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# Phylogeny of *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae* (*Sphaerotheca fuliginea* auct. s.lat.) inferred from rDNA ITS sequences – a taxonomic interpretation

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**Abstract:** Braun, U., Shishkoff, N. & Takamatsu, S. 2001: Phylogeny of *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae* (*Sphaerotheca fuliginea* auct. s.lat.) inferred from rDNA ITS sequences – a taxonomic interpretation. Schlechtendalia 7: 45-52.
Data of a phylogenetic analysis of the *Podosphaera* (*Sphaerotheca*) *fuliginea* complex based on rDNA ITS sequences are taxonomically interpreted. Using a morphological species concept, mainly based on the size of the ascomata and the diameter of the thin-walled apical portion of the asci (oculus), combined with biological data, the present taxonomic status of *P. balsaminae, P. diclipterae, P. fuliginea, P. intermedia, P. pseudofusca* and *P. sibirica* as separate species has been confirmed. *P. fusca* emend. as well as *P. xanthii* emend. are reassessed as complex, compound species. *P. euphorbiae-hirtae* and *P. phaseoli* are reduced to synonymy with *P. xanthii*.

**Zusammenfassung:** Braun, U., Shishkoff, N. & Takamatsu, S. 2001: Phylogeny of *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae* (*Sphaerotheca fuliginea* auct. s.lat.) inferred from rDNA ITS sequences – a taxonomic interpretation. Schlechtendalia 7: 45-52.
Ergebnisse einer phylogenetischen Analyse des *Podosphaera* (*Sphaerotheca*) *fuliginea*-Komplexes auf Grundlage von rDNA-ITS-Sequenzen werden taxonomisch ausgewertet. Unter Anwendung eines morphologischen Artkonzepts, hauptsächlich auf Grundlage der Fruchtkörpergröße und des Durchmessers der dünnwandigen Scheitelregion der Asci (Oculus), in Verbindung mit biologischen Daten, wird der gegenwärtige taxonomische Status von *P. balsaminae, P. diclipterae, P. fuliginea, P. intermedia, P. pseudofusca* und *P. sibirica* bestätigt. *P. fusca* emend. und *P. xanthii* emend. werden neu als komplexe Sammelarten bewertet. *P. euphorbiae-hirtae* und *P. phaseoli* werden zu *P. xanthii* gestellt.

## Introduction

Hirata et al. (2000) published a comprehensive evolutionary analysis of subsect. *Magnicellulatae* (U. Braun) U. Braun & N. Shishkoff of *Podosphaera* sect. *Sphaerotheca* (Lév.) U. Braun & N. Shishkoff (Braun & Takamatsu 2000) based on rDNA ITS sequences. The species concerned are characterised by having relatively small ascomata with very large peridial cells, mycelioid appendages and a single ascus. Salmon (1900) placed all taxa of this complex in *Sphaerotheca humuli* var. *fuliginea* (Schltdl.: Fr.) E.S. Salmon. Pollacci (1905) introduced the combination *Sphaerotheca fuliginea* (Schltdl.: Fr.) Pollacci, but maintained Salmon´s (1900) broad concept of this taxon. Blumer (1933, 1967) reduced the broad concept of *S. fuliginea* somewhat. However, the first significant attempt to split this complex into smaller morphological units was made by Junell (1966). Braun (1987) and most subsequent authors followed Junell´s (1966) concept and introduced additional segregated species. The introduction of *Sphaerotheca fusca* (Fr.) S. Blumer emend. U. Braun (incl. *S. fusca* s.str., *S. erigerontis-canadensis* (Lév.) L. Junell, *S. xanthii* (Castagne) L. Junell, *S. melampyri* L. Junell, *S. elsholtziae* Z.Y. Zhao, *S. cucurbitae* (Jacz.) Z.Y. Zhao) based on morphological criteria has been the most important deviation from Junell´s (l.c.) species concept in this complex. Braun (1987, 1995) supposed a more or less linear

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co-evolution between powdery mildew fungi and their host plants, so that morphologically barely distinguishable taxa on hosts of the more ancestral Rosidae and Moraceae and the more advanced Asteridae and Cucurbitaceae were not lumped in a single species, which is evident in BRAUN´s (1987: 100) key. BRAUN (1987) regarded powdery mildews on ancestral hosts to be ancestral as well and those on hosts of the Asteridae were taken for derived, advanced species, but based on new molecular investigations this view point cannot be considered to be generally true.

On account of molecular examinations published by SAENZ & TAYLOR (1999) and TAKAMATSU et al. (2000), BRAUN & TAKAMATSU (2000) merged *Podosphaera* Kunze and *Sphaerotheca* Lév. and BRAUN & SHISHKOFF (in BRAUN & TAKAMATSU 2000) formally divided *Podosphaera* into sect. *Podosphaera* and sect. *Sphaerotheca*, which was further split into subsect. *Sphaerotheca* and subsect. *Magnicellulatae*.

HIRATA et al. (2000) examined 79 isolates of species belonging to subsect. *Magnicellulatae* from 60 host species of various host plant families and used the results for an evolutionary analysis. For applied and taxonomic purposes, it is, however, necessary to interpret the molecular data and to use them for the creation of a better species concept.

## Species concept in phytopathogenic fungi in general and in the powdery mildew fungi in particular

The species concept in phytopatogenic fungi is a complex, complicated problem, which has been controversially discussed (SKALICKÝ 1968, URBAN 1968). There are two basic types of taxonomists: 'lumpers' (with a wide morphological species concept) and 'spitters' (with a narrow biological species concept, i.e., one species for one host genus or host family). SALMON (1900) treated the Erysiphales as saprophytes on a strict morphological base and even lumped distinct taxa when morphological and morphometrical features overlapped. This approach led to an extremely broad, unnatural species concept. In powdery mildew fungi, JACZEWSKI (1927) maintained the wide morphological species concept of SALMON (1900), but created numerous 'formae', each 'forma' for a single host genus. GOLOVIN´s (1956) monograph of *Leveillula* was based on a similar taxonomic view point, but he introduced one species for each host family and one 'forma' for each host genus. This concept is, however, not tenable, unnatural and does not agree with morphological and molecular data (BRAUN 1987, 1995; KHODAPARAST et al. 2001). BLUMER (1967), JUNELL (1966, 1967a,b), BRAUN (1987, 1995), CHEN et al. (1987) and all subsequent authors applied an integrated concept, based on morphology and biology (host range, biological specialisation). Since 1996, this concept has been supplemented by molecular approaches (HIRATA & TAKAMATSU 1996, TAKAMATSU et al. 1999, SAENZ & TAYLOR 1999, MORI et al. 2000, etc.). All molecular examinations in phytopathogenic fungi clearly demonstrated the important role of the co-evolution between parasite and host and the strong influence of niche separation by host specialisation for the process of speciation. Nowadays species concepts of phytoparasitic fungi should be based on a combination of morphology, biology and molecular information. However, phenotype and morphology should play a fundamental role for the separation and recognition of species, i.e., 'good' species should be morphologically distinguishable. Genetically allied, biologically and physiologically

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deviating but morphologically indistinguishable taxa should be united in compound species ('sensu lato'), which may be separated into biological races ('formae speciales') [SKALICKÝ 1968]. In powdery mildews, such species may be genetically and biologically fairly differentiated (HIRATA et al. 2000, KHODAPARAST et al. 2001), but as far as they are morphologically uniform and when they form distinct clades or subclades, they can be assiged to a single compound species, which may be separated into biological races.

## Taxonomic interpretation of the evolutionary analysis of *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae*

HIRATA et al. (2000) found 27 hapotypes of which 19 consisted of isolates from only one host species, four contained isolates from more than one host species within the Asteraceae and the remaining four haplotypes included isolates from different host families. The subsect. *Magnicellulatae* ingroup formed a distinct clade. 25 haplotypes were arranged in a single large clade with haplotype 1 (*Veronica*) and 2 (*Veronicastrum*) as sister groups. These results fully confirmed the treatment of *Podosphaera fuliginea* (Schltdl.: Fr.) U. Braun & S. Takamatsu and *P. sibirica* (U. Braun) U. Braun & S. Takamatsu as separate species.

The main clade was divided into three groups. The basal group (**group I)** was composed of isolates from hosts belonging to the Asteraceae (*Leontodon, Matricaria, Taraxacum*), Lamiaceae (*Ajuga*), Scrophulariaceae *(Melampyrum*) and Verbenaceae (*Clerodendrum*) characterised by having relatively small ascomata, which can be attributed to *Sphaerotheca erigerontis-canadensis* sensu JUNELL (1966), *S. elsholtziae*, *S. melampyri* and *S. intermedia* U. Braun, respectively. BRAUN (1987) placed all of these taxa, excluding *S. intermedia*, in *S. fusca* emend. (incl. *S. xanthii*) since the differentiation between these species proposed by JUNELL (1966) was not tenable. The taxa concerned are morphologically very close and connected by a continuum of the variability of the features examined. BLUMER (1933, 1967) maintained *S. fusca* as a separate species on *Doronicum* and *Senecio* distinguished from allied species by forming well-developed brown patches composed of pigmented persistent hyphae. JUNELL (1966) confined *S. fusca* to collections on *Doronicum* spp. and assigned collection on *Senecio* spp. to *S. xanthii*. BRAUN (1987) discussed the taxonomy of *S. fusca* in detail and pointed out that this species is not distinct from other *Sphaerotheca* collections on composites.

SHISHKOFF (1999) found a new, very useful morphological feature for taxonomic purposes in the *S. fuliginea* complex. It turned out that the thin-walled apical portion of the ascus (oculus) represents a good, consistent structure for the discrimination of allied species, i.e., a certain ascoma size being correlated with a certain diameter of the oculus. Because of this characteristic, *S. fusca* emend. U. Braun (BRAUN 1987) had to be divided into two species, viz., *P. fusca* s.str. with smaller ascomata and small oculi [8-15 µm diam., Ø 10 µm] and *P. xanthii* with larger ascomata and oculi [15-25(-30) µm diam., Ø 20 µm] (BRAUN & SHISHKOFF, in BRAUN & TAKAMATSU 2000) [Fig. 1]. Species of *Doronicum*, the genus of the type host of *S. fusca*, is also attacked by *S. xanthii*, but the common, widespread *Podosphaera* (*Sphaerotheca*) on hosts of this genus belongs to the 'small species' and is

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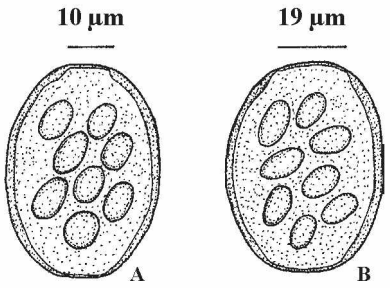



**Fig. 1:** Asci of *Podosphaera fusca* (A) with narrow apical oculus and *P. xanthii* (B) with broad apical oculus.

well-characterised by forming brown mycelium patches on host leaves as already mentioned in the original description of *Erysiphe fusca* by Fries. Therefore, BRAUN & SHISHKOFF (in BRAUN & TAKAMATSU 2000) neotypified *P. fusca* in this sense and reduced *S. erigerontis-canadensis* to synonymy with the latter species.

**Group I** in the tree published by HIRATA et al. (2000) represents *Podosphaera fusca* emend. Collections on *Melampyrum* spp. (*S. melampyri*) and *Ajuga* spp. (*S. elsholtziae*) were included in *S. fusca* s.lat. by BRAUN (1987) since they were morphologically indistinguishable from hosts of this species on composites. The ascomata are relatively small and the oculi of the asci are only 8-15 µm diam. (Ø 10 µm). Therefore, *S. melampyri* and *S. elsholtziae* have to be reduced to synonymy with *S. fusca* emend. The fungus on *Clerodendrum* (Verbenaceae), described as *S. intermedia* U. Braun, has been re-examined. This species is morphologically also very close to *S. fusca* (ascomata small, oculus about 10 µm diam.). The peridial cells are, however, somewhat smaller as in collections of *P. fusca* (mostly 15-30 µm diam.) and the germ tubes belong to the Pannosa-type (HIRATA 1942), which could be confirmed by S. Takamatsu. *P. intermedia* belongs to a separate haplotype and is morphologically distinct from *S. fusca*. Therefore, ***S. intermedia*** should be maintained as a separate species. Numerous other collections of *P. fusca* with small ascomata and oculi have been examined, e.g., on *Agastache scrophulariaefolia* (USA, HAL 465), *Ajuga nipponica* (Japan, HAL 483), *Clinopodium gracile* (Japan, HAL 511) [Lamiaceae]; *Scrophularia variegata* (Armenia, HAL 591), *Siphonostegia* sp. (China, HAL 479) [Scrophulariaceae] and *Solanum dulcamara* (Armenia, HAL 487) [Solanaceae].

Most haplotypes of **group III** are composed of taxa with relatively large ascomata and oculi (15-30 µm diam., Ø 20 µm), which can be summarised as *Podosphaera xanthii* emend. (BRAUN & SHISHKOFF, in BRAUN & TAKAMATSU 2000). *P. xanthii* represents a rather heterogeneous compex of specialised as well as plurivorous races on hosts of the composites, cucurbits, legumes, etc. The process of speciation in this complex is not yet finished and collections of most haplotypes are morphologically indistinguishable from each other, so that they must be placed in a single compound species which has to be called *P. xanthii*. ***Sphaerotheca euphorbiae-hirtae*** U. Braun & Somani (on *Acalypha*) and ***S. phaseoli*** (Z.Y. Zhao) U. Braun (on various legumes) are morphologically indistinguishable from *P. xanthii* (ascomata 75-100 µm diam., Ø 90 µm, oculi 15-23 µm, Ø 18 µm) and belong together with collections on some composites to haplotype 26. ***Podosphaera astragali*** (L. Junell) U. Braun & S. Takamatsu on *Astragalus* and *Trollius* spp. in Europe is clearly distinct from *P. xanthii* (incl. *S. phaseoli*) by small ascomata (55-90 µm diam., Ø 75 µm) and oculi (Ø 10 µm), so that this species probably belongs to the *P. fusca* complex. However, molecular data are not yet available for this taxon.
***P. pseudofusca*** (U. Braun) U. Braun & S. Takamatsu on *Fatoua villosa* (haplotype 20 in

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group III) may be maintained as a separate species, since the features of this fungus are intermediate between *P. fusca* and *P. xanthii*. The ascomata are large (75-100 µm diam., Ø 85 µm), but the oculi of the asci are small (10-15 µm diam, Ø 12 µm). Haplotype 14 (on *Dicliptera japonica* = ***Podosphaera diclipterae*** (Y. Nomura) U. Braun & S. Takamatsu) has similar large ascomata and small oculi, but differs from *P. pseudofusca* in having very long ascoma appendages. ***Podosphaera balsaminae*** (Kari ex U. Braun) U. Braun & S. Takamatsu (haplotype 24) may also be excluded from *P. xanthii* emend. and maintained as a separate species. Numerous collection on *Impatiens noli-tangere* and *I. balsamina* have recently been re-examined by N. Shishkoff and U. Braun. The ascomata are large (65-100 µm diam., Ø 90 µm) as in *P. xanthii*, but the oculi of the asci are intermediate between *S. fusca* and *S. xanthii* (10-20 µm diam., Ø 15 µm). Furthermore, the germination pattern of the conidia seems to be different (SCHMIDT 1999). The occurrence of a collection on *Impatiens textori* in haplotype 15 together with composites is, however, unclear. A single sample on *I. textori* has been examine (HAL 779), which was morphologically indistinguishable from specimens on *I. noli-tangere*.

The status of **group II** (on *Aster ageratoides, A. tataricus, Carpesium abrotanoides, Kalimeris pinnatifida*) causes some problems. It forms a separate subclade between group I and III. All collections on the hosts of group II are generally confined to eastern Asia. Collections on all hosts have been re-examined (MUMH 143, 344, HAL 467, 481, 523). The size of the ascomata (average values ranging from 75 to 85 µm) and the size of the oculi (8-15 µm diam., Ø 10 µm) agree well with those of *P. fusca*. Group II represents a special assemblage of closely allied haplotypes which forms a separate subclade, but the process of speciation connected with the establishment of consistent phenotypical differences is not yet finished, so that this group should be assigned to the morphologically indistinguishable group I (= *P. fusca*).

The results of the present taxonomic interpretation may be summarised as follows:

(1) Group I and II may be merged and represent a single morphological species, i.e., *P. fusca* characterised by having relatively small ascomata (55-90 µm diam., average < 85 µm) and oculi (8-15 µm diam., average 12 µm).

***Podosphaera fusca*** (Fr.) U. Braun & N. Shishkoff, in Braun & Takamatsu, Schlechtendalia 4: 29 (2000) emend.

≡ *Erysiphe fusca* Fr., Symb. mycol. 3: 242 (1829).
≡ *Sphaerotheca fusca* (Fr.) S. Blumer, Beitr. Krypt.-Fl. Schweiz 7(1): 117 (1933).
= *Erysiphe doronici* Duby, Bot. gall.: 870 (1830).
= *Erysiphe erigerontis-canadensis* Lév., in Mérat, Rev. fl. paris.: 459 (1843).
≡ *Sphaerotheca erigerontis-canadensis* (Lév.) L. Junell, Svensk Bot. Tidskr. 60(3): 387 (1966).
= *Erysiphe detonsa* Westend., Herb. Crypt. Belg., Fasc. 11-12, No. 555 (1851), homonym.
≡ *Sphaerotheca detonsa* J. Kickx f., Fl. crypt. Flandres: 375 (1867), as "(Westend.) Kickx".
= *Sphaerotheca erigerontis* Oudem., Verh. Kon. Ned. Akad. Wetensch. Amsterdam, Afd.

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Natuurk., Tweede Sect., 2(2): 84 (1897).
= *Sphaerotheca phtheirospermi* Henn. & Shirai, Bot. Jahrb. Syst. 19: 147 (1900).
= *Sphaerotheca melampyri* L. Junell, Svensk Bot. Tidskr. 60(3) 387 (1966).
= *Sphaerothca elsholtziae* Z.Y. Zhao, Acta Microbiol. Sinica 21(4): 441 (1981).

Almost circumglobal, on hosts of numerous host genera of the Asteraceae, Lamiaceae, Scrophulariaceae and Solanaceae.

Notes: *P. fusca* appears to be homothallic (SHISHKOFF 1999).

(2) Group III represents *P. xanthii* emend., exclusive of *P. balsaminae, P. diclipterae* and *P. pseudofusca*, which is characterised by having large ascomata (75-100 µm diam., average > 85 µm) and large oculi (15-30 µm diam., average 20 µm).

***Podosphaera xanthii*** (Castagne) U. Braun & N. Shishkoff, in Braun & Takamatsu, Schlechtendalia 4: 31 (2000)

≡ *Erysiphe xanthii* Castagne, Cat. pl. Mars.: 181 (1849).
≡ *Sphaerotheca xanthii* (Castagne) L. Junell, Svensk Bot. Tidskr. 60(3): 382 (1966).
= *Erysiphe fuscata* Berk. & M.A. Curtis, Grevillea 5: 159 (1876).
≡ *Sphaerotheca fuscata* (Berk. & M.A. Curtis) Serbinow, Bot. Zap. 18: 72 (1891).
= *Sphaerotheca microcarpa* Hazsl., Mat. Természettud. Közlem. 15: 20 (1878).
= *Meliolopsis calendulae* Malb. & Roum., in Roum., Fungi gall. exs., Cent. XXXVII, No. 3658, Toulouse 1886.
≡ *Sphaerotheca calendulae* (Malbr. & Roum.) Malbr., Bull. Soc. Mycol. France 4: 32 (1888).
≡ *Albigo calendulae* (Malbr. & Roum.) Kuntze, Rev. gen. pl. III: 442 (1892).
= *Sphaerotheca verbenae* Săvul. & Negru, Bul. Sti. Acad. Republ. Populare Române V, 3: 415 (1953).
= *Sphaerotheca indica* Patw., Mycopathol. Mycol. Appl. 23: 129 (1964).
= *Sphaerothca cucurbitae* (Jacz.) Z.Y. Zhao, Acta Microbiol. Sinica 19(2): 148 (1979), nom. inval.

Circumglobal, on hosts of numerous host genera of the Asteraceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Scrophulariaceae, Solanaceae, Verbenaceae and probably of many other families.

Notes: The *P. xanthii* isolates examined were heterothallic (SHISHKOFF 1999). BRAUN (1987) reduced *Sphaerotheca codonopsis* (Golovin) Z.Y. Zhao and *S. catalpae* Wang ex Z.Y. Zhao to synonymy with *S. fusca* s.lat. Type material of the two species has to be re-examined, above all the structure of the oculi of the asci, to find the correct taxonomic position of these taxa.
The host ranges of *P. fusca* and *P. xanthii* overlap each other strongly. Both species occur on hosts of the Asteraceae, Lamiaceae, Scrophulariaceae, Solanaceae and Verbenaceae and have many common host genera or even host species, e.g., *Doronicum, Senecio, Scrophularia* and *Solanum*.

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**Key to the species of the *Podosphaera* (*Sphaerotheca*) *fuliginea* / *P. fusca* complex treated in the present paper**

1 Peridial cells relatively small, 8-30 µm diam., mostly 15-25 µm; on *Clerodendrum* spp. or *Veronicastrum* spp. ..... 2
1* Peridial cells larger, 10-50 µm diam., mostly 20-40 µm; on other hosts ..... 3
2 Ascospores large, 19-25 µm long, average > 20 µm; on *Veronicastrum* spp. ..... *P. sibirica*
2* Ascospores smaller, 14-22.5 µm long, average < 20 µm; on *Clerodendrum* spp. ..... *P. intermedia*
3 Thin-walled apical portion of the asci (oculus) small, 8-15 µm diam., average 12 µm ..... 4
3* Oculus large, 15-30 µm diam., average 20 µm; on a wide range of hosts ..... *P. xanthii* emend.
3** Oculus medium, 10-20 µm diam., average 15 µm; ascomata large, 65-100 µm diam., average 90 µm; on *Impatiens* spp. ..... *P. balsaminae*
4 Ascomata small, 55-90 µm diam., average < 85 µm ..... 5
4* Ascomata larger, 75-100 µm diam., average 85 µm or larger; on *Dicliptera* spp. or *Fatoua* spp. ..... 7
5 Length/width ratio of conidia 1.5-1.9; on many hosts of the Asteraceae, Lamiaceae, Scrophulariaceae, Solanaceae, Verbenaceae ..... *P. fusca* emend.
5* Length/width ration of conidia 1.9-2.1; on *Astragalus* or *Veronica* ..... 6
6 Ascospores ripening early, length/width ratio > 1.5; on *Veronica* ..... *P. fuliginea*
6* Ascospores ripening later, length/width ratio < 1.5; on *Astragalus* ..... *P. astragali*
7 Ascoma appendages very long, usually 1-6 times as long as the ascomatal diam.; on *Dicliptera* spp. ..... *P. diclipterae*
7* Ascoma appendages shorter, 0.5-2 times as long as the ascomatal diam.; on *Fatoua* spp. ..... *P. pseudofusca*

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