Global distribution of *Erysiphe platani*: new records, teleomorph formation and re-examination of herbarium collections

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Erysiphales / Platanus / morphologie / espèces envahissantes / adaptation / Phyllactinia guttata

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doi/10.7872/crym.v35.iss2.2014.163
Abstract – A global survey of the spread of the Platanus powdery mildew, *Erysiphe platani*, has been carried out. *E. platani* teleomorph formation was recorded in countries where the fungus anamorph has been present for several years. The first findings of chasmothecia were recorded in Austria, Czech Republic, France, Italy and Slovakia. New records of *E. platani* (including the teleomorph) were found in Belgium, Croatia and Denmark. The occurrence of this fungus in Sweden and in two countries of North Africa (Algeria and Morocco) was confirmed. Descriptions of morphological features, illustrations, and worldwide distribution of *E. platani* are provided. Herbarium collections of powdery mildews on *Platanus* spp. were re-examined and revised. The occurrence of *Phyllactinia guttata* on *Platanus* is discussed and questioned.

*Erysiphales* / *Platanus* / morphology / invasive species / adaptation / *Phyllactinia guttata*

INTRODUCTION

*Erysiphe platani* (Howe) U. Braun & S. Takam., the North American powdery mildew fungus restricted to species of *Platanus*, has spread from North America across the world. The fungus has been introduced into South America, Africa, Asia, Oceania and many European countries. In Europe, the pathogen was observed for the first time in Italy (Sprenger, 1916) and now occurs in most European countries. Until the beginning of the 21st century, only the anamorph of the fungus could be formed given the environmental conditions in Europe. Since Ranković (2003) first recorded the perfect stage of this fungus in Europe (Montenegro) a stage known only from the USA up until that point, there have been several additional records on the rare occurrence of ascocarps in Europe: Hungary (Pastirčákova & Pastirčák, 2008), Switzerland (Fischer Huelin et al., 2008), Germany (Kirschner, 2011), Spain (Menéndez Valderrey, 2012), and Ukraine (Heluta et al., 2013). The first finding of the fungus in Asia (anamorph only) was most likely in Syria, as recorded by Ali (1987). The first observations of teleomorph formation of *E. platani* in the Asian part of Turkey (Anatolia), China and Japan have recently been published by Sert et al. (2004), Liang et al. (2008) and Meeboon (2013), respectively. The first author of this paper could not find the teleomorph of *E. platani* during field work in Slovakia in the first six years since the discovery of the fungus in that country in November 2004 (Pastirčákova & Pastirčák, 2006), despite the fact that the anamorph occurs every year. Since 2010, however, the fungus has formed the teleomorphic stage in Slovakia year after year. On the basis of new field collections in other countries, re-examination of herbarium specimens, and all available published data, a global survey of the teleomorph formation and occurrence of *E. platani* was carried out. The morphology of both the anamorph and teleomorph of this fungus is presented here. Another aim of this paper was to confirm occurrences in Sweden and North Africa (Algeria, Morocco and Tunisia) recorded in the distribution map (supported only by personal communication) published by Anselmi et al. (1994).

MATERIALS AND METHODS

In order to find the teleomorph of *E. platani*, symptomatic leaves and infected fruits of *Platanus* spp. were collected in the countries where the fungus was known only in its anamorphic stage (Czech Republic, France, Iran, Italy,
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Slovakia), where the fungus was not yet reported (Belgium, Croatia, Denmark), or where the findings were neither supported by herbarium specimens nor effectively published (Algeria, Canada, Georgia, Morocco, Serbia, Sweden).

In order to re-examine and confirm teleomorph formation of *Platanus* powdery mildew fungus, 55 herbarium specimens were borrowed: nine specimens from BPI (U.S. National Fungus Collections, Beltsville, Maryland, USA); two specimens from GZU (Institute for Plant Sciences, University of Graz, Graz, Austria); 11 specimens from KR (State Museum of Natural History, Karlsruhe, Germany); eight specimens from PDD (New Zealand Fungal and Plant Disease Collection, Landcare Research, Auckland, New Zealand); 22 specimens from VPRI (Victorian Department of Environment and Primary Industries, Bundoora, Victoria, Australia); and three specimens from W (Museum of Natural History, Vienna, Austria). Another two specimens from BPI labeled as *Microsphaera platani* Howe on hosts not belonging to the Platanaceae were also examined.

Fresh material was examined by means of a stereo microscope (SZ51, Olympus, Tokyo, Japan) and standard light microscope (BX51, Olympus, Tokyo, Japan). Measurements were carried out in distilled water. Lactophenol blue (Merck, Darmstadt, Germany) was used to stain and observe colourless conidia. For observation of dried herbarium materials, the lactic acid technique was used. The morphological structures of the fungus and symptoms of attacked host organs were photographically documented. Based on data from the literature as well as re-examination of herbarium collections, the geographical distribution of the fungus and its teleomorph formation was established. Distribution of the powdery mildew fungus in different countries has also been investigated by written contact with herbarium curators as well as authors of published papers in which it was not clearly indicated whether the fungus produced the teleomorph.

Voucher specimens of our new collections from Algeria, Belgium, Canada, Croatia, Czech Republic, Denmark, Georgia, Iran, Italy, Morocco, Serbia, Slovakia and Sweden are deposited at NR (Institute of Forest Ecology of Slovak Academy of Sciences, Nitra, Slovakia), and duplicates of two specimens from Algeria and Slovakia are at BPI. Collections from France are deposited in the phytopathological herbarium of ENSA El Harrach, Algiers, Algeria.

**RESULTS AND DISCUSSION**

All specimens of powdery mildew on *Platanus* spp. were found to belong to *E. platani* based on morphological examinations. The following description of the fungus is supported by measurements of both anamorphic and teleomorphic reproductive stages of the herbarium specimens and new field collections listed below. Due to measurements of our new collections, the dimensions are slightly different from the description published previously by the first two authors (Pastirčáková & Pastirčák, 2006, 2008).

*Erysiphe platani* (Howe) U. Braun & S. Takam., Schlechtendalia 4: 12. 2000 *Fig. 1*

Mycelium amphigenous, forming thin to dense white-coloured colonies. Hyphae branched, septate, hyaline, smooth, 4-8 μm wide. Hyphal appressoria lobed to multilobed, solitary or opposite in pairs. Conidiophores erect, unbranched, 90-220(-240) μm long, 1-3 septate, with straight to flexuous foot cells (arising mostly centrally from the top of the hyphal mother cell), and mature conidia borne singly. *Pseudoiodium* type. Primary conidia hyaline, ellipsoid-ovoid, with rounded apices and subtruncate bases, 28.5-43 × 14-22.5 μm. Secondary conidia ellipsoid to doliiform, with truncate ends, hyaline, 30-45(-52) × 13-22.5 μm, usually longer than primary conidia. Conidial germ tubes subterminal, sporadically terminal, moderately long, ending in a lobed appressorium. Mature chasmothecia dark brown to black, scattered, globose, 90-120(-135) μm in diameter, peridial cells irregularly polygonal. Appendages dichotomously branched (three to six times), tips distinctly recurved, 7-15 per chasmothecium, 120-345(-360) μm long, olivaceous brown at the base, paler upwards, uniseptate at the base. Asci shortly stalked, 4-6 per chasmothecium, 45-58 × 25-38 μm, containing 3-6 ascospores. Ascospores ellipsoid to ovoid, 16-26.5 × 10-17.5 μm.

**Specimens examined:**


On leaves of *Platanus* sp. – **AUSTRALIA.** Burnley, VIC, 6 May 1992, leg. et det. I.G. Pascoe (VPRI 17908a); Hawthorn, VIC, 10 Dec 1992, leg. et det. I.G. Pascoe (VPRI 18571a); Burnley, VIC, 12 Dec 1992, leg. I.G. Pascoe, det.
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On multiple fruit of achenes of *P. ×hispanica* – **SLOVAKIA.** Nitra, Akademická Street, 18 Oct 2012, leg. K. Pastirčáková (NR 5084).


**Additional specimens examined:**


**Notes:** White powdery mildew colonies and fruiting bodies are formed on both surfaces of the leaf and also on multiple fruits of achenes (Fig. 1a,b). The fungus attacks both young and mature leaves. Terminal leaves of growing shoots are stunted and distorted. The dense pubescence (many branched dendritic trichomes) normally present on the surface of young *Platanus* leaves, which disappears during maturation, tends to remain on infected leaves. The teleomorph forms in September (in North American and European countries); occasionally, immature chasmothecia can be found in late August. In Asia, the chasmothecia are mature in November. The hybrid plant *Platanus ×hispanica* is more severely and frequently affected by powdery mildew than either of its parent species *P. occidentalis* and *P. orientalis*. The hyperparasitic fungus *Ampelomyces quisqualis* Ces. was frequently observed in conidiophores and fruiting bodies of the fungus (Fig. 1 l,m).

Only the anamorph of *E. platani* was found in specimens from Georgia, Greece, Iran, Morocco, New Zealand, Poland, Slovenia, and Sweden. Although all Australian specimens from VPRI (22 specimens were examined) contained only the anamorph, Braun (1987) found an immature chasmothecia on *Platanus* leaves collected by J.A. Simpson (Australia, Parramatta, N.S.W., 24 Jan 1985, HAL 203). *Oidium obductum* Ellis & Langl. recorded from Australia in 1977 on *P. orientalis* by Threader et al. (1980) and Spencer (1997), most probably refers to the anamorph of *E. platani*.

All of the eight New Zealand specimens (from PDD), including Boesewinkel’s collections of *M. alphitoides* on *P. ×acerifolia*, contained only the *Pseudoidium* anamorph belonging to *E. platani*. Boesewinkel’s (1986: 19-20) description (long conidiophores 250-500 µm, huge conidia 75-86 × 20 µm) based on specimens PDD 49904 and 49905 does not agree with our re-examination of
these specimens; we found conidia with a maximum length of 52 µm. We observed only one extremely long conidiophore in PDD 49904. Heluta et al. (2013: 108, fig. 2c) also observed conidia quite variable in size.

Old North American specimens labeled as *Oidium obductum* (BPI 409688, 409689, 409690, 409691, W 7162) and *Oidium erysiphoides* Fr. (BPI 409564) on *Platanus* spp. contained the anamorph of *Pseudoidium* type belonging to the present species. Mature chasmothecia of *E. platani* were observed in North American specimens of *Microsphaera alni* (GZU 306255, W 1671 and 6925) and *M. platani* (BPI 605840, 605841), and also in a Swiss specimen (KR 26180). Three of the four Austrian specimens collected in early August 2010 (KR 26137, 26142, 26143) contain immature (and a few mature) chasmothecia. Teleomorph formation was confirmed in the specimens of symptomatic leaves of *P. orientalis* collected in the UBC Botanical Garden, Vancouver, Canada (immature fruiting bodies) and *P. ×hispanica* from France and Serbia.

A Romanian collection of *E. platani* (Negrean & Anastasiu, 2006) was not available for re-examination because of the ongoing reorganization of herbarium BUCM (Romanian Academy of Science, Bucharest). We have not received a response from the authors regarding whether they found chasmothecia, so the presence of the teleomorph in this country is uncertain. Dr. Natalia Karpun and Dr. Paul Beales confirmed (personal communication) that only the anamorphic stage of the fungus is present in Russia and the United Kingdom, respectively.

Conclusive evidence of the occurrence of *E. platani* in Belgium, Croatia and Denmark was confirmed by the presence of chasmothecia in our new collections. These are the first reports of this fungus and its perfect stage from these three European countries.

Based only on a personal communication, Anselmi et al. (1994: 165, fig. 3) indicated the occurrence of *M. platani* (currently *E. platani*) in the distribution map. The findings from Sweden and Northern Africa (Algeria, Morocco and Tunisia) have not yet been effectively published. Scholler et al. (2012) did not confirm if the fungus occurs in Southern Sweden. We found the anamorph of *E. platani* on several *P. ×hispanica* in the city centre of Malmö in September 2013. The fourth present author, Z. Bouznad noticed this disease on *P. ×hispanica* and *P. orientalis* in Algeria for the past 15 years, where it has caused great damage. Recently, he found the first fruiting bodies of *E. platani*, on the leaves of *P. ×hispanica* only. The sixth present author, M. El Guilli noticed powdery mildew symptoms on *P. ×hispanica* in Morocco over the past 10 years. Examination of the Moroccan collection (NR 5069) showed the *Pseudoidium* anamorph of *E. platani*. Unfortunately, we have not yet confirmed the occurrence of the fungus in Tunisia. Since the fungus is present in neighbouring countries (Algeria and Morocco), we can assume that *E. platani* also attacks the leaves of *Platanus* spp. in Tunisia. At present, it is clear that the fungus attacks plane trees in both the north and south of Africa.

Two herbarium specimens (both deposited in BPI) assigned to *M. platani* on hosts which do not belong to the family Platanaceae were also re-examined. Due to the agreeing morphology as well as the affinity of the host families, powdery mildew collections on *Acer platanoides* (Aceraceae) and on *Azalea nudiflora* (Ericaceae) have been assigned to *Erysiphe acerina* U. Braun & S. Takam. and *Erysiphe azaleae* (U. Braun) U. Braun & S. Takam., respectively. *E. acerina* differs from *E. platani* in the small chasmothecia (80-95 µm in diam.), shorter appendages (1-1.5 times as long as the chasmothecial diam.), 6-8 spores
per ascus and smaller ascospores (16-20 × 8-10 µm). *E. azaleae* has usually numerous appendages (10-40) and more asci per chasmothecium (4-10). These specimens were annotated by the first present author on July 2012 and returned to BPI. However, at the same time, Braun & Cook (2012) consider *E. acerina* to be a synonym of *Erysiphe syringae-japonicae* (U. Braun) U. Braun & S. Takam. on the basis of their morphological similarity.

The Fungal Databases of Systematic Mycology and Microbiology Laboratory, ARS, USDA (Farr & Rossman, n.d.) contain two specimens (BPI 605840, 605841) marked as *Sphaerotheca platani*. Since there is no such taxon in Index Fungorum, we asked for a loan of these specimens from BPI. We found that the folder containing the two herbarium sheets of *Microsphaera platani* was erroneously labeled as ‘*Sphaerotheca platani* Howe’. Both specimens were examined microscopically and found to be *E. platani* with mature chasmothecia. The names of these two specimens should be corrected in the USDA database.

In addition to *E. platani*, another powdery mildew species *Phyllactinia guttata* (Wallr.) Lév. (syn. *Phyllactinia corylea* (Pers.) P. Karst., *Phyllactinia suffulta* (Rebent.) Sacc.) has been reported to occur on *P. occidentalis* in the USA (Anonymous, 1960) and on *P. orientalis* in China (Teng, 1963, 1996; Chen, 2002 reported as *P. corylea*). The specimens labeled as *Phyllactinia* on *Platanus* were also borrowed for re-examination. To our surprise, the specimens of *P. corylea* (BPI 606615, 859697) collected in the USA contained only the anamorph of *Pseudoidium* type (no clavate conidia, typical for *Ovulariopsis* type, were found) and no chasmothecia. We confirmed the identity of this material as *E. platani*. The specimen BPI 859697 was also annotated by Prof. Uwe Braun on 19 Jul 2010 as *E. platani*. Therefore, we searched for the original paper reporting the American record of *Phyllactinia* on *Platanus*. The authors of older indexes of plant diseases or checklists of fungi in the United States (e.g. Anonymous, 1960; Farr et al., 1989; Horst, 2008) reported the occurrence of *P. guttata* (or its synonyms) on *P. occidentalis* in Indiana, USA. We found that this all stems from Hoffer (1914), who published a record of *P. corylea* on the leaves of ‘sycamore’ in Indiana, but without giving the Latin name of the host or description of the fungus. The common name “Sycamore” is not only widely used to refer to some North American members of the genus *Platanus*, but also to *Acer pseudoplatanus*. There are no Hoffer specimens of powdery mildews deposited at PUL (at Purdue University, West Lafayette, Indiana, USA, where G.N. Hoffer worked as Assistant Professor of Botany) or in any other collections of *Phyllactinia* on *Platanus* deposited at any of the numerous North American herbaria. We believe that the authors of older references mistakenly interpreted Hoffer’s host plant as *‘Platanus occidentalis’*. As original material was unavailable, the identity of the host plant (i.e. *A. pseudoplatanus vs. P. occidentalis*), and thus the occurrence of *Phyllactinia* on *Platanus* in the USA, could not be confirmed.

There is no mention of *Phyllactinia* on *Platanus* from China in Sylloge Fungorum Sinicum (Tai, 1979) and in Flora Fungorum Sinicum, Vol. 1, Erysiphales (Chen et al., 1987), although Teng (1963 in Chinese, and later in an English version edited by R.P. Korf in 1996) published *P. orientalis* as a host of *P. guttata* in China before these two monographs were compiled. *Platanus* is also absent as a host of *Phyllactinia* in the latest powdery mildew monograph (Braun & Cook, 2012). There are no voucher specimens of *Phyllactinia* on *Platanus* in
herbaria HMAS (Institute of Microbiology CAS, Beijing, China) and CUP (Cornell University, Ithaca, New York, USA) where Teng’s collections are deposited. Although *P. corylea* on *P. orientalis* has recently been recorded in China (Chen, 2002), we had no opportunity to examine and verify original specimens recorded by M.M. Chen or S.C. Teng. Prof. Mo-Mei Chen (currently at University of California, Berkeley; personal communication) could not confirm the existence of voucher specimens for her record. As far as we can ascertain, voucher specimens of *Phyllactinia* on *Platanus* are apparently not deposited at any Chinese herbarium. So, the Chinese record is also unclear as material was not available. We assume that the fungus was probably dislodged by wind, or possibly misidentified (like the American specimens).

Re-examination of the original herbarium specimens, new collections of powdery mildew on *Platanus* spp., and previous published data on this fungus confirm its occurrence in 44 countries on all continents of the world. Ten years have passed since the first finding (Ranković, 2003) of the teleomorph of *E. platani* outside North America. Presently, the fungus produces a teleomorph not only in North America, but also in North Africa (Algeria), Australia, Asia (China, Japan, Turkey) and in 15 European countries. Table 1 provides an up-to-date list of all countries where the fungus has been reported including information on anamorph and teleomorph formation based on data in the literature as well as the results of our examinations.

The anamorph appears to be more adaptable to new environmental conditions and this could explain why some fungal species are much more widely dispersed in their anamorphic form. According to Cooper (2013), the pattern of many powdery mildew introductions where the initial populations are represented only by the anamorphic stage, and only much later after establishment is the sexually reproducing stage encountered. In Italy, about 90 years after the first Italian finding of *E. platani* (Sprenger, 1916), the fungus has formed teleomorphic reproductive structures, which were found in Italian specimens NR 5078 and KR 25961 collected in 2007 and 2009, respectively. Menéndez Valderrey (2012) recorded the first teleomorph of the fungus in Northern Spain about 27 years after discovery of the fungus in the country in 1985 by Gallego & Honrubia (1990). The Spanish specimen (KR 26162) collected in October 2010 still contains no teleomorph. The fungus started to produce the perfect stage almost 14 years after the first finding of its anamorph in Japan (Tanda, 1999; Meeboon, 2013). Interestingly, *E. platani* (reported as *M. platani* but without the teleomorph) was found in Brunei on the north coast of the island of Borneo, in Southeast Asia (Sivapalan et al., 1999), in an area with a tropical climate (the average temperature varies between 27.7°C in May and 26.7°C in December, and high humidity above 80%). So far the teleomorph has not been found in that country.

Favourable climate conditions allow the growth of *E. platani* and the development of both of its reproductive stages. Rapid spread and the ability to adapt to new conditions will enable this powdery mildew species to produce the teleomorph in other countries where the fungus presently only occurs in its anamorphic stage. Based on the phylogenetic analyses of *É. platani* collections from different geographic areas, Scholler et al. (2012) suggest that differences between European and extra-European materials indicate a considerable rate of mutation of this powdery mildew species.
Table 1. Global occurrence of asexual (anamorph) and sexual (teleomorph) reproductive stages of *Erysiphe platani* on *Platanus* spp.

<table>
<thead>
<tr>
<th>Geographic region</th>
<th>Reproductive stages</th>
<th>References</th>
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<tbody>
<tr>
<td><strong>Anamorph</strong></td>
<td><strong>Teleomorph</strong></td>
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<tr>
<td><strong>North America</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canada</td>
<td>+</td>
<td>Braun (1987), this paper</td>
</tr>
<tr>
<td>USA</td>
<td>+</td>
<td>Glawe (2003)</td>
</tr>
<tr>
<td><strong>South America</strong></td>
<td></td>
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<tr>
<td>Argentine</td>
<td>+</td>
<td>Braun <em>et al.</em> (2000)</td>
</tr>
<tr>
<td>Brazil</td>
<td>+</td>
<td>Inokuti <em>et al.</em> (2008)</td>
</tr>
<tr>
<td>Chile</td>
<td>+</td>
<td>Luisi &amp; San Martin (1987)</td>
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<tr>
<td><strong>Europe</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Austria, Czech Republic, Italy, Slovakia</td>
<td>+</td>
<td>Braun &amp; Cook (2012), Pastirčáková &amp; Pastirčák (2006), this paper</td>
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<tr>
<td>Bulgaria</td>
<td>+</td>
<td>Fakirova (1991)</td>
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<td>France</td>
<td>+</td>
<td>Viennot-Bourgin (1982), this paper</td>
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<td>Georgia</td>
<td>+</td>
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<tr>
<td>Germany</td>
<td>+</td>
<td>Kirschner (2011), Scholler <em>et al.</em> (2012)</td>
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<td>Greece</td>
<td>+</td>
<td>Vakalounakis &amp; Klironomou (1995)</td>
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<td>Hungary</td>
<td>+</td>
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<td>+</td>
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<td>Portugal</td>
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<td>Sequeira (1981)</td>
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<td>Gallego &amp; Honrubia (1990), Menéndez Valderrey (2012)</td>
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<td>+</td>
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<td>+</td>
<td>Fischer Huelin <em>et al.</em> (2008)</td>
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<td>Ukraine</td>
<td>+</td>
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<td>United Kingdom</td>
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<td>Jones &amp; Baker (2007)</td>
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<tr>
<td>Azerbaijan</td>
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<td>Guseinov (1992)</td>
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<tr>
<td>Brunei</td>
<td>+</td>
<td>Sivapalan <em>et al.</em> (1999)</td>
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<tr>
<td>China</td>
<td>+ +</td>
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<tr>
<td>Iran</td>
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<td>Khodaparast &amp; Abbasi (2009), Sharifi <em>et al.</em> (2013), this paper</td>
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<tr>
<td>Japan</td>
<td>+ +</td>
<td>Tanda (1999), Meeboon (2013)</td>
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<tr>
<td>Korea</td>
<td>+</td>
<td>La <em>et al.</em> (2013)</td>
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<tr>
<td>Russia</td>
<td>+</td>
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<tr>
<td>Syria</td>
<td>+</td>
<td>Ali (1987)</td>
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<tr>
<td>Turkey (Asian part)</td>
<td>+ +</td>
<td>Sert <em>et al.</em> (2004)</td>
</tr>
<tr>
<td><strong>Africa</strong></td>
<td></td>
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<tr>
<td>Algeria</td>
<td>+</td>
<td>Anselmi <em>et al.</em> (1994), this paper</td>
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<td>Morocco</td>
<td>+</td>
<td>Anselmi <em>et al.</em> (1994), this paper</td>
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<tr>
<td>Rep. of South Africa</td>
<td>+</td>
<td>Gorter &amp; Eicker (1985)</td>
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<tr>
<td>Tunisia</td>
<td>b</td>
<td>Anselmi <em>et al.</em> (1994)</td>
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<td><strong>Oceania</strong></td>
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<tr>
<td>New Zealand</td>
<td>+</td>
<td>Boesewinkel (1986)</td>
</tr>
</tbody>
</table>

*a* presence of chasmothecia is not unambiguously clear; *b* occurrence of fungus is not convincingly confirmed
CONCLUSIONS

Our collections represent the first records of *E. platani* for Belgium, Croatia and Denmark. First discoveries of its teleomorph in Austria, Czech Republic, France, Italy and Slovakia, and the occurrence of this fungus in Sweden and in two countries of North Africa – Algeria and Morocco – were confirmed. On the basis of revision of herbarium collections, doubtful reports in older references, and non-existence of voucher specimens, the occurrence of *P. guttata* on *Platanus* is questioned. All this indicates that *E. platani* is the only powdery mildew species that attacks *Platanus* spp.

Acknowledgements. The authors sincerely thank the curators of herbaria BPI, GZU, KR, PDD, VPRI and W for loans of specimens. Sincere thanks are also extended to curators of many North American and Chinese herbaria for providing information on their powdery mildew collections. We are indebted to Nana Bitsadze (Agricultural University of Georgia, Tbilisi, Georgia), Seyed Akbar Khodaparast (University of Guilan, Rasht, Iran), Dragiša Savić (National Park Fruska Gora, Serbia), Piero Braccini (ARSIA – Regione Toscana, Florence, Italy) and Eric La Fountaine (UBC Botanical Garden, Vancouver, Canada) for kindly providing material. Paul Beales (The Food and Environmental Research Agency, York, UK) and Natalia Karpun (Russian Academy of Agricultural Sciences, Sochi, Russia) are thanked for information on British and Russian records of the fungus, respectively. We also thank Philippe Clerc (Conservatoire et Jardin botaniques, Geneva, Switzerland) for the translation of the French text on the Swiss record; and Mo-Mei Chen (University of California, Berkeley, USA), Wen-Ying Zhuang (Institute of Microbiology, Chinese Academy of Sciences, Beijing, China) and Tiezhi Liu (Chifeng University, China) for providing Chinese literature and its translation. We are grateful to Scott LaGreca (Cornell University, Ithaca, USA) for kindly correcting the text. This study was supported by the Scientific Grant Agency of the Ministry of Education of the Slovak Republic and of Slovak Academy of Sciences, project VEGA 2/0071/14.

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