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PHYLOGENY OF *ERYSIPHE* SPECIES ON THE FABACEAE SENSU LATO

co-evolution, Erysiphales, Erysiphe, Fabaceae

Summary

Eleven species of *Erysiphe* R. Hedw. ex DC.: Fr. emend. Heluta (Erysiphales) are recorded from the Fabaceae sensu lato. *E. cercidis* T. Xu and *E. deserticola* Speg. occur on the Caesalpinioideae, and only one species, *E. desmanthi* (U. Braun) Heluta comb. nov., is found on the Mimosoideae. The other 8 are parasites of the Faboideae. Morphological analysis of all 11 species shows that their ancestral form was similar to *E. glycines* var. *lespedezae* (R.Y. Zheng & U. Braun) U. Braun & R.Y. Zheng. Allocation of these species to phylogenetic groups of the Fabaceae indicates that their evolution occurred in parallel with that of their hosts, but with some delay in time. *E. pisi* DC. probably developed from an ancestral form on Palaeosophoreae, and still occurs on *Sophora* species. Some parasites of more recent taxonomic groups of Fabaceae, which are morphologically identical to *E. pisi*, probably developed from the same primary ancestor, but not from the parasite of Palaeosophoreae (ancient «*E. pisi*»). The latter probably gave origin to *E. trifolii* Grev. and *E. thermopsidis* R.Y. Zheng & G.Q. Chen. Rapid evolution of the Palaeomillettieae did not initiate speciation in *Erysiphe*. Probably only two taxa developed at this stage: *E. glycines* var. *glycines* (from the ancestral form already mentioned) and *E. puerariae* R.Y. Zheng & G.Q. Chen (from the ancestor of the *E. trifolii*-type). Subsequent speciation splash occurred on the Palaeogalegeae, where and when *E. cruchetiana* S. Blumer, *E. viciae-unijugae* (Homma) U. Braun, and *E. caulicola* (Petrak) U. Braun developed.

Introduction

An analysis of the species distribution of powdery mildew fungi (Erysiphales) by subfamilies of the Fabaceae sensu lato indicates that there were at least two main stages in their evolution: the first occurred long before divergence of the Caesalpinioideae, Mimosoideae and Faboideae; the second was connected only with the Faboideae [12]. Out of 47 members of the Erysiphales known to occur on the Fabaceae, 38 species have been recorded on plants of the third subfamily, and most of those belong in *Erysiphe* DC.: Fr. emend. Heluta and *Microsphaera* Lev. (10 and 21 respectively). The other parasites of the Faboideae belong to the genera *Uncinula* Lev. (6 species), *Sphaerotheca* Lev. and *Phyllactinia* Lev. (3 each), *Pleochaeta* Sacc. & Speg. (2 species), *Brasiliomyces* Vieg. and *Leveillula* Arn. (1 each). Representatives of the genera *Brasiliomyces*, *Pleochaeta*, *Phyllactinia* and *Uncinula* are probably now merely a few relics of groups of powdery mildews which previously flourished, doubtless also on ancestors of the modern legumes, that is to say, their origin was connected with earlier stages of evolution of the order Erysiphales. A collective species, *Leveillula taurica* sensu lato is the youngest representative on the Fabaceae. and a member of the youngest genus of this order [3, 4]. It is not inconceivable that now biotypes of

this genus are gradually colonizing new hosts of different families of the Magnoliophyta. Species of *Sphaerotheca* are probably fortuitous on the Fabaceae, because they occur in small numbers and have anamorphs of the *Oidium* sensu stricto type, whereas other parasites on legumes have anamorphs which are either evolutionary more recent or unrecorded. Species of the remaining two genera, *Erysiphe* and *Microsphaera*, form an apparently phylogenetic unified group, because, as noted formerly [1, 4, 5, 7, 10, 11], there are many taxa intermediate between them. Those closer to *Erysiphe* are morphologicaly more simple and earlier in origin, and it is accordingly necessary to carry out a precise examination of the relationships between species of the genus *Erysiphe* recorded on members of the Fabaceae sensu lato. The present paper addresses this interesting problem.

Results and discussion

As already noted [12], comparative analysis of morphological features of *Erysiphe* species gives very little information about how evolution occurred within this genus, but it is possible to determine more archaic or more recent taxa based on the presence in them of features judged to be primitive. In this case it is essential to look first at the number of spores in the ascus. During evolution this changed from eight to two (single-spored asci are formed very rarely). Appendage shape is also noteworthy. In different species of the genus *Erysiphe* it can vary from simple and mycelium-like to more complex — dichotomously branched and differentiated from mycelium.

As pointed out above, eleven representatives of the genus *Erysiphe* have been recorded on plants of the family Fabaceae sensu lato. Only two (*E. cercidis* and *E. deserticola*) are found on the Caesalpinioideae and one (*Microsphaera trifolii*) is known on the Mimosoideae. The others are parasitic on members of the Faboideae. As will be seen from the table, all species parasitizing legumes are morphologically rather similar, but the Chinese endemic species *E. cercidis* is distinguished on account of a number of features which are at the extremes of the full range of variation. It has the smallest conidia and ascocarps, the fewest and shortest asci (which contain the shortest ascospores); the number of ascospores in the ascus is 2—7; appendages are simple and mycelium-like. It is therefore possible to regard this taxon as archaic in comparison with the other species. It is not inconceivable that this species has the most ancient origin by comparison with the other representatives of the genus *Erysiphe* described on legumes. *E. deserticola*, another parasite of Caesalpinioideae, is known only from Argentina. Its teleomorph has not been adequately studied; its anamorph is similar to the anamorph of *E. pisi* [11]. The small number of ascospores in the ascus (2—4) is peculiar to this species, and its host-specific character and especially its geographical distribution also testify to its considerable isolation from other representatives of the genus *Erysiphe* on the subfamilies Mimosoideae and Faboideae.

The fungus *E. puerariae* also is distinguished by some special features. Its ascocarps contain few asci, which are the widest among *Erysiphe*-like parasites of legumes; ascospores of this species are also the largest, and *E. puerariae* has very few appendages (1—4, more seldom up to 7) which may branch dichotomously once or twice at the apex. This combination of features suggests that this species is evolutionarily advanced and that it has a relationship with the genus *Microsphaera*. *Erysiphe caulicola* also differs somewhat from other species of this group. It has the largest ascocarps, the most asci containing the greatest number of ascospores (up to 7), and short appendages. *E. trifolii* and *E. thermopsidis* are also of special interest. The former has appendages differentiated from mycelium more than in any other species [2, table V], with apices which can divide dichotomously more than once. On the basis of these features, Braun [8] has transferred this species to the genus *Microsphaera*. *E. thermopsidis* has short simple, often uncinate appendages which make this species close to the genus *Uncinula*. Furthermore, it has conidia as small as those of *E. cercidis*. Among the

other species, *E. viciae-unijugae* and *E. cruchetiana* are also distinguished. They have frequently- and irregularly-branched, almost coralloid appendages. It is also worth noting *E. glycines*, and particularly its variety *lespedezae* with its archaic number of ascospores (8, rarely 6—7).

Some features of *Erysiphe* species recorded from legumes

Species	Dimensions of conidia	Diameter of ascocarps	Number of asci	Dimensions of asci	Number of ascospores	Dimensions of ascospores
E. caulicola (Petrak) U. Braun	30—45 x 14—18	(100)110—185(210)	5—15	60—80 x 30—45	(2)4—7	16—25 x 10—14
E. cercidis T. Xu	27—35 x 13—17	65—100(110)	3—5(7)	33—55 x 29—40	2—7	14—20 x 9—14
E. cruchetiana Blumer	30—40 x 15—20	90—120	4—10	54—70 x 35—45	(2)3—4(5)	18—24 x 11—15
E. deserticola Speg.	25—40 x 13—20	100—150	—	50—60 x 25—35	2—4	—
E. desmanthi (U. Braun) Heluta	—	70—95(105)	3—5	40—55 x 24—40	3—4	15—22 x 11—15
E. glycines Tai var. *glycines*	25—50 x 13—32	(75)85—130(150)	4—10	50—65 x 30—45	(3)4—7(8)	16—25 x 15—18
var. *lespedezae* (Zheng & U. Braun) U. Braun & Zheng	—	—	(5)6—11(14)	50—80 x 30—50	(6)—8	14—24 x 10—14
E. pisi DC.	24—55 x 14—22	(80)85—150	(3)4—8(13)	40—85 x 25—55	(2)3—6	18—25 x 10—17
E. puerarie Zheng & Chen	—	(70)90—110	3—7	46—76 x 38—56	3—6	23—28 x 15—18
E. thermopsidis Zheng & Chen	25—35 x 13—18	80—120	(4)6—10	35—70 x 25—45	(2)3—5	16—25 x 9—14
E. trifolii Grev.	30—45 x 16—21	(80)90—150(180)	3—12	45—80 x 25—50	(2)3—5(6)	18—30 x 10—16
E. viciae-unijugae (Homma) U. Braun	25—38 x 13—20	85—135(145)	4—10	50—70 x 35—45	(3)4—6(7)	18—25 x 10—15

N o t e s. Information on *Erysiphe* species is adduced by U. Braun [11], with our additions; the dimensions are given in mkm; there are extreme values in round brackets.

It is thus possible to demonstrate that, on legumes, some more or less separate species and groups of the genus *Erysiphe* exist. These are: 1) *E. cercidis*; 2) *E. deserticola*; 3) *E. caulicola*, *E. glycines* and *E. pisi*; 4) *E. cruchetiana* and *E. viciae-unijugae*; 5) *E. puerariae* and *E. trifolii*; 6) *E. thermopsidis*. A clear transition from *Erysiphe* to *Microsphaera* (via group 5) and *Uncinula* (via the last species) can also be traced.

It is however a very difficult problem to make any diagram of the relationships of *Erysiphe* species based purely on their morphology. Therefore, working on the hypothesis that evolution in *Erysiphe* was connected with that of legumes, an attempt will now be made to analyse the distribution of species of this genus by phylogenetic groups of the Fabaceae sensu lato.

As already noted, only *E. cercidis* and *E. deserticola* are found on representatives of the subfamily Caesalpinioideae, and in morphology these two species stand somewhat apart from the other *Erysiphe* species parasitizing legumes. In all probability, they are species which developed during the first stage of evolution of powdery mildews parasitizing legumes. On plants of the subfamily Mimosoideae only one species, *E. trifolii*, was known. Braun [9] has reported *Microsphaera trifolii* (=*E. trifolii* sensu Heluta and some other mycologists working on powdery mildews) var. *desmanthi* U. Braun on *Desmanthus brachylobus* Benth.; but this

variety differs considerably from *M. trifolii* var. *trifolii* in morphology, because it has significantly smaller ascocarps, warty appendages, a small number of asci and few ascospores. In addition, this fungus develops on stems. These features, together with the specific taxonomic position of host plant, are sufficient grounds to regard this taxon as a separate species — *E. desmanthi* (U. Braun) Heluta comb. nov.[1] On the one hand, it is similar to *E. cercidis* (dimensions of ascocarps, asci and ascospores, and number of asci); on the other, this species is similar to *E. deserticola* (number of ascospores). It is not improbable that these three species have one common ancestor, from which *E. desmanthi* has evolved the most. *Microsphaera trifolii* var. *trifolii* has also been reported on species of *Acacia* Mill. and *Albizzia* Durazz., but this information needs critical verification, because an incorrect identification of the fungus is possible: such mistakes are common in records of powdery mildew fungi parasitizing legumes [10].

Most *Erysiphe* species recorded on legumes are found on representatives of the subfamily Faboideae. As may be seen from Fig. 1, the number of these species is greater on the evolutionarily advanced groups of this subfamily[2]. Thus, it can be supposed that evolution in the genus *Erysiphe* took place in parallel to that of the Faboideae, but with some delay in time. The ancestral form of these parasites was probably similar to the present species *E. glycines*, because the variety *lespedezae* of this species has the greatest number of features judged here to be archaic — eight ascospores in ascus and very simple appendages. *E. pisi* DC. may have developed on the Palaeosophoreae or perhaps an even more early ancestral form owing to reduction of the number of its ascospores. It still occurs on plants of the genus *Sophora* L. This species has been thought to occur on legumes descended from the Palaeosophoreae groups, but it is quite possible that these organisms have not developed from «*E. pisi*» parasitizing Palaeosophoreae, but they each separately evolved from an *E. glycines*-like ancestor. In that way, on papilionaceous plants we have a complicated picture of taxa with similar morphology which evolved through different paths at different times. Only by recognizing such an hypothesis can we explain the fact that the morphologically primitive and archaic *E. glycines* continues to exist in our time and is parasitic on plants belonging to the evolutionary advanced tribes Desmodieae, Phasoleae and Vicieae, while it is not recorded on representatives of the groups related to the Genistoid alliance, Millettioid and Robinioid complexes. It is probable that the archaic «*E. pisi*» gave origin to *E. trifolii* (through further evolution of appendages which led to their differentiation from mycelium as happened in species of the genus *Microsphaera*) and to *E. thermopsidis* (through the same process, but with appendages similar to those of morphologically primitive representatives of the genus *Uncinula*), because these two species are known on plants of various groups of the Genistoid and Galegoid alliances. In any event the close relationship of *E. glycines*, *E. pisi* and *E. trifolii* seems beyond question since the spreading of first and second of them correlates with the rank of tribes in their hosts. A similar situation is observed in *E. pisi* and *E. trifolii* at the rank of tribes or, at least at the rank of complexes. The process of reduction of ascospore number is also reliable: cytological investigations [13] have demonstrated that in the ascus of powdery mildews eight primary nuclei are formed. All or part of this number (depending on the actual fungal species) can become the basis for differentiation of ascospores. The phenomenon of reduction of ascospores numbers can also be traced for present taxa of the genus *Erysiphe*. For example, in asci of *E. glycines* var. *lespedezae* recorded on representatives of the genus *Lespedeza* Michx. (tribe *Desmodieae*) in China, Japan and the far east of Russia eight ascospores are

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[1] Bas.: *Microcphaera trifolii* var. *desmanthi* U. Braun, Mycotaxon **19**: 375 (1984).

[2] In this place and further, all information on the legumes is taken from the monograph by G.P. Yakovlev [6].

formed. Furthermore, specimens from the same region and from North America are found on plants of the genus *Desmanthus* Desv. (the same tribe), and on the basis of this feature they have an intermediate place between var. *lespedezae* and var. *glycines* [11]. The last of them also parasitizes representatives of some genera of the line represented by Phaseolus and the more advanced group of the Galegoid complex.

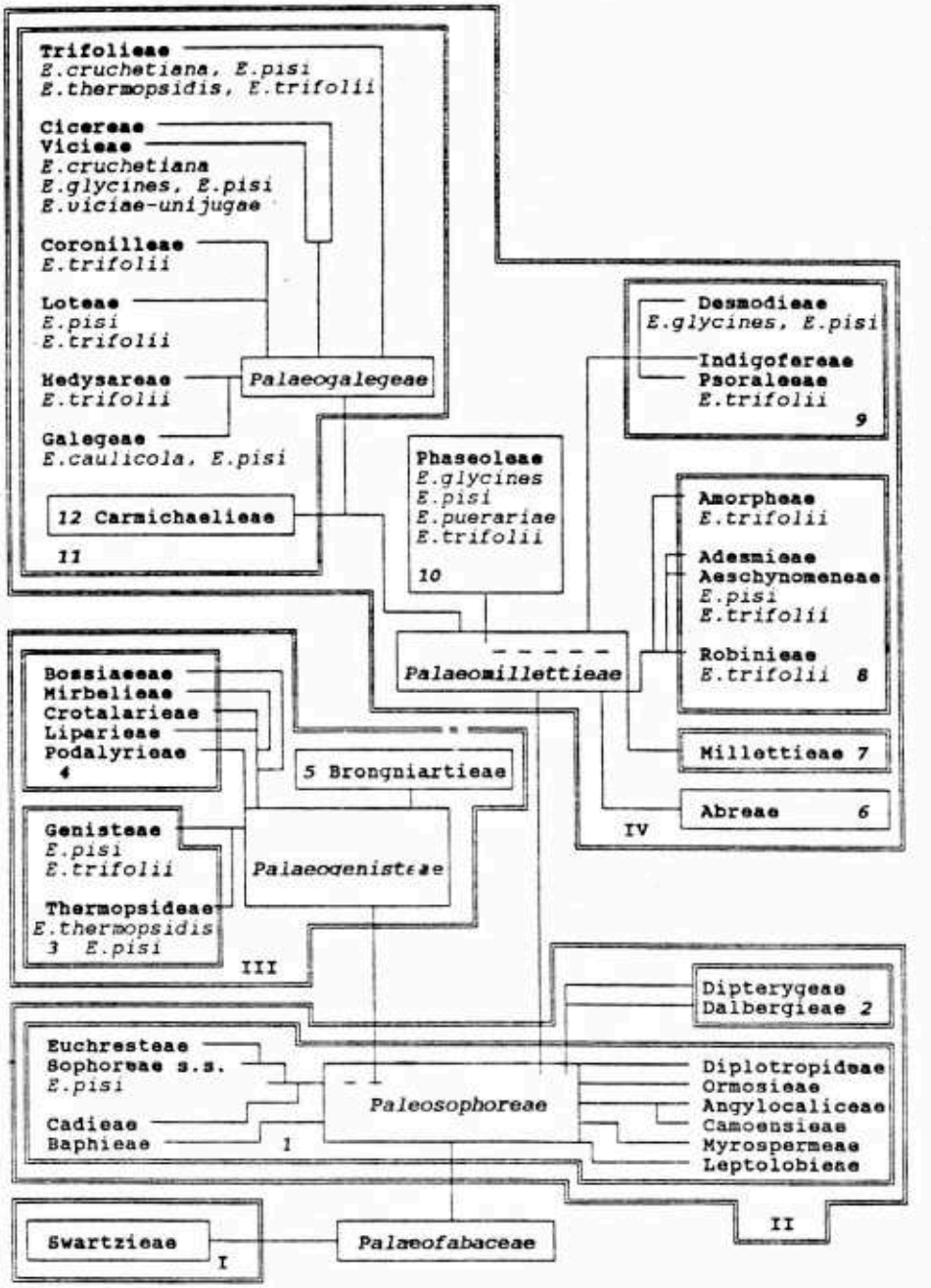

Fig. 1. Distribution of species of the genus *Erysiphe* by phylogenetic groups of the subfamily Faboideae. I. Swartzioid line. II. Sophoroid alliance: 1 — Sophoroid complex; 2 — Dalbergioid complex. III. Genistoid alliance: 3 — Genistoid complex; 4 — Podalyrioid complex; 5 — Brogniartioid line. IV. Millettioid alliance: 6 — Abroid line; 7 — Millettioid centre; 8 — Robinioid complex; 9 — Desmodioid complex; 10 — Phaseoloid line; 11 — Galegoid complex; 12 - Carmichaelioid line

Rapid evolution of the Palaeomillettieae did not apparently initiate speciation in the genus *Erysiphe*, because we do not find any new additional common taxa for plants of different complexes and lines of the Millettioid alliance. Probably at this stage only a reduction of ascospore numbers took place in forms like *E. glycines* var. *lespedezae*. The selection of present biotypes of *E. glycines* var. *glycines* recorded on representatives of the Phaseoloid line and the Galegoid complex of papilionaceous plants was a result of this process. It is not inconceivable that on the Palaeomillettiae, *E. puerariae* originated from an ancestral form like *E. trifolii*: both have spread on plants of the Phaseoloid line and have similar morphological features. Further selection of *Erysiphe* species takes place on the Palaeogalegeae, because only on representatives of this group have such species as *E. cruchetiana*, *E. viciae-unijugae*, and *E. caulicola* developed. The first of these is similar to *E. pisi* and is regarded, even by Braun [8], as a variety of this species. However, *E. cruchetiana* has appendages branched and arranged in a more complicated manner. *E. viciae-unijugae* also has such appendages, though their ramification is even more intensive. Both species have spread onto plants of the same genus (*Lathyrus* L.), but they have different geographic distributions (the first is European; the second is Asian) and are probably very recently evolved variants of a common ancestor like *E. pisi*. What places *E. caulicola* takes in the diagram of relationships remains something of a mystery. It may be near *E. glycines* (they have such common features as a large number of asci, an archaic number of ascospores in ascus, and simple appendages), but in this case the range of host plants for *E. caulicola* is likely to be considerably broader then has been established to date.

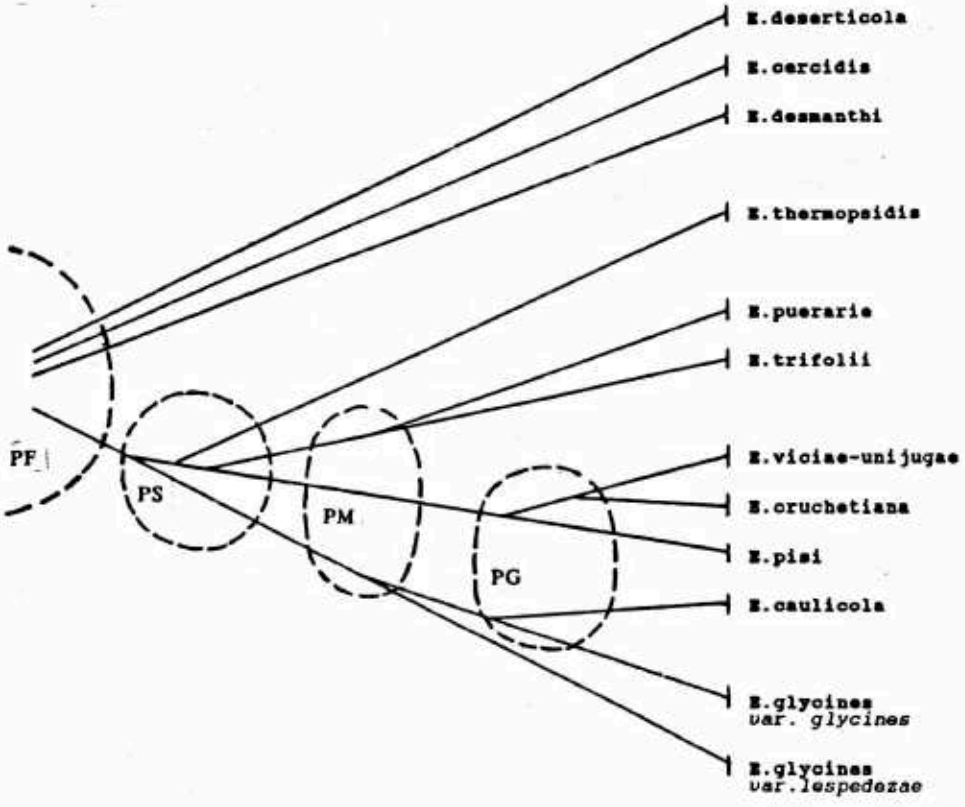

Fig. 2. Diagram of the probable pylogenetic connections of species of the genus Erysiphe registered on legumes (PF — Palaeofabaceae, PG — Palaeogalegeae, PM — Palaeomillettieae, PS — Palaeosophoreae)

Conclusions

The information presented here about species of the genus *Erysiphe* recorded on legumes suggests a correlation between their morphology and their parasitism of particular groups of the Fabaceae sensu lato. In any event the parasites of the Mimosoideae and Caesalpinioideae stand somewhat aside from the rest, because they have strongly expressed morphological features (see table) which are probably evidence of their having the longest evolutionary history. Nevertheless, something like *E. glycines* var. *lespedezae* can be considered as the ancestral form of most *Erysiphe* species found on legumes. A summary of the phylogenetic connections of the species of the genus *Erysiphe* recorded on the Fabaceae sensu lato is shown on Fig. 2.

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ФІЛОГЕНІЯ ВИДІВ РОДУ *ERYSIPHE* — ПАРАЗИТІВ БОБОВИХ

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На бобових (Fabaceae s. l.) виявлено 11 видів борошнисторосяних грибів з роду *Erysiphe* DC.: Fr. emend. Heluta: два — *E. cercidis* T. Xu та *E. deserticola* Speg. — на цезальпінієвих (Caesalpinioideae) і лише один — *E. desmanthi* (U. Braun) Heluta comb. nov. — на мімозових (Mimosoideae); решта є паразитами метеликових (Faboideae). На основі результатів аналізу морфологічних ознак усіх 11 представників роду *Erysiphe* встановлено, що їх анцестральною формою був вид, близький до *E. glycines* var. *lespedezae* (Zheng & U. Braun) U. Braun & Zheng. Аналіз приуроченості видів роду до філогенетичних груп бобових свідчить про те, що еволюційний процес

у роді відбувався паралельно до еволюції рослин-живителів, проте з певною затримкою в часі. Ще на Palaeosophoreae, мабуть, від вищезгаданої анцестральної форми виник *E. pisi* DC., який зберігся на видах роду *Sophora* L. Вірогідно, що морфологічно ідентичні йому паразити інших еволюційно просунутіших груп бобових виникли від того ж анцестора, а не від древнього «*E. pisi*» — паразита палеософорових. Проте від останнього, мабуть, ще на Palaeosophoreae взяли початок *E. trifolii* Grev. і *E. thermopsidis* Zheng & Chen. Активна еволюція палеомілєттієвих не ініціювала видоутворення в роді *Erysiphe*. Мабуть, тут виникли лише *E. glycines* var. *glycines* (від первісної анцестральної форми паразитів бобових) і *E. puerariae* Zheng & Chen — від анцестора типу *E. trifolii*. Подальший сплеск видоутворення відбувся на Palaeogalegeae, на представниках яких виникли *E. cruchetiana* Blumer, *E. viciae-unijuga* (Homma) U. Braun и *E. caulicola* (Petrak) U. Braun.

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ФИЛОГЕНЕЗ ВИДОВ РОДА *ERYSIPHE* — ПАРАЗИТОВ БОБОВЫХ

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На бобовых (Fabaceae s. l.) зарегистрировано 11 видов мучнисторосяных грибов из рода *Erysiphe* DC.: Fr. emend. Heluta: два — *E. cercidis* T. Xu и *E. deserticola* Speg. — на цезальпиниевых (Caesalpinioideae) и только один — *E. desmanthi* (U. Braun) Heluta comb. nov. — на мимозовых (Mimosoideae); остальные являются паразитами мотыльковых (Faboideae). На основании анализа морфологических признаков всех 11 представителей рода *Erysiphe* установлено, что их анцестральной формой был вид, близкий к *E. glycines* var. *lespedezae* (Zheng & U. Braun) U. Braun & Zheng. Анализ приуроченности видов рода к филогенетическим группам бобовых свидетельствует о том, что эволюционный процесс в роде шел параллельно эволюции их растений-хозяев, но с некоторой задержкой во времени. Ещё на Palaeosophoreae, очевидно, от упомянутой анцестральной формы произошел *E. pisi* DC., который сохранился на видах рода *Sophora* L. Очень вероятно, что морфологически идентичные ему паразиты других эволюционно более продвинутых групп бобовых произошли от того же анцестора, а не от древнего «*E. pisi*» — паразита палеософоровых. Но от последнего, наверное, еще на Palaeosophoreae взяли начало *E. trifolii* Grev. и *E. thermopsidis* Zheng & Chen. Активная эволюция палеомиллетиевых не инициировала видообразование в роде *Erysiphe*. Возможно, здесь возникли только *E. glycines* var. *glycines* (от первичной анцестральной формы паразитов бобовых) и *E. puerariae* Zheng & Chen — от анцестора типа *E. trifolii*. Дальнейший всплеск видообразования произошел на Palaeogalegeae, на представителях которых появились *E. cruchetiana* Blumer, *E. viciae-unijugae* (Homma) U. Braun и *E. caulicola* (Petrak) U. Braun.