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Podosphaera lini (Ascomycota, Erysiphales) revisited and reunited with *Oidium lini*

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Abstract

Podosphaera lini (Erysiphaceae) has recently been detected on linseed, *Linum usitatissimum* var. *crepitans*, in England and represents the first unequivocal record of this powdery mildew species from Great Britain. The history of powdery mildew on linseed/flax in the UK is critically discussed. DNA sequence data (ITS + 28S rDNA) have been retrieved, from the British material and a specimen from Germany, to be used for phylogenetic analyses. The position of *P. lini* as a species of its own in the genus *Podosphaera*, close to *P. macularis* (hop powdery mildew), was confirmed in the ITS-based phylogeny. The phylogenetic results, in concordance with the morphological traits of the flax powdery mildew (small peridial cells of the chasmothecia), place this species in *Podosphaera* sect. *Sphaerotheca* subsect. *Sphaerotheca*. *Oidium lini*, described from Croatia by Škorič in 1926, was later erroneously reduced to a synonymy with *Golovinomyces orontii*. *Oidium lini* has been reassessed and is now regarded as a synonym of *Podosphaera lini*. *Oidium lini*, cited in the literature as a name published by Bondartsev in 1913, is critically discussed and reviewed. The name *O. lini* was most likely never validly introduced and is doubtful.

Key words – powdery mildew – *Linum* – phylogeny – taxonomy – *Oidium*

Introduction

The history of powdery mildew on flax in Europe dates back a long time and is ambiguous. Škorič (1926) described *Oidium lini* on flax, *Linum usitatissimum*, in Croatia. Salmon & Ware (1928) found an identical fungus on flax in a greenhouse of Cambridge University, England. The asexual morph of this species, with conidia maturing in chains and fibrosin bodies, is now referred to as the *Fibroidium* morph of *Podosphaera lini* fide Braun & Cook (2012: 97). Jaczewski (1927: 218) had reduced *Oidium lini* Škorič to synonymy with *Erysiphe cichoracearum* DC., together with "*Oidium lini* Bondartsev". The synonymy of *E. cichoracearum* and *O. lini* appears incorrect, because *E. cichoracearum* has a *Euoidium* asexual morph, fide Braun & Cook (2012: 294) that has conidia maturing in chains without fibrosin bodies. Furthermore, a valid introduction of

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Bondartsev's name could not be traced (Jaczewski's, l.c., reference to "Bolezni Rastenii 1913: 326" has been proved wrong, see Discussion). Soon after Škorič (l.c.) described *O. lini*, the first record of a powdery mildew on flax in Britain was made by Salmon & Ware (1928) on the stems and leaves of seedlings of flax in a greenhouse at Cambridge University. Homma (1928) then reported *O. lini* Škorič as well as *Erysiphe polygoni* (with a *Pseudoidium* asexual morph) on flax in Japan. Hammarlund (1945) showed that flax belongs in the host range of *Erysiphe polyphaga* Hammarl. (= *Golovinomyces orontii* (Castagne) Heluta s. lat.), a polyphagous powdery mildew with a *Euoidium* asexual morph, and this was supported by other authors, including Allison (1934) and Stone (1962). Blumer (1967: 303) discussed the putative identity of the *Linum* powdery mildew and used the name "*Oidium lini* Bonartsev" (*O. lini* Škorič was not cited), but he regarded *O. lini* as possible synonym of *E. polyphaga*. Zvetkov (1970) found the sexual morph of a *Sphaerotheca* species on flax in Russia and described it as *Sphaerotheca lini*. Zhao (1979) collected this species in Xinjian, China, and published a drawing of conidiophores, conidia and a chasmothecium. The name *S. lini* was later reallocated to *Podosphaera* (Braun & Takamatsu 2000). Takamatsu et al. (2010) included the first sequence retrieved from *P. lini* collected in Switzerland in a comprehensive molecular analysis of *Podosphaera* species on rosaceous hosts, however, the authors did not include any detailed discussion of the flax powdery mildew. Schmidt & Scholler (2012) examined conidiophores and conidia of *P. lini* collected in Germany and provided a detailed description and illustration, including the peculiarities of the conidial germination. Braun & Cook (2012) continued to follow Jaczewski's (1927) and Blumer's (1967) treatment of "*Oidium lini* Bondartsev" by treating *O. lini* Škorič as part of the *Erysiphe cichoracearum* (sensu latissimo) complex. The authors reduced these names to synonymy with *Golovinomyces orontii*, although these taxa were already regarded as synonyms of *P. lini* by Sałata (1985). In 2018, the asexual morph of a powdery mildew was found on *Linum usitatissimum* var. *crepitans* (linseed) in Great Britain. This powdery mildew was identified as *P. lini* by Preston & Cook (2019). The authors discussed why the first record of *O. lini* Škorič on linseed in Britain in 1927 had not been officially recognized as belonging to *P. lini*. In order to confirm the identity of the collection from UK and to clarify the phylogenetic affinity of *P. lini*, molecular sequence analyses have been carried out and supplemented by an analysis of a sequence retrieved from a German specimen.

Materials & Methods

The finding in the field

On 12 July 2018, an inconspicuous powdery mildew was collected growing on linseed, *Linum usitatissimum* var. *crepitans*, in the Cambridge University Botanic Garden. The specimen was suspected to be the asexual morph of *Podosphaera lini*. Microscopic examinations of the sample were conducted to confirm the identity of the powdery mildew. At this time the flax plants had finished flowering and the felt of fungal mycelium on their leaves was quite old and brownish but some conidiophores bearing catenescent conidia with fibrosin bodies could be discerned. By 16 September these plants were dead, but a new generation of young infected plants appeared with abundant fresh conidiophores. These were suitable for use in the morphological study as well as the DNA extraction, ITS sequencing and the phylogenetic study. Following the morphological and phylogenetic analyses the finding was placed in the correct historic and taxonomic perspective.

Additional samples were collected on 24 October, but were heavily parasitized by the hyperparasitic fungus *Ampelomyces quisqualis* which is common on *Podosphaera* and other powdery mildew species in Cambridgeshire. At no stage were chasmothecia detected. The plants grew in the Systematic Beds with *L. grandiflorum* and *L. perenne* subsp. *anglicum*. Neither species showed any sign of powdery mildew, even though other nearby plant species supported *Golovinomyces orontii* and other powdery mildews.

Morphological studies

For the microscopic examination, a modified method of Shin & La (1993) was used involving

stripping mycelium bearing conidiophores from three leaves with 19 mm wide 'crystal clear' adhesive transparent tape. The tape was mounted with the adhesive surface uppermost on a slide with concentrated lactic acid, covered with a cover slip and heated gently (crystal clear tape, supplied by Pritt or Staples, was not deformed or discoloured by this process). The examination was done with a compound microscope at × 60 magnification and photomicrographs were taken with a hand-held camera (Panasonic model no. DMC–L56 with Lumex Optical Image Stabilizer). From the three leaves, a total of 20 conidia and 13 conidiophores were measured. There were no obvious differences between upper and lower leaf surfaces and no significant differences (P = 0.05) amongst the separate leaves.

Molecular phylogeny

Sequences of the rDNA ITS (including 5.8S rDNA) and D1/D2 domains of the 28S rDNA were retrieved as described in Götz et al. (2018). New sequences obtained in this study were deposited in GenBank under the accession numbers MK749431 and MK749432. These sequences were combined with the sequences of *Podosphaera* species (Table 1) used in Takamatsu et al. (2010). These sequences were aligned using MUSCLE (Edgar 2004), implemented in MEGA7 (Kumar et al. 2016) and manually refined. This alignment was deposited in TreeBASE (http://www.treebase.org/) under the accession number S24154. Phylogenetic trees were obtained from the data by the maximum parsimony (MP) and maximum likelihood (ML) methods according to the procedures described in Braun et al. (2019).

Table 1 Sequences downloaded from GenBank (in alphabetical order) used in this study

Species	**Host**	**Sources**	**GenBank Accession No.**	**References**
Fibroidium diosteae	*Diostea juncea*	MUMH 2498	AB525944	Takamatsu et al. 2010
Fibroidium diosteae	*Diostea juncea*	MUMH 4938	AB525946	Takamatsu et al. 2010
Podosphaera amelanchieris	*Amelanchier laevis*	MUMH 4968	AB525927	Takamatsu et al. 2010
Podosphaera aphanis	*Fragaria chiloensis*	MUMH 1871	AB525933	Takamatsu et al. 2010
Podosphaera aphanis	*Fragaria* × *ananassa*	VPRI 19031	AF073355	Cunnington et al. 2003
Podosphaera caricicola	*Carica papaya*	MUMH 1853	AB525918	Takamatsu et al. 2010
Podosphaera cerasi	*Prunus avium*	UC1512302	AF011316	Saenz & Taylor 1999
Podosphaera cercidiphylli	*Cercidiphyllum japonicum*	MUMH s67	AB026140	Takamatsu et al. 2000
Podosphaera clandestina	*Crataegus monogyna*	MUMH 2429	AB525930	Takamatsu et al. 2010
Podosphaera clandestina	*Crataegus oxyacantha*	MUMH 1869	AB525931	Takamatsu et al. 2010
Podosphaera curvispora	*Aria alnifolia*	MUMH 3266	AB525928	Takamatsu et al. 2010
Podosphaera epilobii	*Epilobium ciliatum*	MUMH 1873	AB525926	Takamatsu et al. 2010
Podosphaera ferruginea	*Sanguisorba officinalis*	MUMH 469	AB027232	Takamatsu et al. 2000
Podosphaera filipendulae	*Filipendula purpurea*	TPU 1842	AB022385	Mori et al. 2000
Podosphaera fugax	*Geranium nepalense*	MUMH 343	AB026134	Takamatsu et al. 2000

Table 1 Continued.

Species	Host	Sources	GenBank Accession No.	References
Podosphaera japonica	*Stephanandra incisa*	MUMH 831	AB525943	Takamatsu et al. 2010
Podosphaera leucotricha	*Malus domestica*	VPRI 17729	AF073353	Cunnington et al. 2003
Podosphaera macularis	*Humulus lupulus*	MUMH 2926	AB525917	Takamatsu et al. 2010
Podosphaera minor	*Spiraea nipponica*	MUMH 269	AB026137	Takamatsu et al. 2000
Podosphaera minor	*Spiraea japonica*	MUMH 327	AB026150	Takamatsu et al. 2000
Podosphaera minor	*Spiraea japonica*	MUMH 2535	AB525941	Takamatsu et al. 2010
Podosphaera negeri	*Escallonia rubra*	MUMH 1478	AB525919	Takamatsu et al. 2010
Podosphaera negeri	*Escallonia virgata*	MUMH 2515	AB525921	Takamatsu et al. 2010
Podosphaera pannosa	*Rosa rubiginosa*	MUMH 1476	AB525937	Takamatsu et al. 2010
Podosphaera pannosa	*Rosa maltiflora*	MUMH 819	AB525939	Takamatsu et al. 2010
Podosphaera prunicola	*Prunus laurocerasus*	UC1512310	AF011317	Saenz & Taylor 1999
Podosphaera sp.	*Agrimonia pilosa*	MUMH 49	AB026141	Takamatsu et al. 2000
Podosphaera sp.	*Pyracantha* aff. *crenatoserrata*	MUMH 2450	AB525935	Takamatsu et al. 2010
Podosphaera sp.	*Pyracantha crenulata*	MUMH 1870	AB525936	Takamatsu et al. 2010
Podosphaera sp.	*Stachyurus praecox*	MUMH 830	AB525942	Takamatsu et al. 2010
Podosphaera spiraeae	*Aruncus dioidus*	MUMH s63	AB026152	Takamatsu et al. 2000
Podosphaera spiraeae	*Spiraea cantoniensis*	MUMH s60	AB026143	Takamatsu et al. 2000
Podosphaera spiraeae	*Spiraea japonica*	TPU 1752	AB026149	Takamatsu et al. 2000
Podosphaera spiraeae	*Spiraea thunbergii*	TPU 1877	AB026153	Takamatsu et al. 2000
Podosphaera spiraeae	*Spiraea cantoniensis*	MUMH 2490	AB525940	Takamatsu et al. 2010
Podosphaera violae	*Viola maculata*	BCRU 04343	AB525947	Takamatsu et al. 2010

Results

Phylogenetic analyses

About 1240 bp long sequences spanning the end of 18S rDNA, ITS1-5.8S rDNA-ITS2, and 28S rDNA D1/D2 domains were obtained from two specimens collected in Germany and UK. These sequences were aligned with 37 ITS sequences retrieved from GenBank (Table 1). The ITS sequence alignment matrix consisted of 39 sequences and 479 characters, of which 90 characters (18.8%) were variable and 60 (12.5%) were informative for parsimony analysis. *Podosphaera curvispora* Y. Nomura and *P. leucotricha* (Ellis & Everh.) E.S. Salmon were used as the outgroup

species in accordance with Takamatsu et al. (2010). A total of 220 equally parsimonious trees with 159 steps were constructed by the MP analysis. Tree topologies were almost consistent among the trees, except for branching orders of the terminal branches and branch lengths. One of the trees with the maximum likelihood value is shown in Fig. 1. The ML tree topology was almost identical to the MP tree and only bootstrap supports were shown in the MP tree. The two ITS sequences determined in this study were identical to a sequence of *P. lini* (AB525925) from a specimen collected in Switzerland. These three sequences grouped in a clade with strong bootstrap support (MP = 98%, ML = 100%). A clade comprising *P. filipendulae* (Z.Y. Zhao) T.Z. Liu & U. Braun (AB022385), *P. ferruginea* (Schltdl.: Fr.) U. Braun & S. Takam. (AB027232), *P. macularis* (Wallr.: Fr.) U. Braun & S. Takam. (AB525917), and *Podosphaera* sp. on *Agrimonia pilosa* (AB026141) was a sister to the *P. lini* clade with 80% (MP) and 92% (ML) bootstrap supports. A phylogenetic analysis using 28S rDNA D1/D2 sequences generated a tree similar to the ITS trees (tree not shown).

Taxonomy and morphology

Characteristics and measurements made on the British material were almost identical to those given for the holotype. However, some additional characteristics and mean values for the British material are given in square brackets.

Podosphaera lini (Zvetkov) U. Braun & S. Takam., Schlechtendalia 4: 30, 2000 Figs 2–3

≡ *Sphaerotheca lini* Zvetkov, Mikol. Fitopatol. 4(5): 484, 1970.

= *Oidium lini* Škorič, Glasn. Šumske Pokuse 1: 108, 1926.

≡ *Acrosporium lini* (Škorič) Subram., Hyphomycetes (New Delhi): 837, 1971.

Illustrations: Zhao (1979: 37, fig. 13), Sałata (1985: 14, fig. 4A), Braun (1987: 121, pl. 17, fig. D, 1995: 257, pl. 13, fig. A), Paulech (1995: 68, fig. 21), Schmidt & Scholler (2012: 62–63, fig. 10–11), Braun & Cook (2012: 146, fig. 94).

Literature: Zhao (1979: 36), Sałata (1985: 58), Braun (1987: 121, 1995: 71), Fakirova (1991: 126), Paulech (1995: 68), Schmidt & Scholler (2012: 61), Braun & Cook (2012: 146).

Mycelium on leaves (amphigenous), stems and inflorescences, at first thin, effuse, later often forming dense patches or a complete covering, primary mycelium delicate, secondary mycelium persistent, white, later turning yellowish or brownish, forming a dense felt, persistent hyphae flexuous, but not geniculate, walls thin, later becoming moderately thick, smooth to rough, sparingly septate and branched, cells 60–85 µm long and (2.5–)3–8(–12) µm wide [$\bar{x}$ 69 × 7.6 µm]; hyphal appressoria rare [to numerous], nipple-shaped or with slightly crenulate margin; conidiophores straight to curved, 75–210 µm long and 8.5–13.5 µm wide [$\bar{x}$ 134 × 11 µm, mostly curved, rarely straight, arising laterally from one end of the subtending hyphal mother cell, occasionally arising from its top surface], foot-cells 25–135 µm long [$\bar{x}$ 46 × 10 µm], cylindrical, sometimes somewhat swollen at the base or occasionally widening apically, straight to slightly curved, followed by 1–3 shorter cells, forming catenescent conidia [3–6 per chain, not very swollen]; conidia cylindrical, subcylindrical, almost ellipsoid (20–)25–35(–39) × (9–)12–16(–18.5) µm (range of fresh and dried conidia), [$\bar{x}$ 33.5 × 12.4 µm], length/width ratio 1.7–4.2 [$\bar{x}$ 2.7], hila 7.4–14.8 µm diam., germ tubes perihilar, occasionally lateral, 10–40 × 5–8.5 µm, slightly constricted at the base, with a tendency to become forked, about 50% with septum. Chasmothecia gregarious, immersed in mycelial patches or layers, 80–125 µm diam.; peridium cells irregularly shaped, 8–30 µm diam.; appendages in the lower half, not very numerous and relatively short, simple, distinction between hyphae and appendages difficult, 5–9 µm wide, hyaline, later pigmented, sparingly septate, walls thin, smooth to rough; ascus broad ellipsoid-ovoid, very thin-walled, rapidly swelling in water, 70–110 × 50–70 µm, sessile, 6–8-spored; shape and size of the ascospores variable, oblong, ellipsoid-ovoid to subglobose, 15–25 × 9–16 µm, colorless, sometimes poorly developed.

Holotype – Russia, Novgorod Oblast, Novgorod Rayon, Borki, on *Linum usitatissimum* (= *L. indehiscens* var. *elongatum*), 21 Aug. 1969, S. Zvetkov (LE 43185).

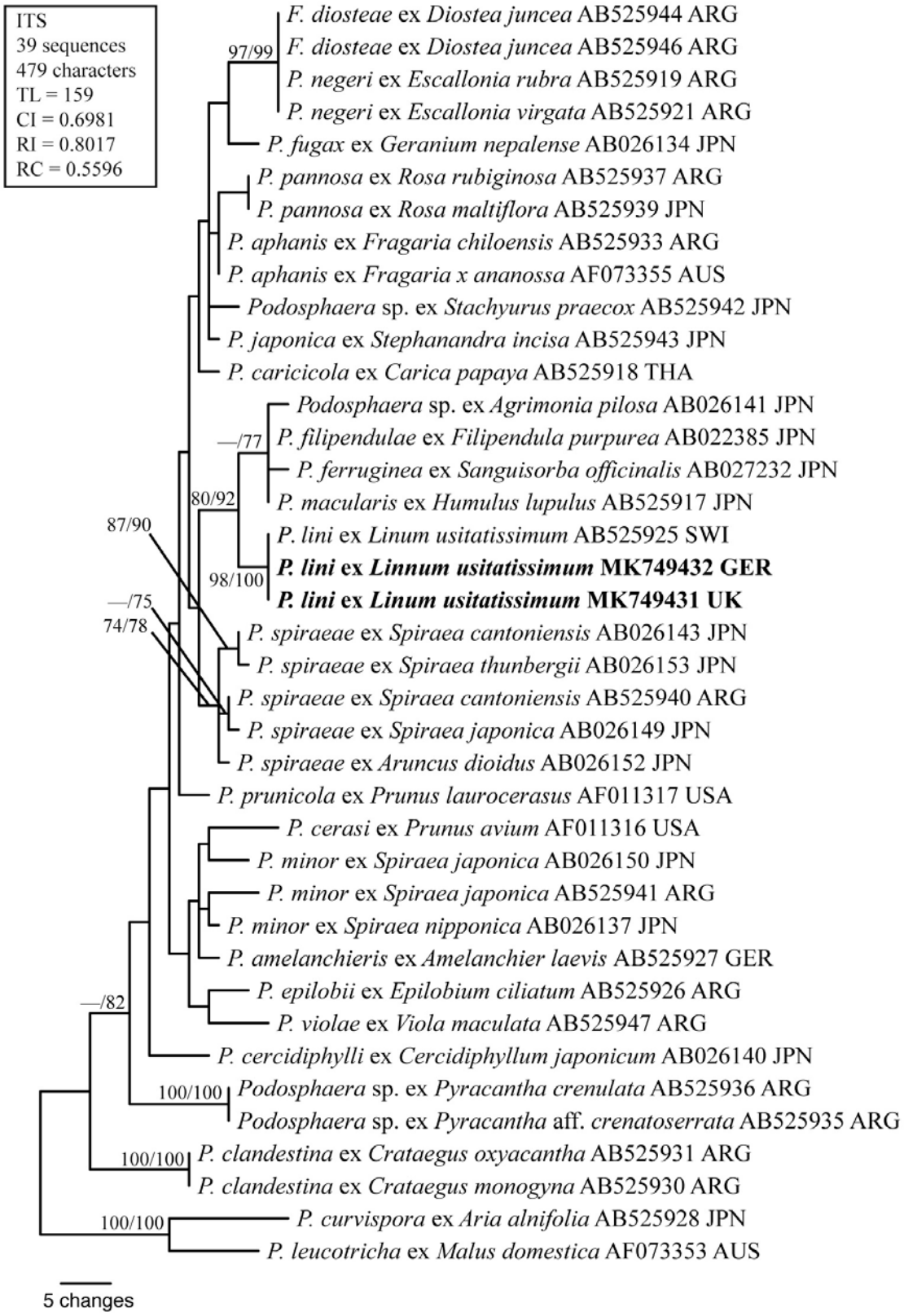

Fig. 1 – Phylogenetic analysis of the rDNA ITS regions for 39 sequences from clade 2 of *Podosphaera* (according to Takamatsu et al. 2010). This tree is a phylogram of the maximum likelihood tree of the 220 equally parsimonious trees with 159 steps, which was found using a heuristic search with TBR branch swapping. Horizontal branch lengths are proportional to the number of substitutions that were inferred to have occurred along a particular branch of the tree. BS (> 70%) values by the maximum parsimony (MP) and maximum likelihood (ML) methods are shown on/under the respective branch. Sequences determined in this study are highlighted in boldface. *F.* = *Fibroidium*; *P.* = *Podosphaera.*

Fig. 2 – Powdery mildew caused by *Podosphaera lini* on *Linum usitassimum* var. *crepitans* (linseed) in July 2018, UK, Cambridge. A Overall view. B Close-up of infected leaf and non-infected fruit. This picture is copyright of C.D. Preston.

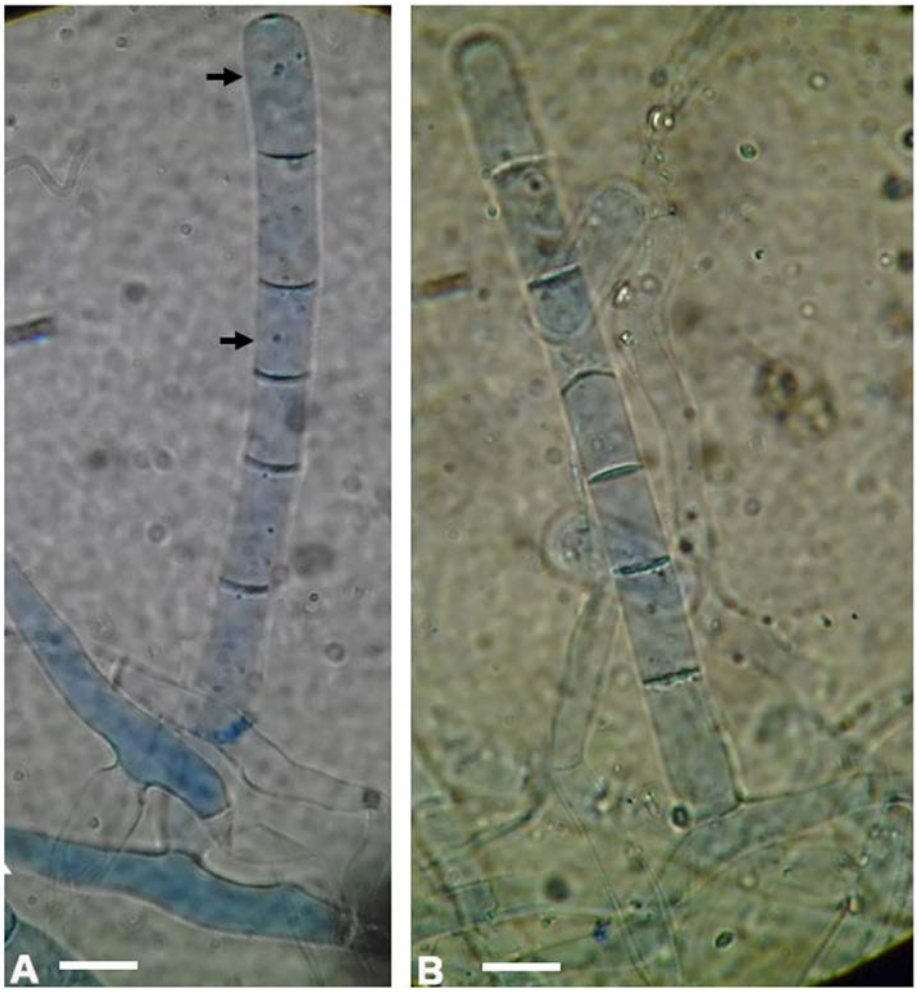

Fig. 3 – Conidiophores of *Podosphaera lini* ex linseed, CGE 1093. A Somewhat curved structure. B Straight structure. Black arrows indicate fibrosin bodies. Bars = 10 µm. This picture is copyright of R.T.A. Cook.

Additional material examined: Germany, Schleswig-Holstein, Lübeck, Kannenbruch/ Krummesser Heide, border of Heidteich, 2229/2, on *Linum usitatissimum*, 30 Aug. 2008, A. Schmidt (KR 0002832). UK, Cambridge, Cambridge University Botanic Garden, on *Linum usitatissimum*, var. *crepitans*, 16 Sep. 2018, C.D. Preston (CGE 1093, HAL 3309 F).

Host range and distribution: on *Linum* spp., Linaceae; *L. catharticum*, Europe [Poland (Mułenko et al. 2008), Slovakia (Paulech 1995)]; *L. usitatissimum*, Asia [China (Zhao 1979, Amano 1986)], Europe [Bulgaria (Fakirova 1991, Braun 1995), Germany (Brandenburger & Hagedorn 2006, Schmidt & Scholler 2012), Poland (Sałata 1985, Braun 1995, Mułenko et al. 2008), Russia (Zvetkov 1970, Braun 1995), Slovakia (Paulech 1995), Switzerland (Takamatsu et al. 2010), UK (Preston & Cook 2019)].

Discussion

In the summer of 2018 a powdery mildew on flax in England (Cambridge) was morphologically identified as *Podosphaera lini.* The presence of fibrosin bodies in the catenescent conidia of the collection from Cambridge proved that it was a *Fibroidium* morph of *Podosphaera* rather than a *Euodium* of *Golovinomyces*. The comparatively unswollen immature conidia, the narrow, cylindrical shape of the mature conidia, and the high L/W ratio were all sufficient evidence to identify the pathogen as *Podosphaera lini.* This was the first unequivocal record of *P. lini* from the UK. The first record on flax from the UK referred to *Oidium lini* Škorič (Salmon & Ware 1928, Moore 1959). Škorič (1926) in the original (Croatian) description of the fungus had described catenate conidia (2–3 per chain), 26–41 × 12–15 µm, with fibrosin bodies and stated 'according to all characteristics *Oidium lini* sp. nov. belongs to one of the *Sphaerotheca* species'. The absence of the sexual morph deterred the author from unequivocally placing the pathogen in this holomorph genus and the author's approach was upheld by Homma (1928: 333). Such inhibition to name a holomorph was common at the time and continued until the late 20th century when the asexual morph was proved to be as important as or more important than the sexual morph, as witnessed by the scanning electron microscope studies of Cook et al. (1997). Hence, linseed powdery mildew in Britain was reported as *Oidium lini* by Mercer et al. (1994). The authors Gladders et al. (1999) and Perryman & Fitt (2000) referred to the powdery mildew as *Sphaerotheca lini* (now *Podosphaera lini*) which followed in line with the finding of the sexual morph in Russia by Zvetkov (1970). This was despite *O. lini* being erroneously reduced to synonym with *Erysiphe cichoracearum* f. *lini* Jacz. by Jaczewski (1927). The synonymy referred to the plurivorous powdery mildew species *Golovinomyces orontii* s. lat. It remained as this species until the present day (Amano 1986, Ing 1990, Braun & Cook 2012). The species was also reported as such on flax (old records often under *Erysiphe cichoracearum* sensu latissimo) from various countries, including Asia (India; Iraq; Israel; Kazakhstan; Russia, Siberia; Saudi Arabia; Uzbekistan), Caucasus (Armenia, Georgia), Europe (Estonia, Germany, Italy, Norway, Romania, Russia, Sweden, Switzerland, UK, Ukraine, former Yugoslavia), and North America (USA) [Amano (1986), Geluta (1989), Simonyan (1994), Braun (1995), Sharma & Khare (1995), Brandenburger & Hagedorn (2006), Voytyuk et al. (2009), Jage et al. (2010)]. However, *G. orontii* s. lat. has recently been revised on the basis of phylogenetic analyses and morphological reassessments and split into three closely allied species and a new distantly related species on *Vinca* (Braun et al. 2019). *Golovinomyces* on flax was not included in these analyses and so the true affinity of *Golovinomyces* on *Linum* spp. is still unclear and in need of phylogenetic clarification.

Takamatsu et al. (2010) included a single ITS rDNA sequence retrieved from a collection on *Linum usitatissimum* in Switzerland in a broad-based phylogenetic analysis of *Podosphaera* spp. on rosaceous hosts, but without any discussion. In order to substantiate the phylogenetic position and relationship of *P. lini*, the British collection and the German sample described and illustrated in Schmidt & Scholler (2012), have been used here to generate additional ITS sequences. The *P. lini* sequences from Germany, UK and Switzerland form a small well supported clade close to sequences obtained from various other *Podosphaera* species, including *P. macularis* (hop powdery

mildew), confirming the position of *P. lini* as a species of its own within the genus *Podosphaera* sect. *Sphaerotheca* subsect. *Sphaerotheca*.

Oidium lini, described by Škorič (1926), has become an ambiguous name. Jaczewski (1927) reduced this name to synonymy with *Erysiphe cichoracearum* f. *lini* (= *Golovinomyces orontii* s. lat.), and Blumer (1967) as well as Braun (1987, 1995) and Braun & Cook (2012) followed this interpretation, which is, undoubtedly wrong. Škorič (1926) mentioned in the original (Croatian) description: catenate conidia (2–3 per chain), 26–41 × 12–15 µm, with fibrosin bodies and stated that 'according to all characteristics *Oidium lini* sp. nov. belongs to one of the *Sphaerotheca* species' (translation provided by Professor Diminic Danko, University of Zagreb, Croatia). Type material of this species has not been traced, but based on Škorič's original description (in particular the mention of fibrosin bodies), *O. lini* can now be interpreted as the asexual (*Fibroidium*) morph of *P. lini*. The identity of the name "*Oidium lini* Bondartsev" is doubtful. It is included in the databases of fungal names (Index fungorum, MycoBank), but without an exact bibliographic reference. Jaczewski (1927: 473) cited "Bolezni Rastenii 1913, str. 326" (this citation refers to Zhurnal "Bolězni Rastenii"). The reference concerned has been checked by M. Zhurbenko (St. Petersburg, Russia): Issue 5–6 (7th year) was published in 1913, but there is no description of *O. lini* on page 326, and the entire volume does not contain any publication of Bondartsev. However, Lebedeva (1913) published a paper in this volume starting on page 326. On page 331, the name "*Oidium lini* A. Bond." is listed, but without any description (Lebedeva recorded "*O. lini*" from Voronesh guberniya [governorate]). Thus, "*O. lini* Bondartsev" is invalid according to Art. 38.1 (a) of the Code (ICN) [Jaczewski (1927: 473) noted that this species is probably identical with *Erysiphe cichoracearum* f. *lini*, suggesting that he had never seen any material, and moreover, Jaczewski (l.c.) did not validate this name, since he did not add any descriptive data [nom. nud., Art. 38.1 (a)] and also because he cited *O. lini* Škorič as a synonym [nom. illeg., superfl., Art. 52.1]. The origin of Lebedeva's (l.c.) citation of *O. lini* remains quite unclear. She possibly obtained this name from Bondartsev (in litt.). Thus, this name has to be cited as follows:

Oidium lini Bondartsev, in Lebedeva, Zhurn. "Bolěsni Rast." 5–6: 331, 1913, nom. inval [Art. 38.1 (a)].

The identity of *O. lini* Bondartsev, cited in Lebedeva (1913) and Jaczewski (1927) is quite unclear, due to the ability of several powdery mildew species to infect *Linum* spp., viz., *Erysiphe lini* Tanda [with a *Pseudoidium* morph distinct from that of Homma's (1928) '*E. polygoni*'], *Golovinomyces orontii* s. lat., *Leveillula taurica* s. lat., and *Podosphaera lini* (Braun & Cook 2012). The undifferentiated application of the name *Oidium lini* poses an additional problem for the interpretation of the distribution data of flax/linseed powdery mildews. Records of *O. lini* or *Oidium* sp. on *Linum* spp. may refer to *E. lini*, *G. orontii* s. lat. or *P. lini*. There are numerous unclear records of *O. lini* and *Oidium* sp. on *Linum* spp. from different parts of the world, including Africa (Egypt, Ethiopia, Kenya, Libya, Morocco, Tanzania), Asia (Bangladesh, China, India, Pakistan, Russia [Siberia], Taiwan, Turkey), Australia, almost throughout Europe, North America (Canada) and South America (Argentina, Brazil, Peru) [Amano 1986]. *Oidium* sp. on *Linum usitatissimum* was reported from Estonia (Karis 1987) and Ukraine (Geluta 1989). Liu (2010: 268, fig. 129) described and illustrated *Oidium* sp. on *Linum stelleroides* from China (Inner Mongolia). Many authors have specifically listed *Oidium lini* on *Linum usitatissimum*, for instance, Otani (1988) from Japan, Paul & Thakur (2006) and Sharma & Khare (1995) from India and Severoglu & Ozyigit (2012) from Turkey; Eliade (1990) on various *Linum* species, including *L. usitatissimum*, from Romania; Grigaliūnaitė (1997) on various *Linum* spp. from Lithuania, and Paulech (1995) on *Linum austriacum*, *L. catharticum* and *L. usitatissimum* from Slovakia. The clarification of the distribution and host range of flax powdery mildew in general and *Podosphaera lini* in particular requires detailed morphological examinations and analyses of sequence data worldwide.

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