

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

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Résumé – Une enquête globale a été menée sur la propagation d'*Erysiphe platani* agent causal de l'oïdium du platane. Le téléomorphe d'*E. platani* a été découvert dans les pays où l'anamorphe existe déjà depuis plusieurs années. Les premières observations des chasmothèces de ce champignon ont été réalisées en Autriche, en République tchèque, en France, en Italie et en Slovaquie. Par ailleurs, la présence de l'holomorphe d'*E. platani* a été signalée en Belgique, en Croatie et au Danemark. La présence de ce champignon en Suède et dans deux pays d'Afrique du Nord (Algérie et Maroc) a été confirmée. Cette étude donne la description des caractéristiques morphologiques, ainsi que les illustrations et la distribution mondiale d'*E. platani*. En outre, les collections d'herbiers de l'oïdium de *Platanus* spp. ont été réexaminées et révisées. La présence de *Phyllactinia guttata* sur le platane est discutée.

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

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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 (Pastirčáková & 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 (Pastirčáková & 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,

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.

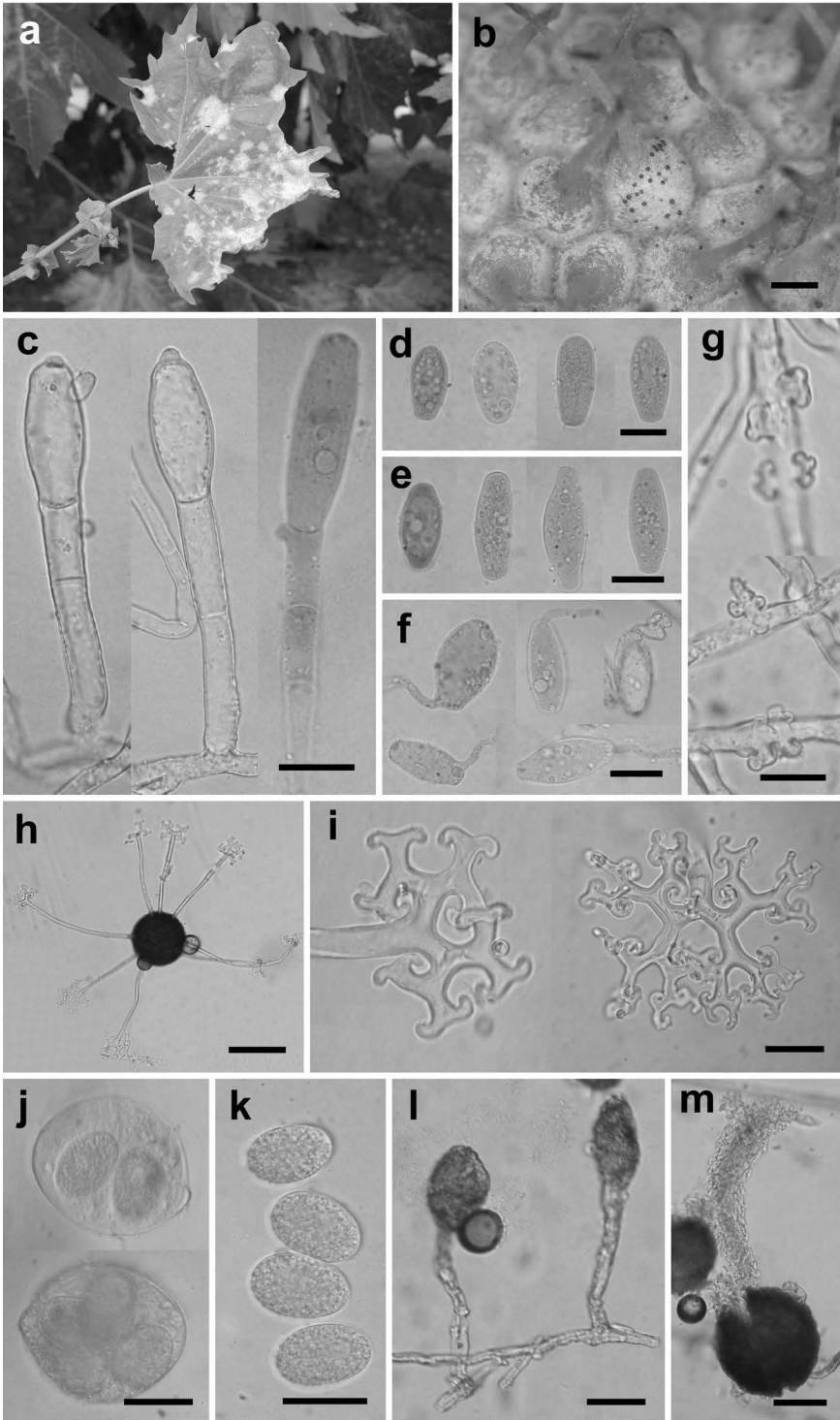
Voucher specimens of our new collections from Algeria, Belgium, Canada, Croatia, Czech Republic, Denmark, Georgia, Iran, Italy, Morocco, Serbia, Slovakia and Sweden are deposited at NR (Institute of Forest Ecology of Slovak Academy of Sciences, Nitra, Slovakia), and duplicates of two specimens from Algeria 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*

- = *Microsphaera platani* Howe, Bull. Torrey Bot. Club 5: 4. 1874.
- = *M. penicillata* f. *platani* Jacz., Karm. Opred. Grib., Vyp. 2. Muchn.-rosj. Griby (Leningrad): 359. 1927.
- = *M. alni* auct. p.p.
- = *M. alphitoides* auct. p.p.
- = *M. penicillata* auct. p.p.



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, *Pseudoidium* type. Primary conidia hyaline, ellipsoid-ovoid, with rounded apices and subtruncate bases, 28.5–43 \times 14–22.5 μm . Secondary conidia ellipsoid to doliiform, with truncate ends, hyaline, 30–45(–52) \times 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 \times 25–38 μm , containing 3–6 ascospores. Ascospores ellipsoid to ovoid, 16–26.5 \times 10–17.5 μm .

Specimens examined:

On leaves of *Platanus digitata* Gordon (synonym of *P. orientalis* var. *digitata*) – **AUSTRALIA**. Bendigo, VIC, 4 Feb 1992, leg. unknown, det. I.G. Pascoe (VPRI 17793a).

On leaves of *Platanus xhispanica* Mill. ex Münchh. (syn. *P. xacerifolia* (Aiton) Willd.) – **ALGERIA**. Ain Taya (25 km from Algiers, near the Mediterranean Sea), 12 Oct 2013, leg. et det. Z. Bouznad and A. Kedad (BPI 892891, NR 5096). – **AUSTRALIA**. Denman, NSW, 27 Nov 1992, leg. K. Allen, det. A. Sivapalan (VPRI 18531a); Castle Hill, NSW, 15 Dec 1992, leg. J.A. Simpson, det. A. Sivapalan (VPRI 18614a); Seven Hills, NSW, 15 Dec 1992, leg. J.A. Simpson, det. A. Sivapalan (VPRI 18617a); Denman, NSW, 16 Dec 1992, leg. J.A. Simpson, det. A. Sivapalan (VPRI 18629a); Perth, WA, 25 Jan 1994, leg. M. Stuart, det. A. Sivapalan (VPRI 19800a); South Perth, WA, 15 Dec 1994, leg. K. Adcock, det. A. Sivapalan (VPRI 20437a). – **AUSTRIA**. Kärnten, Spittal an der Drau, Porcia Castle Park, 3 Aug 2010, leg. et det. M. Lutz (KR 26143); Kärnten, Villach-Land, in front of Firehouse, 4 Aug 2010, leg. et det. M. Lutz (KR 26141); Kärnten, Villach, Cineplex parking lot, 7 Aug 2010, leg. et det. M. Lutz (KR 26142); Kärnten, Villach, Italiener Strasse, parking lot, 13 Aug 2010, leg. et det. M. Lutz (KR 26137). – **BELGIUM**. Ghent, Coupure Links, 10 Oct 2013, leg. M. Höfte and L. Tyvaert (NR 5095). – **CROATIA**. Zagreb, Maksimir Park, 23 Sep 2013, leg. D. Diminić (NR 5076). – **CZECH REPUBLIC**. Břeclav, Jan Palach Square and Slovácká Street, 23 Oct 2011, leg. M. Pastirčák (NR 5079, 5080); Olomouc, railway station, 31 Aug 2013, leg. M. Pastirčák (NR 5082); Přerov, Tovární Street, bus terminal, 31 Aug 2013, leg. M. Pastirčák (NR 5083). – **DENMARK**. Copenhagen, Jarmers Plads, 14 Oct 2013, leg. K. Adamčíková (NR 5085). – **FRANCE**. Marseille, Cours Belsunce, 5 Dec 2011, leg. Z. Bouznad; Bordeaux, Quai des Chartrons, 23 Dec 2013, leg. Z. Bouznad. – **GEORGIA**. Chiatura, 20 Aug 2013,

◀ Fig. 1. *Erysiphe platani*. **A**. white powdery colonies on the leaf of *Platanus xhispanica*; **B**. infected achenes; **C**. conidiophores; **D**. primary conidia; **E**. secondary conidia; **F**. germinating conidia; **G**. hyphal appressoria; **H**. chasmothecium; **I**. apices of appendages; **J**. asci with ascospores; **K**. ascospores; **L**. pycnidia of *Ampelomyces quisqualis* which has formed in place of a conidium atop the conidiophore of *E. platani*; **M**. chasmothecium parasited by *A. quisqualis*. Sources: (**A**, **C**–**M**) NR 5098; (**B**) NR 5084. Scale bars: (**B**) 1 mm, (**C**–**G**, **I**–**L**) 20 μm , (**H**) 100 μm , (**M**) 50 μm . Photo M. Pastirčák.

leg. et det. N. Bitsadze (NR 5070); Perevisa, 23 Aug 2013, leg. et det. N. Bitsadze, parasited by *Ampelomyces quisqualis* (NR 5071); Tbilisi, 28 Aug 2013, leg. et det. N. Bitsadze (NR 5072). – **ITALY**. Toscana, Firenze, 2007, leg. C. Parrini and P. Braccini (NR 5078); Latium, Viterbo, Monte Romano, Piazza Dante, 21 Nov 2009, leg. et det. M. Scholler (KR 25961). – **MOROCCO**. Kénitra, Boulevard Mohammed V, 10 Aug 2013, leg. M. El Guilli (NR 5069). – **NEW ZEALAND**. Auckland, Dec 1984, leg. et det. H.J. Boesewinkel as *Microsphaera alphitoides* (PDD 49904); Auckland, Waitakere, Mar 1985, leg. et det. H.J. Boesewinkel as *M. alphitoides* (PDD 49905); Christchurch Botanical Garden, Mid Canterbury, 9 Feb 2002, leg. et det. J.A. Cooper (PDD 80131); Christchurch, Mid Canterbury, 20 Mar 2004, leg. et det. J.A. Cooper (PDD 79781); Lincoln, Mid Canterbury, 17 Mar 2011, leg. et det. J.A. Cooper (PDD 96152). – **POLAND**. Sandomierska Basin, Krakow-Nowa Huta, near Hutnik Stadium, tree avenue, 6 Sep 2010, leg. I. Piatek and M. Piatek, det. M. Piatek, parasited by *A. quisqualis*, according to us the host plant was incorrectly identified as *P. orientalis* (KR 29490a). – **SERBIA**. Novi Sad, city, 10 Oct 2013, leg. D. Savić (NR 5077). – **SLOVAKIA**. Piešťany, Bratislavská cesta, 13 Sep 2010, leg. M. Pastirčák, parasited by *A. quisqualis* (NR 5098); Nitra, Akademická Street, 10 Oct 2010, leg. K. Pastirčáková (NR 5099); Piešťany, Adama Trajana Street, 28 Oct 2011, leg. M. Pastirčák (NR 5100); Nitra, Mikovíniho Street, 17 Oct 2013, leg. K. Pastirčáková (BPI 892892, NR 5101). – **SLOVENIA**. Ljubljana, city, Congress Square, 8 Aug 2010, leg. et det. M. Lutz (KR 26144); Ljubljana, city, parking lot near Ljubljana Castle, 8 Aug 2010, leg. et det. M. Lutz (KR 26145); Julische Alpen, Bovec, city, SE parking lot, 12 Aug 2010, leg. et det. M. Lutz (KR 26146). – **SPAIN**. Catalonia, Barcelona, Plaza de Catalunya, 6 Oct 2010, leg. U. Fischer, det. M. Lutz (KR 26162). – **SWEDEN**. Malmö, Stortorget Square, 4 Sep 2013, leg. K. Adamčíková (NR 5073, 5074). – **SWITZERLAND**. Geneve, Quai Wilson, 29 Oct 2008, leg. et det. A. Bolay (KR 26180).

On leaves of *Platanus occidentalis* L. – **USA**. Vicksburg, MS, 4 Jul 1888?, leg. S.M. Tracy as *Oidium erysiphoides* (BPI 409564); Urmeyville, IN, Sep 1890, leg. et det. E.M. Fisher as *Microsphaeraalni* (W 6925); Charleston, WV, 8 Aug 1894, leg. et det. E.T. and S.A. Harper as *Oidium obductum* on *Platanus americana* (W 7162); San Paula, CA, 10 Sep 1908, leg. P.E. Smith, det. G.G. Hedgcock as *Phyllactinia corylea* (BPI 606615); Bucks County, PA, Aug 1937, leg. R.S. Kirby as *P. corylea*, rev. U. Braun as *Erysiphe platani*, 19 Jul 2010 (BPI 859697).

On leaves of *Platanus orientalis* L. – **AUSTRALIA**. Melbourne, VIC, 27 Apr 1979, leg. et det. G. Marks, parasited by *A. quisqualis* (VPRI 17630a); Farrer, ACT, 4 Jan 1993, leg. C.A. Grgurinovic, det. A. Sivapalan (VPRI 18690a); Barton, ACT, 15 Feb 1993, leg. G.A. Kile, det. A. Sivapalan (VPRI 18824a); Geelong, VIC, 12 Feb 2007, leg. I. Rogers, det. J.H. Cunningham (VPRI 40670a). – **CANADA**. British Columbia, Vancouver, UBC Botanical Garden, 14 Nov 2013, leg. E. La Fontaine (NR 5097). – **GREECE**. Samos Island, Pythagorion, Chora, 3 Aug 1984, leg. J. Poelt, det. U. Braun on 27 May 1986 as *M. platani* (GZU 306254). – **IRAN**. Rasht, Guilan, 19 Aug 2013, leg. S.A. Khodaparast (NR 5075). – **NEW ZEALAND**. Auckland, Dec 1984, leg. et det. H.J. Boesewinkel as *M. alphitoides* (PDD 49906). – **USA**. Near Gettysburg, PA, July 1935, leg. D.R. Sumstine, det. J.A. Stevenson as *O. obductum* (BPI 409691); Toledo, OH, 30 Sep 1937, leg. P.E. Tilford, det. R.W. Davidson as *O. obductum* (BPI 409690).

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, 17 Dec 1992, leg. I.G. Pascoe, det.

A. Sivapalan (VPRI 18622a); Burnley, VIC, 14 Jan 1993, 23 Feb 1993, 26 Feb 1993, 17 May 1993, leg. et det. A. Sivapalan (VPRI 18735a, 18844a, 18853a, 19222a); St. Kilda, VIC, 29 Jan 1993, leg. et det. A. Sivapalan (VPRI 18766a); Perth, WA, 27 Feb 1993, leg. E. Davison, det. A. Sivapalan (VPRI 18864a); Melbourne, VIC, 20 Feb 1998, leg. et det. J.H. Cunnington as *Microsphaera* sp. (VPRI 21733a). – **NEW ZEALAND**. Auckland City, Albert Park, 6 Mar 2005, leg. et det. C.F. Hill (PDD 82343); Auckland, Lynfield, s.d., leg. et det. C.F. Hill as *M.alni* (PDD 47071). – **USA**. Charleston, WV, 8 Aug 1894, leg. et det. E.T. and S.A. Harper as *O. obductum* (BPI 409689); Richmond, VA, 22 July 1938, leg. H.C. Riely, det. J.A. Stevenson as *O. obductum*, parasited by *A. quisqualis* (BPI 409688); Pittsburg, PA, 12 Sep 1940, leg. et det. D.R. Sumstine as *M. platani* (BPI 605840); Philadelphia, PA, 10 Oct 1940, leg. et det. D.R. Sumstine as *M. platani* (BPI 605841); Concordia, MO, s.d., leg. et det. C.H. Demetrio as *M.alni* (GZU 306255, W 1671).

On multiple fruit of achenes of *P. ×hispanica* – **SLOVAKIA**. Nitra, Akademická Street, 18 Oct 2012, leg. K. Pastirčáková (NR 5084).

On multiple fruit of achenes of *Platanus* sp. – **AUSTRALIA**. Burnley, VIC, 6 Jul 1993, leg. I.G. Pascoe, det. A. Sivapalan (VPRI 19354a). – **NEW ZEALAND**. Auckland, Lynfield, s.d., leg. et det. C.F. Hill as *M.alni* (PDD 47071).

Additional specimens examined:

On *Acer platanoides* L. – **USA**. Oregon, Clackamas Co., 16 Jun 2003, leg. et det. M. Putnam as *M. platani* (BPI 878399).

On *Azalea nudiflora* L. (synonym of *Rhododendron periclymenoides* (Michx.) Shinners) – **USA**. Pennsylvania, Delaware Co., s.d., leg. Wm. Trimble as *M. platani* (BPI 558576).

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. The identity of an Austrian record of *Sphaerotheca castagnei* Lév. (an illegitimate name; according to current taxonomy, it is a synonym of various species because of its various historical uses) on *P. occidentalis* reported by Amano (1986) is unclear, since material was not available for study.

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* L. There are no Hoffer specimens of powdery mildews deposited in 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 Sinicorum (Tai, 1979) and in Flora Fungorum Sinicorum, 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 *E. 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.

Geographic region		Reproductive stages		References
		Anamorph	Teleomorph	
North America	Canada	+	+	Braun (1987), this paper
	USA	+	+	Glawe (2003)
South America	Argentina	+		Braun <i>et al.</i> (2000)
	Brazil	+		Inokuti <i>et al.</i> (2008)
	Chile	+		Luisi & San Martin (1987)
Europe	Austria, Czech Republic, Italy, Slovakia	+	+	Braun & Cook (2012), Pastirčáková & Pastirčák (2006), this paper
	Bulgaria	+		Fakirova (1991)
	France	+	+	Viennot-Bourgin (1982), this paper
	Georgia	+		Gvritishvili (2008), this paper
	Germany	+	+	Kirschner (2011), Scholler <i>et al.</i> (2012)
	Greece	+		Vakalounakis & Klironomou (1995)
	Hungary	+	+	Pastirčáková & Pastirčák (2008)
	Montenegro	+	+	Mijušković (1993), Ranković (2003)
	Poland, Slovenia	+		Braun & Cook (2012), this paper
	Portugal	+		Sequeira (1981)
	Romania	+	<i>a</i>	Negrean & Anastasiu (2006)
	Serbia	+	+	Karaman <i>et al.</i> (2012), this paper
	Spain	+	+	Gallego & Honrubia (1990), Menéndez Valderrey (2012)
	Sweden	+		Anselmi <i>et al.</i> (1994), this paper
	Switzerland	+	+	Fischer Huelin <i>et al.</i> (2008)
	Ukraine	+	+	Heluta <i>et al.</i> (2013)
United Kingdom	+		Jones & Baker (2007)	
Belgium, Croatia, Denmark	+	+	This paper	
Asia	Azerbaijan	+		Guseinov (1992)
	Brunei	+		Sivapalan <i>et al.</i> (1999)
	China	+	+	Liang <i>et al.</i> (2008)
	Iran	+		Khodaparast & Abbasi (2009), Sharifi <i>et al.</i> (2013), this paper
	Israel	+		Halperin (1989), Voytyuk <i>et al.</i> (2009)
	Japan	+	+	Tanda (1999), Meeboon (2013)
	Korea	+		La <i>et al.</i> (2013)
	Russia	+		Karpun (2012)
	Syria	+		Ali (1987)
	Turkey (Asian part)	+	+	Sert <i>et al.</i> (2004)
Africa	Algeria	+	+	Anselmi <i>et al.</i> (1994), this paper
	Morocco	+		Anselmi <i>et al.</i> (1994), this paper
	Rep. of South Africa	+		Gorter & Eicker (1985)
	Tunisia	<i>b</i>		Anselmi <i>et al.</i> (1994)
Oceania	Australia	+	+	Braun (1987), Cunnington (2003)
	New Zealand	+		Boesewinkel (1986)

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.

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