e. *P. fusca* s. str.) are situated at the basal position, while *P. fuliginea*, a sister taxon to the *P. fusca* s. l. complex, has asci with large oculi. Thus, the process of speciation within *Podosphaera* on *Orobanchaceae*, similar to that observed in fungi parasitizing *Asteraceae*, is not yet finished. If our hypothesis is correct, in future molecular investigations conducted on European materials, samples of *Podosphaera* on *Orobanchaceae* could form a distinct clade within Group 1. In this case we will have either to accept that *P. fusca* s. str. combines haplotypes both with small and large oculi, or, avoiding confusion in the *P. fusca* s. l. complex, to re-erect from synonymy *Sphaerotheca melampyri* L. Junell for parasites on *Melampyrum* and to transfer this species to *Podosphaera*, having introduced a new combination. It is obvious that more sequence data is required to clarify phylogenetic relationship within *P. fusca* s. l. using large collections from Europe.

In Ukraine *P. fusca* s. str. and *P. xanthii* are common; for the last two decades numerous data on their distribution was accumulated (Fig. 2, *6*, *7*). Both species usu-

Table 2. **Relationship of *Podosphaera fusca* s. str. and *P. xanthii* with genera, tribes and subfamilies of *Asteraceae***

Subfamily	Tribe	Genus	Fungus
Asteroideae	**Anthemideae**	Lepidotheca	*P. fusca* s. str.
	Astereae	*Conyza*	*P. fusca* s. str.
		Erigeron	*P. fusca* s. str.
		Phalacroloma	*P. fusca* s. str.
	Calendulaeae	*Calendula*	*P. xanthii*
		Dimorphotheca	*P. xanthii*
	Coreopsideae	*Bidens*	*P. xanthii*
		Coreopsis	*P. xanthii*
		Cosmos	*P. xanthii*
		Dahlia	*P. xanthii*
	Heliantheae	*Helianthus*	*P. xanthii*
		Xanthium	*P. xanthii*
	Inuleae	*Pulicaria*	*P. xanthii*
	Madieae	*Arnica*	*P. xanthii*
	Senecioneae	*Adenostyles*	*P. xanthii*
		Doronicum	*P. fusca* s. str.
		Senecio	*P. xanthii*
Cichorioideae	*Arctotideae*	*Gazania*	*P. xanthii*
	Cichorieae	*Crepis*	*P. fusca* s. str.
		Hieracium	*P. fusca* s. str.
		Lapsana	*P. fusca* s. str.
		Leontodon	*P. fusca* s. str.
		Taraxacum	*P. fusca* s. str.

Table 3. **Size of the ascus oculi in *Podosphaera* collected on *Orobanchaceae* in Ukraine**

Host plant species	Locality Region	*KW* number	Size of ascus oculi	Average size of ascus oculi
Melampyrum arvense	Vinn	28217F	5,5—11,5	8,5
Melampyrum arvense	ARC	26955F	5,0—12,0	8,5
Melampyrum arvense	ARC	32616F	8,0—11,0	9,5
Odontites vulgaris	Od	27530F	7,0—12,0	9,5
Odontites vulgaris	Kyiv	27257F	7,0—13,5	10,0
Melampyrum argyrocomum	Luh	32615F	8,5—12,5	10,5
Melampyrum arvense	ARC	32617F	8,0—13,5	10,5
Euphrasia parviflora	Vinn	37834F	7,0—14,0	10,5
Melampyrum arvense	Khark	26957F	11,0—12,0	11,5
Rhinanthus sp.	Zak	32631F	9,5—13,5	11,5
Odontites luteus	ARC	32629F	8,0—14,5	11,5
Melampyrum cristatum	Vinn	37835F	11,5—12,5	12,0
Melampyrum pratense	Lv	32622F	11,0—15,5	13,5
Melampyrum pratense	Kyiv	27519F	8,5—18,5	13,5
Melampyrum pratense	Kyiv	32621F	10,5—18,0	14,0
Melampyrum pratense	Vol	32620F	9,0—20,0	14,5
Melampyrum nemorosum	Cherk	26961F	13,0—17,0	15,0
Melampyrum pratense	Kyiv	27520F	11,0—20,5	15,5
Melampyrum nemorosum	Kyiv	26958F	13,5—20,0	16,5
Melampyrum pratense	Chernih	28219F	14,0—23,5	18,5
Melampyrum pratense	Vol	32619F	17,5—23,0	20,0

ally occur under similar conditions; however, the former can be found at higher altitudes while the latter is more frequent on cultivated plants and weeds.

Conclusions

At least seven species of *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae* are known in Ukraine. Taxonomic status of *P. delphinii*, *P. helianthemi* and *P. plantaginis*, species close to *P. fusca* s. str., is unclear, and these fungi require further molecular analyses. Samples on *Impatiens noli-tangere* show large chasmothecia, as well as asci with small oculi, and belong to *P. balsaminae*. *Podosphaera fuliginea* has small chasmothecia and wide oculi of the asci. In Ukraine *Podosphaera fusca* s. str. parasitize *Asteraceae* and *Scrophulariaceae*, whereas *P. xanthii* infects *Asteraceae*, *Cucurbitaceae*, *Solanaceae* and *Verbenaceae*. There is strict relationship between these fungi and host genera from the mentioned families. Furthermore, none of the genera is known to be infected by both species. Thus, the table provided in this paper is a reliable tool for distinguishing *P. fusca* s. str. and *P. xanthii*. Within *Asteraceae*, only species of two subfamilies, *Asteroideae* and *Cichorioideae*, are recorded as host plants of these fungi. On representatives of less advanced subfamilies, *Mutisioideae* and *Carduoideae*, these species do not occur in Ukraine. On *Cichorioideae*, almost exclusively (except for one occasion) *P. fusca* s. str. is reported, while *Asteroideae* comprises hosts for both species; however, it is host specific at the tribe level. Within hosts of *Orobanchaceae*, no hiatus

between *P. fusca* s. str. and *P. xanthii* is observed. In this case, species differentiation in *Podosphaera* is apparently not complete. Relationships of *P. fusca* s. str. and *P. xanthii*, respectively, with genera of host plants revealed by Japanese mycologists are confirmed. Thus, results of the research based upon the sample sources generally confined to East Asia, appear to be true for Europe. It can be therefore concluded that enlargement of the diameter of the ascus oculi in *Podosphaera* may have occurred multiple times independently in various phylogenetic lineages. Further comprehensive phylogenetic analysis of *P. fusca* s. l. including a broad range of European specimens is required.

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ВИДОВА ДИФЕРЕНЦІАЦІЯ КОМПЛЕКСУ *MAGNICELLULATAE* (*PODOSPHAERA*, *ERYSIPHALES*) НА ЗІБРАНИХ В УКРАЇНІ МАТЕРІАЛАХ

В Україні зареєстровано сім видів підсекції *Magnicellulatae* секції *Sphaerotheca* роду *Podosphaera*, причому статус *P. delphinii*, *P. helianthemi* і *P. plantaginis* не ясний, ці види близькі до *P. fusca* s. str. і потребують молекулярно-філогенетичного дослідження. Зразки з *Impatiens noli-tangere* мають великі хазмотеції і сумки з відносно маленькими порами. Вони належать до *P. balsaminae*. *Podosphaera fuliginea* має дрібні хазмотеції і сумки з великими порами. *Podosphaera fusca* s. str. в Україні паразитує на представниках родин *Asteraceae* і *Scrophulariaceae*, *P. xanthii* — *Asteraceae*, *Cucurbitaceae*, *Solanaceae* та *Verbenaceae*. Спостерігається облігатна приуроченість цих грибів до певних родів згаданих родин. Не відомо жодного роду, на представниках якого були б знайдені обидва види. Таким чином, наведена в статті таблиця може бути надійним посібником для ідентифікації *P. fusca* s. str. та *P. xanthii*. Серед складноцвітих указаними грибами уражуються тільки види двох підродин — *Asteroideae* та *Cichorioideae*. На представниках інших, менш просунутих підродин (*Mutisioideae* і *Carduoideae*), в Україні ці гриби не розвиваються. На рослинах підродини *Cichorioideae* паразитує, за єдиним виключенням, *P. fusca* s. str., тоді як представники *Asteroideae* можуть бути живителями обох видів грибів. При цьому спостерігається спеціалізація грибів навіть на рівні колін. На видах родини *Orobanchaceae* гіатус між *P. fusca* s. str. та *P. xanthii* відсутній. Очевидно, в даному випадку видова диференціація роду *Podosphaera* ще не завершилася. Розподіл *P. fusca* s. str. та *P. xanthii* за родами рослин-живителів збігається з результатами, отриманими японськими мікологами головним чином на східно-азійських матеріалах. Таким чином, закономірності, встановлені при дослідженні цих матеріалів, є, очевидно, правильними і для Європи. Робиться висновок, що збільшення пори сумки в роді *Podosphaera* відбувалося неодноразово в різних філогенетичних лініях. Молекулярно-філогенетичне дослідження *P. fusca* s. l. продовжує залишатися актуальним і має бути проведене з широким залученням європейських матеріалів.

Ключові слова: *таксономія*, *борошнисторосяні гриби*, Sphaerotheca, Podosphaera fusca, *Європа*

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ВИДОВАЯ ДИФФЕРЕНЦИАЦИЯ КОМПЛЕКСА *MAGNICELLULATAE* (*PODOSPHAERA*, *ERYSIPHALES*) НА СОБРАННЫХ В УКРАИНЕ МАТЕРИАЛАХ

В Украине зарегистрировано семь видов подсекции *Magnicellulatae* секции *Sphaerotheca* рода *Podosphaera*, причем статус *P. delphinii*, *P. helianthemi* и *P. plantaginis* не ясен, эти виды близки к *P. fusca* s. str. и нуждаются в молекулярно-филогенетическом исследовании. Образцы с *Impatiens noli-tangere* имеют крупные хазмотеции и сумки с относительно маленькими порами. Они принадлежат к *P. balsaminae*. *Podosphaera fuliginea* имеет мелкие хазмотеции и сумки с крупными порами. *Podosphaera fusca* s. str. в Украине паразитирует на представителях семейств *Asteraceae* и *Scrophulariaceae*, *P. xanthii* — *Asteraceae*, *Cucurbitaceae*, *Solanaceae* и *Verbenaceae*. Наблюдается облигатная приуроченность этих грибов к определенным родам указанных семейств. Не известно ни одного рода, на представителях которого были бы найдены оба вида. Таким образом, приведенная в статье таблица может быть надежным пособием для идентификации *P. fusca* s. str. и *P. xanthii*. Среди сложноцветных указанными грибами поражаются только виды двух подсемейств — *Asteroideae* и *Cichorioideae*. На представителях других, менее продвинутых подсемейств (*Mutisioideae* и *Carduoideae*), в Украине эти грибы не развиваются. На растениях подсемейства *Cichorioideae* паразитирует, за единственным исключением, *P. fusca* s. str., тогда как представители *Asteroideae* могут быть хозяевами обеих видов грибов. При этом наблюдается специализация грибов даже на уровне колен. На видах семейства *Orobanchaceae* гиатус между *P. fusca* s. str. и *P. xanthii* отсутствует. Очевидно, в данном случае видовая дифференциация рода *Podosphaera* еще не завершилась. Распределение *P. fusca* s. str. и *P. xanthii* по родам питающих растений совпадает с результатами, полученными японскими микологами преимущественно на восточно-азиатских материалах. Таким образом, закономерности, установленные при исследовании этих материалов, являются, очевидно, правильными и для Европы. Делается вывод, что увеличение поры сумки в роде *Podosphaera* происходило неоднократно в разных филогенетических линиях. Молекулярно-филогенетическое исследование *P. fusca* s. l. продолжает оставаться актуальным и должно быть проведено с широким привлечением европейских материалов.

К л ю ч е в ы е с л о в а: таксономия, *мучнисторосяные грибы*, Sphaerotheca, Podosphaera fusca, *Європа*.