UDC 582.282.112+582.736/739

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DISTRIBUTION OF *ERYSIPHE* AND *MICROSPHAERA* SPECIES (ERYSIPHALES) BY PHYLOGENIC GROUPS OF LEGUMES

Erysiphales, Microsphaera, Erysiphe, Fabaceae, phylogeny, co-evolution

Summary

Most species of *Erysiphe* R. Hedw. ex DC.: Fr. emend. Heluta and *Microsphaera* Lev. (Erysiphales, Ascomycota) parasitizing legumes (Fabaceae s. l.) are connected with papilionaceous plants (Faboideae). Numbers of powdery mildew species are correlated with evolution of their host groups. The Swartzioid line has no powdery mildew fungi. The Sophoroid alliance has 5 species. The Genistoid alliance has 7, and the Milettioid alliance has 22 species, 20 of which are parasitic on the Galegoid complex, the most advanced phylogenetic group of papilionaceous plants. Powdery mildew fungi do not develop on representatives of archaic tropical tribes, even though they were of primary importance in evolution of the Faboideae. Thus, evolution of these fungi occurred later than that of their papilionaceous hosts. Practically all tribes, including hosts of *Microsphaera* species (a more advanced genus), are also hosts of *Erysiphe*, a less advanced genus. This corroborates the close phylogenic relationship between these two genera. Analysis of distribution of their species by phylogeny of their papilionaceous hosts also confirms the hypothesis already proposed by the author that «colonization» of woody plants was an important factor in the morphological evolution of the order Erysiphales.

Many authors [5, 6, 8—11 et al.] have stated that the genera *Erysiphe* and *Microsphaera* are phylogenetically connected, but a detailed analysis of this connexion has never been made. The present author shares this opinion [1, 2], and believes that the evolutionary transition from *Erysiphe* to *Microsphaera* is of important theoretical interest. This transition is represented by a sequence of taxa, which starts from morphologically simple species possessing primitive ascocarps with mycelium-like basal appendages, and terminates in evolutionary advanced species having ascocarps with short equatorial appendages well differentiated from mycelium. This *Erysiphe—Microsphaera* transition, in contrast to the similar *Erysiphe—Uncinula* and *Sphaerotheca—Podosphaera* transitions, has plenty of intermediate species. This makes comparative morphological analysis and reconstruction of the origin and subsequent evolution of *Microsphaera* much easier. With even a brief analysis of the three transitions, we can see their parallelism. It is therefore arguable that an evolutionary pattern established in one transition will be inherent in the others, and perhaps even throughout the whole order.

An analysis of phylogenetical relationships in the *Erysiphe—Microsphaera* complex [12—14] based on parasites of legumes (22 species) has therefore already been started, because parasitism on a phylogenetically uniform group of host plants can be a good indicator of such relationships for powdery mildew fungi. Phylogenetical relationships of

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species of the genus *Erysiphe* parasitizing legumes were analysed [13], which established that their evolution was connected with evolutionary events in the Fabaceae s. l., and that a taxon similar to the present *Erysiphe glycines*, especially one of its varieties, var. *lespedezae* (R.Y. Zheng & U. Braun) U. Braun & R.Y. Zheng, seems to represent an ancestral form. In another paper [14], a comparative analysis of morphological features of the *Microsphaera* species also recorded on legumes was carried out, confirming the present paper's hypothesis. In addition, it concluded that some groups of the genus *Microsphaera* parasitizing legumes originated from different ancestral taxa belonging to the ancient portion of the genus *Erysiphe*. Based on analysis of morphological features, a diagram of probable relationships of *Microsphaera* species recorded on legumes has been worked out, but lack of space prevented a discussion of the distribution of these species by phylogenetical groups of host plants. Such an analysis can, however, throw additional light on evolution of powdery mildew fungi, and therefore forms the subject of the present work.

Each subfamily of the Fabaceae s. l. has its own specific set of powdery mildews (Table). This set is very scarce in the Caesalpinioideae and Mimosoideae. Only *Erysiphe cercidis*, *E. deserticola*, *Microsphaera diffusa* and *M. ravenelii* were, for example, recorded on the Caesalpinioideae. Direct relationships between these species based on morphology were not established [12—14]. Indeed, *Erysiphe cercidis* and *E. deserticola* seemed taxonomically rather distant from other species of the *Erysiphe—Microsphaera* complex recorded on legumes. Furthermore, no intermediate species are known connecting *M. ravenelii* with other species of the complex. *M. diffusa*, probably an aggregate of several species, needs further investigation and subsequent subdivision. The species which could be segregated from *M. diffusa* are probably connected with an ancestor similar to *E. glycines* [14].

Distribution of species of the genera *Erysiphe* Hedw. ex DC.: Fr. emend. Heluta and *Microsphaera* Lev. by subfamilies of the Fabaceae s. l. and phylogenetic groups of the Faboideae

Species of the Erysiphales	Caesalpinioideae	Mimosoideae	Faboideae	Phylogenetical groups of the Faboideae									
				Swartzioid line	Sophoroid alliance		Genistoid alliance		Millettioid alliance				
					Sophoroid complex	Dalbergioid complex	Podalyrioid complex	Genistoid complex	Millettioid centre	Robinioid complex	Desmodioid complex	Phaseoloid line	Galegoid complex
Erysiphe caulicola (Petr.) U. Braun	-	-	*	-	-	-	-	-	-	-	-	-	*
E. cercidis T. Xu	*	-	-	-	-	-	-	-	-	-	-	-	-
E. cruchetiana S. Blumer	-	-	*	-	-	-	-	-	-	-	-	-	*
E. deserticola Speg.	*	-	-	-	-	-	-	-	-	-	-	-	-
E. glycines F.L. Tai	-	-	*	-	-	-	-	-	-	-	*	*	*
E. pisi DC.	-	-	*	-	*	-	-	*	-	*	*	*	*
E. puerariae R.Y. Zheng & G.Q. Chen	-	-	*	-	-	-	-	-	-	-	-	*	-
E. thermopsidis R.Y. Zheng & G.Q. Chen	-	-	*	-	-	-	-	*	-	-	-	-	*
E. trifolii Grev.	-	*	*	-	-	-	-	*	-	*	*	*	*
E. viciae-unijugae (Homma) U. Braun	-	-	*	-	-	-	-	-	-	-	-	-	*
Microsphaera acaciae (S. Blumer) U. Braun	-	*	-	-	-	-	-	-	-	-	-	-	-
M. alhagi (Golovin) U. Braun	-	-	*	-	*	-	-	-	-	-	-	-	*
M. astragali (DC.) Trevis.	-	-	*	-	-	-	-	-	-	-	-	-	*
M. bauemleri Magnus	-	-	*	-	-	-	-	-	-	-	-	-	*
M. chouardii Durrieu	-	-	*	-	-	-	-	-	-	-	-	-	*

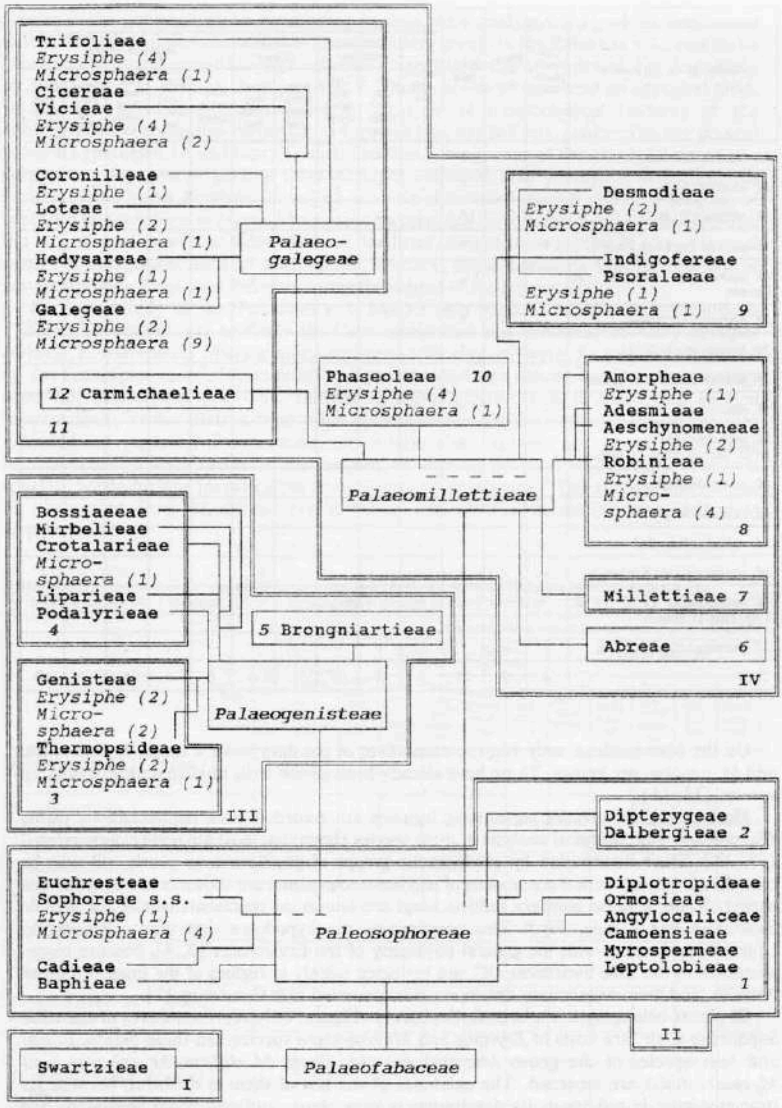
Species of the Erysiphales	Caesalpinioideae	Mimosoideae	Faboideae	Phylogenetical groups of the Faboideae									
				Swartzioid line	Sophoroid alliance		Genistoid alliance		Millettioid alliance				
					Sophoroid complex	Dalbergioid complex	Podalyrioid complex	Genistoid complex	Millettioid centre	Robinioid complex	Desmodioid complex	Phaseoloid line	Galegoid complex
M. cladrastidis Jacz.	-	-	*	-	*	-	-	-	-	-	-	-	-
M. coluteae Kom.	-	-	*	-	*	-	-	-	-	-	-	-	*
M. crispula U. Braun	-	-	*	-	-	-	-	-	-	-	-	-	*
M. diffusa Cooke & Peck	*	-	*	-	*	-	*	-	-	*	*	*	*
M. guarinonii Briosi & Cavara	-	-	*	-	-	-	-	*	-	-	-	-	-
M. hedysari U. Braun	-	-	*	-	-	-	-	-	-	-	-	-	*
M. longissima M.Y. Li	-	-	*	-	-	-	-	-	-	-	-	-	*
M. ludens (Salm.) S. Blumer	-	-	*	-	-	-	-	-	-	-	-	-	*
M. palczewskii Jacz.	-	-	*	-	-	-	-	-	-	*	-	-	*
M. pseudacaciae (P.D. Marchenko) U. Braun	-	-	*	-	-	-	-	-	-	*	-	-	-
M. ravenelii Berk.	*	-	-	-	-	-	-	-	-	-	-	-	-
M. rayssiae Mayor	-	-	*	-	-	-	-	*	-	-	-	-	-
M. robiniae F.L. Tai	-	-	*	-	-	-	-	-	-	*	-	-	-
M. seravschanica Korbonsk.	-	-	*	-	-	-	-	-	-	-	-	-	*
M. swainsoniae (Y.N. Yu & Y.Q. Lai) U. Braun	-	-	*	-	-	-	-	-	-	-	-	-	*
M. thermopsidis U. Braun	-	-	*	-	-	-	-	*	-	-	-	-	-
Total	4	2	27	0	5	0	1	6	0	6	4	5	20

On the Mimosoideae, only two representatives of powdery mildew fungi, *E. desmanthi* and *M. acaciae*, are known. These have already been shown to be phylogenetically isolated species [13, 14].

Most of the *Erysiphales parasitizing* legumes are recorded from papilionaceous plants (Faboideae). Morphological analysis of these species shows that most are quite closely related [13, 14]. Their distribution by phylogenetic groups of papilionaceous plants will now be considered (phylogenetical connexions of papilionaceous plants are shown in the figure of this paper). None of these powdery mildew fungi are known on representatives of the archaic Swartzioid line (Table, Fig.). This corroborates the hypothesis that they originated in Laurasia, and agrees with the general phylogeny of the Erysiphales [3, 4], because representatives of the tribe Swartzieae DC. are restricted mainly to regions of the tropical Central America, and their evolutionary development is connected with Gondwana [7].

Of plants belonging to the archaic Sophoroid alliance, only representatives of the tribe Sophoreae s. str. are hosts of *Erysiphe* and *Microsphaera* species. On these plants, *E. pisi* and four species of the genus *Microsphaera* (*M. alhagi, M. diffusa, M. coluteae*, and *M. cladrastidis*) are recorded. The existence of the last of them is doubtful, because its type specimen is unknown, its description is very short, and additional specimens are absent. It is not inconceivable that this species was mistakenly described by A.A. Jaczewsky [8].

Larger numbers of powdery mildew fungi are recorded on representatives of the Genistoid alliance. They are *E. pisi, E. trifolii, E. thermopsidis, M. diffusa, M. guarinonii, M. rayssiae* and *M. thermopsidis*. Almost all, excluding *M. diffusa*, are connected with the tribes Genisteae (Adans.) Beath and Thermopsideae Yakovl. belonging to the Genistoid alliance.



Quantitative distribution of species of the *Erysiphe—Microsphaera* complex by phylogenetic groups [7] of the Faboideae. I. Swartzioid line. II. Sophoroid alliance: *1* — Sophoroid complex; *2* — Dalbergioid complex. III. Genistoid alliance: *3* — Genistoid complex; *4* — Podalyrioid complex; *5* — Brogniartioid line. IV. Millettioid alliance: *6* — Abroid line; *7* — Millettioid centre; *8* — Robinioid complex; *9* — Desmodioid complex; *10* — Phaseoloid line; *11* — Galegoid complex; *12* — Carmichaelioid line (numbers of species of *Erysiphe—Microsphaera* complex are in round brackets)

The largest number of species of the genera *Erysiphe* and *Microsphaera* was recorded on plants of some phylogenetic groups of the Millettioid alliance. But significantly no

species were found on representatives of the Abroid line and Millettioid centre belonging to this alliance. *E. pisi, E. trifolii, M. diffusa, M. palczewskii, M. pseudacaciae* and *M. robiniae* parasitize plants of the Robinioid complex. The same species of the genus *Erysiphe, E. glycines* and *M. diffusa* are recorded on representatives of the Desmoid complex. *E. glycines, E. pisi, E. puerariae, E. trifolii* and *M. diffusa* were found on plants belonging to the Phaseoloid line. However, powdery mildew species are most rich on the Galegoid complex. *E. caulicola, E. cruchetiana, E. glycines, E. pisi, E. thermopsidis, E. trifolii, E. viciae-unijugae, M. alhagi, M. astragali, M. baeumleri, M. chouardii, M. coluteae, M. crispula, M. diffusa, M. hedysari, M. longissima, M. ludens, M. palczewskii, M. seravschanica* and *M. swainsoniae* parasitize these plants.

An analysis of distribution of powdery mildew fungi by phylogenetical groups of legumes draws attention to the fact that the *Erysiphe—Microsphaera* complex is distinctly connected to advanced tribes of papilionaceous plants, evolution of which took place mostly in subtropical and temperate zones of the northern hemisphere. Powdery mildews do not occur on tropical, mainly archaic tribes, even though they were in a key position during evolution of papilionaceous plants. This suggests that evolution of the *Erysiphe—Microsphaera* complex lagged considerably behind evolution of their hosts. Absence of a direct correlation between levels of advancement of host plants and their parasites is a result of this evolutionary event. Analysis of the figure presented above and the list of powdery mildews recorded on plants belonging to different phylogenetical groups of the Faboideae supports this conclusion. Another pattern can be established through analysis of this figure: practically all tribes, representatives of which are hosts of the evolutionary more advanced genus *Microsphaera*, also include hosts of the less advanced genus *Erysiphe*. This is further evidence of a close phylogenetical connexion between both genera.

As is evident from the figure, most species of the genus *Microsphaera* have been recorded on plants of the tribes Galegeae, Sophoreae and Robinieae, which are mainly trees and shrubs in subtropical and temperate zones. Species of *Erysiphe*, in contrast, are usually parasites of herbaceous plants of the tribes Trifolieae, Viciеae and Phaseoleae. Such a distribution supports the hypothesis already expressed [2] that colonization of woody plants was and is an active factor in the morphological evolution of powdery mildew fungi.

Acknowledgements

The research described in this publication was made possible in part by Grant № U4F000 from the International Science Foundation. I wish to express my gratitude to Drs. David W. Minter (CABI Bioscience, Egham, Surrey, UK) and Sergei L. Mosyakin (M.G. Kholodny Institute of Botany, Kyiv, Ukraine) for their help and comments on the manuscript.

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Recommended for publication
by A.S. Buchalo

Submitted 15.12.1996

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РОЗПОДІЛ ВИДІВ *ERYSIPHE* ТА *MICROSPHAERA* (ERYSIPHALES) ЗА ФІЛОГЕНЕТИЧНИМИ ГРУПАМИ FABACEAE s. l.

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Установлено, що переважна більшість представників *Erysiphe—Microsphaera* комплексу (порядок Erysiphales, Ascomycotina), зареєстрованих на бобових (Fabaceae s. l.), приурочена до метеликових (підродина Faboideae). Кількість видів борошнистросяних грибів збільшується відповідно до еволюційної просунутості філогенетичних груп їх рослин-господарів: шварціоїдна лінія — жодного виду, софороїдний союз — 5 видів, геністоїдний — 7 і мілеттіоїдний — 22 види (20 з них є паразитами найпросунутішого філогенетичного об'єднання метеликових — галегоїдного комплексу). На представниках архаїчних тропічних триб, навіть якщо вони займають центральне місце в еволюції метеликових, борошнистросяні гриби даного комплексу родів не розвиваються. Таким чином, еволюція грибів *Erysiphe—Microsphaera* комплексу значно запізнюється порівняно з такою метеликових.

Практично всі триби, на представниках яких зареєстровані гриби просунутішого роду *Microsphaera* Lev., включають також і господарів видів з менш просунутого роду *Erysiphe* Hedw. ex DC., що додатково свідчить про наявність тісного філогенетичного зв'язку між цими двома родами порядку Erysiphales. Аналіз розподілу видів *Erysiphe—Microsphaera* комплексу за філогенетичними групами метеликових також підтверджує раніше запропоновану автором гіпотезу про те, що опанування борошнистросяними грибами деревних рослин є важливим фактором морфологічної еволюції в порядку Erysiphales.

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РАСПРЕДЕЛЕНИЕ ВИДОВ *ERYSIPHE* И *MICROSPHAERA* (ERYSIPHALES) ПО ФИЛОГЕНЕТИЧЕСКИМ ГРУППАМ FABACEAE s. l.

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Установлено, что подавляющее большинство представителей *Erysiphe—Microsphaera* комплекса (порядок Erysiphales, Ascomycotina), зарегистрированных на бобовых (Fabaceae s. l.), приурочено к мотыльковым (подсемейство Faboideae). Количество видов мучнисторосяных грибов возрастает с эволюционной продвинутостью филогенетических групп их хозяев: шварциоидная линия — ни одного вида, софороидный союз — 5 видов, генистоидный — 7 и милеттиоидный — 22 вида (20 из них — паразиты наиболее продвинутого филогенетического объединения мотыльковых — галегоидного комплекса). На представителях архаичных тропических триб, даже если они занимают центральное место в эволюции мотыльковых, мучнисторосяные грибы данного комплекса родов не развиваются. Таким образом, эволюция грибов *Erysiphe—Microsphaera* комплекса значительно запаздывает по сравнению с эволюцией мотыльковых.

Практически все трибы, на представителях которых зарегистрированы грибы более продвинутого рода *Microsphaera* Lev., включают также и хозяев видов из менее продвинутого рода *Erysiphe* Hedw. ex DC., что дополнительно свидетельствует о наличии тесной филогенетической связи между этими двумя родами порядка Erysiphales. Анализ распределения видов *Erysiphe—Microsphaera* комплекса по филогенетическим группам мотыльковых также подтверждает ранее высказанную автором гипотезу о том, что освоение мучнисторосяными грибами древесных растений является важным фактором морфологической эволюции в порядке Erysiphales.