Discovery of a cryptic species, *Erysiphe salicina* sp. nov., and reconstruction of the phylogeny of powdery mildews on *Populus* and *Salix* spp.

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**Abstract**

Recently performed phylogenetic-taxonomic analyses of species belonging to *Erysiphe* sect. *Uncinula* on willows (*Salix* spp.) demonstrated a much higher diversity than previously assumed. Phylogenetic analyses and morphological examinations of Chinese *Erysiphe* collections on *Salix abscondita* (= *S. raddeana*), *S. sinica* and *S. taraikensis*, all belonging to *Salix* subgen. *Vetrix* sect. *Vetrix*, revealed an additional cryptic species which is described as *Erysiphe salicina*. The new species is morphologically and phylogenetically distinguished from all other powdery mildew species. The phylogeny of the new species and closely related species on *Populus* and *Salix* spp. (*Salicaceae*) was reconstructed and discussed using a combined alignment of the internal transcribed spacer (ITS) regions and partial 28S rDNA sequences. The present phylogenetic analyses suggest that the recently described *E. salicicola* (on *Salix gracilistyla* in Republic of Korea) has to be reduced to synonymy with *E. salicis-gracilistylae* comb. nov. (= *Uncinula salicis-gracilistylae*).

**Keywords** *Erysiphaceae* • *Erysiphe* • *Salicaceae* • Willows • Taxonomy • New species • New combination

**Introduction**

The genus *Salix* L. (*Salicaceae*), commonly known as willows, consists of ~450 species, mainly distributed throughout the Northern Hemisphere (Skvortsov 1999; Fang et al. 1999; Gulyaev et al. 2022). *Salix* comprises valuable ecological species that are commonly used in conservation and environmental projects for habitat restoration and erosion control (Kuzovkina and Quigley 2005; Kuzovkina and Volk 2009). Subgeneric classification of *Salix* has remained in a process of endless revision (Gulyaev et al. 2022). Chen et al. (2010) proposed an infrageneric classification of *Salix* with four subgenera: *Salix*, *Chosenia*, *Triandrae*, and *Vetrix*. Species of the genus *Salix* are diverse in China (275 spp., Fang et al. 1999). *Salix sinica* (K. S. Hao ex C. F. Fang and Skvortsov) G. Zhu is a species originally described as *S. caprea* var. *sinica* K. S. Hao (Zhu 1998). It is considered a species of its own, according to the current taxonomic
Salix spp. are commonly infected by powdery mildews almost worldwide. Four genera, six species, and two varieties of powdery mildews have been recorded parasitizing Salix spp., viz., Podosphaera schlechtendalii Lév., Phyllactinia populi (Jacz.) Y.N. Yu, Pleochaeta salicicola R.Y. Zheng and G.Q. Chen, Erysiphe adunca (Wallr.) Link var. adunca and var. salicis-gracilistylae (Homma) U. Braun and S. Takam., E. capreae DC. ex Duby, and E. pseudoregularis U. Braun (Braun and Cook 2012). The three species of Erysiphe sect. Uncinula on willows are mainly distributed in Asia (China, India, Japan, Korea, Russia [Siberia and Far East]), Europe, and North America (Braun and Cook 2012). Recently, a comprehensive morphological and phylogenetic revision of the E. adunca complex has been conducted by Darsaraei et al. (2021). They reinstated E. salicis DC. (on Salix spp. belonging to various subgenera of Salix in Asia and Europe) as a recognized species of its own, introduced the new combination Erysiphe salicis var. salicis-gracilistylae and reduced Erysiphe pseudoregularis to synonymy with E. capreae. The morphological characteristics of a powdery mildew found in China on Salix sinica, S. taraikensis, and S. abscondita turned out to be different from all recognized Erysiphe spp. on Populus and Salix spp. in terms of morphology and phylogenetic position. Furthermore, the phylogenetic position and taxonomic status of Erysiphe salicicola, recently described from the Republic of Korea on Salix gracilistyla var. melanostachys (Boonme et al. 2021), have been reassessed. Sequences retrieved from the new Chinese species and from E. salicicola have been added to the comprehensive phylogenetic analyses recently published by Darsaraei et al. (2021) in order to update the phylogeny of Erysiphe (sect. Uncinula) spp. on Salicaceae.

**Materials and methods**

**Specimens examined**

Twenty-eight specimens of Erysiphe species on Salix and Populus were collected in China and Russia. They are now deposited in the Herbarium of Mycology of Jilin Agricultural University (HMJAU). Details of these specimens are provided in Table 1.

**Morphological examinations**

Anamorphs and telemorphs of dried herbarium specimens were examined in lactic acid using a light microscope (Axio Scope A1, ZEISS, Germany). The sizes of diverse structures of the anamorphs and telemorphs were measured with at least 30 repetitions. If possible, measurements of microscopic structures were made at a magnification of ×1000, and 95% confidence intervals were determined.

**DNA extraction, PCR, and sequencing**

Whole-cell DNA was extracted by the Chelex-100 method (Hirata and Takamatsu 1996; Walsh et al. 1991) from mycelia and chasmothecia. The complete internal transcribed spacer (ITS) region (including 5.8S rDNA) and 5′-end of the 28S rDNA (including D1 and D2 domains) of the fungi were amplified by polymerase chain reaction (PCR) using the primer sets ITS5/ITS4, PM10/PM2, PM5/PM6 for the ITS region and LSU1/LSU2, PM3/TW14 and PM28F/PM28R for the partial of 28S rDNA region. The details of the primers are presented in Table 2. The reaction components were 2 μL of the total genomic DNA, 12.5 μL premixed PCR mixtures (TaKaRa, Tokyo, Japan), 1 μL of each primer (10 μM) and sterile ddH2O up to a final volume of 25 μL. The PCR reactions were conducted under the following thermal cycling conditions: an initial predenaturation step of 5 min at 95 °C, 35 cycles of 30 s at 95 °C, followed by 1 min at 56 °C for annealing, and 30 s at 72 °C for extension, and a final extension step of 8 min at 72 °C. The PCR products were subjected to electrophoresis in a 1.2% agarose gel in 0.5 × TBE buffer. The amplicons were sent to Sangon Biotech (Shanghai, China) for direct sequencing in the forward and reverse direction using the same primers as for the PCR. The accession numbers are shown in Table 1. Details of the sequences retrieved from GenBank are shown in Supplementary Table 1.

**Molecular phylogenetic analysis**

The obtained sequences, including the complete ITS and partial 28S rDNA from twenty-eight herbarium specimens, were aligned with other sequences retrieved from GenBank. Multiple sequence alignments were conducted by MUSCLE implemented in MEGA-X (Kumar et al. 2018). Alignments were further manually refined and deposited in TreeBASE (http://www.treebase.org/) under the accession number S28710. Phylogenetic trees were obtained from the data using the maximum parsimony (MP) and maximum likelihood (ML) methods. MP analysis was performed in PAUP 4.0 (Swofford 2002) with the heuristic search option using the tree bisection reconnection (TBR) algorithm with 100 random sequence additions to find the global optimum tree. All sites were treated as unordered and unweighted, with gaps treated as missing data. The strength of internal branches of the resulting trees was tested with bootstrap (BS) analysis using 1000 replications with the step-wise addition option set as simple (Felsenstein 1985). Tree scores, including tree length, consistency index (CI), retention index (RI), and rescaled consistency index (RC), were also calculated. The ML analysis was performed using raxmlGUI 2.0 (Edler et al. 2020), under a GTRGAMMA
Table 1  Information about specimens of *Erysiphe* species on *Salix* and *Populus* spp. used in this study

| Species                     | Herbarium No.          | Host Plant | Location                        | Coordinates          | Altitude(m) | Collection Date | ITS+28S rDNA Accession No. |
|-----------------------------|------------------------|------------|---------------------------------|----------------------|-------------|----------------|---------------------------|
| *Erysiphe salicina* sp. nov.| HMJAU-PM91918          | *Salix sinica* | Yichun, Heilongjiang Province, China | 130°24′38″E; 48°53′42″N | 177         | 2014/08/30 | MZ474877                  |
|                            | HMJAU-PM91919          | *S. sinica*  | Tahe, Heilongjiang Province, China | 124°41′28″E; 52°20′20″N | 384         | 2018/10/06 | MZ474891                  |
|                            | HMJAU-PM91920          | *S. taraikensis* | Heihe, Heilongjiang Province, China | 127°29′55″E; 49°57′47″N | 114         | 2014/09/17 | MZ474875                  |
|                            | HMJAU-PM91921          | *S. sinica*  | Heihe, Heilongjiang Province, China | 127°29′55″E; 49°57′47″N | 114         | 2014/09/17 | MZ474880                  |
|                            | HMJAU-PM91922          | *S. sinica*  | Jagedaqi, Heilongjiang Province, China | 124°7′29″E; 50°25′57″N | 398         | 2015/09/01 | MZ474876                  |
|                            | HMJAU-PM91923          | *S. sinica*  | Tahe, Heilongjiang Province, China | 123°31′41″E; 52′47″5″N | 776         | 2016/09/23 | MZ474883                  |
|                            | HMJAU-PM91924          | *S. sinica*  | Tahe, Heilongjiang Province, China | 125°16′41″E; 52′41′33″N | 376         | 2016/09/25 | MZ474881                  |
|                            | HMJAU-PM91925          | *S. sinica*  | Harbin, Heilongjiang Province, China | 127°23′1″E; 45′29′35″N | 374         | 2019/08/24 | MZ474882                  |
|                            | HMJAU-PM91979          | *S. taraikensis* | Heihe, Heilongjiang Province, China | 127°29′55″E; 49°57′47″N | 114         | 2014/09/17 | MZ498832                  |
|                            | HMJAU-PM91989          | *S. abscondita* | Beijing, China | 115°34′19″E; 39′50′15″N          | 1133        | 2018/10/19 | MZ598845                  |
| *E. salicis-gracilistyloae* comb. nov. | HMJAU-PM91964          | *Salix sp.*  | Harbin, Heilongjiang Province, China | 126°3′519″E; 45′47′29″N | 120        | 2019/09/14 | OL739284                  |
|                            | HMJAU-PM91965          | *S. wilhelmianna* | Changchun, Jilin Province, China | 116°29′16″E; 40′30′13″N | 216         | 2018/09/17 | OL763835                  |
|                            | HMJAU-PM91972          | *S. babylonica* | Harbin, Heilongjiang Province, China | 126°3′519″E; 45′47′29″N | 120         | 2019/09/14 | OL763833                  |
|                            | HMJAU-PM91914          | *S. ernestii* | Harbin, Heilongjiang Province, China | 127°21′51″E; 45′30′14″N | 374         | 2019/08/24 | OL763836                  |
| *E. salicis*                | HMJAU-PM91968          | *S. abscondita* | Erdao Baihe, Jilin Province, China | 128°5′46″E; 42°40′44″N | 678         | 2020/09/05 | OL770127                  |
| *E. capreae*               | HMJAU-PM91963          | *S. acutifolia* | Nizhnekadyuckhenskaya, Rostov region, Russia | 47°46′05″N; 40′5′56″E | 30          | 2018/10/06 | OL739394                  |
|                            | HMJAU-PM91973          | *S. waldichiana* | Heihe, Heilongjiang Province, China | 127°29′36″E; 49′57′28″N | 112         | 2014/09/17 | OL763832                  |
|                            | HMJAU-PM91974          | *S. waldichiana* | Heihe, Heilongjiang Province, China | 127°28′43″E; 49′57′11″N | 123         | 2017/09/01 | OL739522                  |
|                            | HMJAU-PM91975          | *S. waldichiana* | Heihe, Heilongjiang Province, China | 127°28′43″E; 49′57′11″N | 123         | 2017/09/01 | OL763834                  |
|                            | HMJAU-PM91976          | *S. eriocarpa* | Erdao Baihe, Jilin Province, China | 127°52′30″E; 42′27′29″N | 681         | 2020/09/02 | OL739580                  |
|                            | HMJAU-PM91977          | *Salix sp.* | Erdao Baihe, Jilin Province, China | 127°23′10″E; 42′27′29″N | 681         | 2020/09/02 | OL739581                  |
|                            | HMJAU-PM91986          | *S. waldichiana* | Heihe, Heilongjiang Province, China | 127°29′36″E; 49′57′28″N | 112         | 2014/09/17 | OL739609                  |
|                            | HMJAU-PM91987          | *Salix sp.* | Mohe, Heilongjiang Province, China | 122°21′58″E; 53′29′15″N | 291         | 2016/09/26 | OL739612                  |
| *E. advenca*               | HMJAU-PM91910          | *Populus × canadensis* | Shakhty, Rostov region, Russia | 47°42′16″N; 40°12′18″E | 110         | 2018/10/3 | OL744369                  |
|                            | HMJAU-PM91980          | *P. davidiana* | Erdao Baihe, Jilin Province, China | 128°4′33″E; 42°24′48″N | 668         | 2020/09/04 | OL744370                  |
| *E. mandshurica*           | HMJAU-PM91981          | *P. koreana* | Erdao Baihe, Jilin Province, China | 128°6′52″E; 42′26′12″N | 682         | 2020/09/06 | OL744371                  |
|                            | HMJAU-PM91982          | *P. koreana* | Mohe, Heilongjiang Province, China | 122°21′58″E; 53′29′15″N | 291         | 2016/09/26 | OL744376                  |
|                            | HMJAU-PM91983          | *P. adenopoda* | Shennongjia, Hubei Province, China | 110°9′12″E; 31′29′12″N | 1727        | 2020/09/27 | OL744377                  |
model. The BS supports and trees were obtained by running rapid bootstrap analysis of 1000 pseudo-replicates followed by a search for the tree with the highest likelihood.

Results

Taxonomy

_Erysiphe salicina_ J. Feng, S.-Y. Liu and Y. Li, _sp. nov._

MycoBank, MB840551

Mycelium epiphyllous, effuse or in patches, sometimes confluent and covering the entire leaf surface, white, moderately thick, evanescent to persistent (Fig. 1a–c). Hyphal cells about 3–6 μm wide; hyphal appressoria solitary or in opposite pairs, lobed to multilobed, coral-like (Fig. 1d–g); conidiophores arising from the upper surface of the mother cell, erect, 48–87 μm long, foot-cells cylindrical, straight, occasionally slightly sinuous at the base, 17–59 × 4–7 μm, followed by 0–2 usually shorter cells, forming conidia singly (Fig. 1h); conidia ellipsoid-cylindrical, usually 20–29 × 8–14 μm, with a length/width ratio varying from 1.8 to 2.9 (Fig. 1i–l), germ tubes almost terminal, short, conidial appressoria multiloculate, some showing longitubus pattern, produced laterally, near the middle or in perhilral position (Fig. 1m, n). Chasmothecia gregarious or scattered, 112–149 μm diam. (Fig. 1o); peridium cells irregularly polygonal to rounded, 8–16 μm diam. (Fig. 1p); appendages numerous, 22–53 per chasmothecium, rarely more, ± equatorial, straight and stiff, simple, 104–169 μm long (0.8–1.3 times as long as the chasmothecial diam.), width almost equal throughout or somewhat wider above, i.e., coiled part somewhat enlarged, width usually about 5–8 μm near the base, 13–19 μm towards the coiled tip (Fig. 1q–s), aseptate, hyaline, wall thin throughout, smooth, occasionally somewhat rough at the base, apices tightly or loosely uncinate-circinate or subhelicoid; asci 5–7, ellipsoid-obovoid, saccate, 57–79 × 29–50 μm, short-stalked, sometimes almost sessile, 4–7-spored (Fig. 1t–w); ascospores oblong ellipsoid-ovoid, 24–34 × 11–17 μm, colourless (Fig. 1x).

Diagnosis: Differs from all known _Erysiphe_ species on hosts belonging to _Salix_ in having hyphal appressoria in opposite pairs, short conidiophores only up to 87 μm, small conidia at most 30 μm in length and 14 μm in width, chasmothecia with few and short appendages and large ascospores exceeding a length of 30 μm, and by forming a monophyletic clade separate to all other _Erysiphe_ species in phylogenetic analyses.

Type: China, Heilongjiang Province, Yichun, Jiayin Maolanggou National Forest Park, on _Salix sinica_, 16 Aug. 2014, Shu-Yan Liu and Feng-Yun Zhao (HMJAU-PM91918 = holotype; HMAS249775 = isotype); ex-holotype sequence → MZ474877 (ITS+LSU).

Etymology: Composed of the name of the host genus, Salix, + Latin adjectival suffix -ina = belonging to.

Host range and distribution: On _Salix _having hyphal appressoria in opposite pairs, short conidiophores only up to 87 μm, small conidia at most 30 μm in length and 14 μm in width, chasmothecia with few and short appendages and large ascospores exceeding a length of 30 μm, and by forming a monophyletic clade separate to all other _Erysiphe_ species in phylogenetic analyses.

Specimens examined: China, Heilongjiang Province, Tahe County, Qixia Mountain Botanical Garden, on _S. sinica_, 6 Oct. 2018, Feng-Yun Zhao, Zhen-Zhen Wang, Wei-Wen Yan (HMJAU-PM91919); Heilongjiang Province, Heihe City, Aihui Town, Aihui National Forest Park, 17 Sep. 2014, Feng-Yun Zhao, Jian Liu, Shu-Rong Tang, Peng-Lei Qiu (HMJAU-PM91921); Heilongjiang Province, Jiagedaqi, Beishan Park, 1 Sep. 2015, Wen-Tao Jiang, Jia-Ni Li, Lei Zhao, Feng-Yun Zhao (HMJAU-PM91922); Heilongjiang Province, Tahe County, Zhangling Forest Farm, 23 Sep. 2016, Feng-Yun Zhao, Guan-Xiu Guan, Jia-Ni Li, Peng-Lei Qiu (HMJAU-PM91923); Heilongjiang Province, Tahe

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**Table 2** Primers used in this study

| Fragment        | Name   | Direction | Primer sequences (5′ → 3′)            | Reference                          |
|-----------------|--------|-----------|--------------------------------------|------------------------------------|
| ITS region      | ITS5   | Forward   | GGAAGTAAAAAGTCTGTAACAGG              | White et al. (1990)                |
|                 | ITS4   | Reverse   | TCCCTCGGTATATGAGT                  | White et al. (1990)                |
|                 | PM10   | Forward   | GCCTGGAAGTTGTTCAAAC                | Bradshaw and Tobin (2020)          |
|                 | PM2    | Reverse   | TCACCTCGGGTTAATCTGAGGT             | Cunningham et al. (2003)           |
|                 | PM5    | Forward   | TTGCTTTGGGCGGCCG                   | Takamatsu and Kano (2001)          |
|                 | PM6    | Reverse   | GYRCYCTGTCCAGGAGG                  | Takamatsu and Kano (2001)          |
| partial 28S rDNA| LSU1   | Forward   | ACCCGCTGAACCTAAGCATA               | Scholín et al. (1994)              |
|                 | LSU2   | Reverse   | CTTTGGTCGCGTTTTCAAGA               | Scholín et al. (1994)              |
|                 | PM3    | Forward   | GKCCTYTMCCGCGGTAGT                | Takamatsu and Kano (2001)          |
|                 | TW14   | Reverse   | GCTATCCTGAGGAACCTTC                | Mori et al. (2000)                 |
|                 | PM28F  | Forward   | TACGGCGGAGTGAAGCCG                  | Bradshaw and Tobin (2020)          |
|                 | PM28R  | Reverse   | ACGTTCATCTTACATTCGCC               | Bradshaw and Tobin (2020)          |
Erysiphe salicis-gracilistylae (Homma) Khodap., S. Takam., and U. Braun, comb. nov.

Basionym: Uncinula salicis-gracilistylae Homma (as “salici-gracilistylae”), Trans. Sapporo Nat. Hist. Soc. 11(3): 173, 1930.

Synonyms: Uncinula adunca var. salicis-gracilistylae (Homma) U. Braun, Mycotaxon 15: 147, 1982.

Erysiphe adunca var. salicis-gracilistylae (Homma) U. Braun and S. Takam., Schlechtendalia 4: 16, 2000.

Erysiphe salicis var. salicis-gracilistylae (Homma) Darsaraei, Khodaparast, S. Takam. and U. Braun, in Darsaraei et al., Mycological Progress 20(4): 531, 2021.

Erysiphe salicicola Hyang B. Lee, P.M. Kirk, and T.T.T. Nguyen, in Boonmee et al., Fungal Diversity 111: 157, 2021, syn. nov.

Description, typification, including epitype, phylogeny, host range and distribution, see Darsaraei et al. (2021), under E. salicis var. salicis-gracilistylae.

Specimens examined: China, Heilongjiang Province, Harbin, Jinlongshan National Forest Park, on Salix ernestii, 24 Aug. 2019, Jing Feng, Han-Xing Gao (HMJAU-PM91914); Jilin Province, on S. wilhelmsiana, 17 Sep. 2018, Shu-Rong Tang (HMJAU-PM91965); Heilongjiang Province, Harbin, Sun Island Scenic Spot, on S. babylonica,
Phylogenetic analysis

Twenty-eight nucleotide sequences spanning the ITS1-5.8S rDNA-ITS2 and 28S rDNA D1/D2 domains were generated in this study. These sequences were aligned with 42 sequences of *E. adunca* s. lat. taken from Darsaraei et al. (2021) and 2 sequences of *E. salicicola* (Boonmee et al. 2021). A sequence
of *E. australiana* (AB022408) was used as an outgroup taxon in accordance with Takamatsu et al. (2015). The alignment consisted of 73 sequences and 1269 characters, of which 133 characters were variable and 141 were informative for parsimony analysis. The maximum parsimony tree (*TL = 397, CI = 0.8615, RI = 0.9726, RC = 0.8378*) with the highest likelihood value is shown in Fig. 2. The ML tree topology was almost identical to the MP tree and only bootstrap supports are shown in the MP tree. The 72 ingroup sequences are divided into five groups. Three groups (Groups I, II, and III) consist of sequences from powdery mildews on *Salix* spp. and the other two groups (Groups IV and V) are composed of sequences from powdery mildews on *Populus* spp. All five groups are supported by BS analyses with 70% or higher. Group I contains all *Erysiphe salicina* sequences obtained from powdery mildews on *Salix* spp. and forms an independent clade supported by a bootstrap value of 100%. Group II contains two sister clades, viz., *E. salicis-gracilistylae* (≡ *E. salicis* var. *salicis-gracilistylae*), including two sequences obtained from *E. salicina*, and *E. salicis* supported by a bootstrap value of 100%.

**Discussion**

*Salix* is a common host genus for powdery mildews of various genera. Four genera, seven species and two varieties of powdery mildews are currently recognized on *Salix* spp. (Braun and Cook 2012; Yu and Lai 1979; Zheng and Chen 1978; Boonmee et al. 2021; Darsaraei et al. 2021). Powdery mildews in the genus *Erysiphe* are the predominant species infecting *Salix* hosts and are geographically widespread. Molecular phylogenetic analyses play an important role in the fungal taxonomy of the powdery mildews. Genetic evaluations are the main method to discover new species, above all cryptic species within complexes (Kirschner et al. 2020; Qiu et al. 2020; Yamaguchi et al. 2021). The recently published phylogenetic-taxonomic revision of the *Erysiphe adunca* complex (Darsaraei et al. 2021) is a case in point, and provides the basis for the present examinations and analyses. The comparative morphology and phylogenetic analysis from the current study elucidate several issues with this group of fungi including the recent publication of the species *E. salicicola*. The morphology of *E. salicicola* is consistent with *E. salicis-gracilistylae* (≡ *Uncinula salicis-gracilistylae*), and sequences retrieved from *E. salicis-gracilistylae* clade within the *E. salicis-gracilistylae* clade, suggesting that *E. salicicola* has to be reduced to synonymy with *E. salicis-gracilistylae*. This clade and corresponding taxonomic have been discussed in detail in Darsaraei et al. (2021). Owing to uncertainties in the interpretation of the cluster concerned, either as species clade or as subclade of the *E. salicis* clade led to the maintenance of this taxon as variety, as in previous treatments (Braun and Cook 2012). However, sequences retrieved from the new species recently described from Republic of Korea and the present new phylogenetic analysis confirm a robust, strongly supported cluster that can be treated as species clade. The host range within this clade is also different from that of *E. salicis*. However, the treatment of this taxon as a species of its own requires the introduction of the new combination *Erysiphe salicis-gracilistylae*.

Powdery mildews found on multiple *Salix* spp. in China have been morphologically and phylogenetically examined. The species is genetically and morphologically distinct from all allied *Erysiphe* species on *Populus* and *Salix* spp. and is thus described as *E. salicina* sp. nov. This species is morphologically different from *E. capreae* and *E. salicis* in having shorter conidiophore foot-cells [17–59 × 4–7 μm vs (25–)35–90 (–110) × 5–9 μm in *E. capreae* and 15–45 × 5–9 μm in *E. salicis*] and smaller conidia (20–29 × 8–14 μm vs 25–45 × 10–24 μm in *E. capreae* and 23–40 × 10–18 μm in *E. salicis*). The ascospores are larger (24–34 × 11–17 μm) compared to *E. salicis* (16–29 × 9–16 μm) and *E. salicis-gracilistylae* (19–24 × 10–18 μm). In addition, *Erysiphe salicina* has chasmothecia with fewer appendages per chasmothecium [22–53 vs (33–)50–400 in *E. capreae*, 25–95 in *E. salicis* and *E. salicis-gracilistylae*], and appendages with enlarged uncinate-circinate apices (vs tightly uncinate-circinate, not enlarged apices in *E. salicis* and *E. salicis-gracilistylae*). Furthermore, the appendages are regular, i.e., without constrictions and swellings, compared to *E. salicis-gracilistylae*, and they arise equatorially, as in *E. salicis* and *E. salicis-gracilistylae*, compared to *E. capreae* that are not equatorial or only somewhat in the upper half, and have a tendency to point upwards at maturity. *Erysiphe adunca* s. str. on *Populus* spp. (*Salicaceae*) is genetically as well as morphologically also distinguished from *E. salicina* by having much longer conidiophores, 70–150 μm, and foot-cells, 40–110 μm, larger conidia, 28–38 × 14–18 μm, and much longer chasmothecial appendages, 1–3 times as long as the chasmothecial diam. (Darsaraei et al. 2021).

At first glance, the result was unexpected, because the most common host plant of the new species, *S. sinica*, was originally described as *S. caprea* var. *sinica*, i.e., this taxon is closely related to *S. caprea* and both species pertain to *Salix* subgen. *Vetrix* sect. *Vetrix*. *Salix caprea* is the principal host of *E. capreae*, which is common in the northern hemisphere. Before our analysis we expected *E. capreae* also on *S. sinica*. The occurrence of a separate species on two hosts belonging to *Salix* subgen. *Vetrix* sect. *Vetrix*, which is morphologically and phylogenetically close to *E. salicis*, suggests a higher and not yet fully elucidated diversity of *Erysiphe* on *Salix* spp. in Asia, and in particular China. We hypothesize that future research...
will reveal additional cryptic species, hidden under previous reports as *Erysiphe (Uncinula) adunca*.

There are additional open questions that will require analyses. For example, Zhu (1998) supposed that *S. sinica* collections from northern and northeastern China have often been misidentified as *S. caprea*. *Erysiphe* spp. on these hosts require further examinations in northeastern China. *Erysiphe salicis* has not yet been verified for China and future collection efforts are needed to elucidate whether *E. salicis* is distributed in China. Additionally, *Erysiphe adunca* on *Populus* spp. in China needs to be evaluated. It is currently known that *E. adunca* is a common and widely distributed species on a wide range of *Populus* spp. in Asia, Europe and North America (Darsaraei et al. 2021). Several *Uncinula* spp., based on Chinese specimens on poplars, have been described (Zheng and Chen 1977), but all names were reduced to synonymy with *E. adunca* (Braun and Cook 2012; Darsaraei et al. 2021). It is still unclear whether all Chinese *Erysiphe* collections on *Populus* spp. pertain to two *Erysiphe* species viz. *E. adunca* and *E. mandschurea*. It cannot be excluded that, comparable to *Erysiphe* on willows, the diversity of *Erysiphe* on poplars is much higher than previously assumed, most notably in China.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11557-022-01793-1.

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**Author contribution** Jing Feng, Shu-Yan Liu, and Uwe Braun were involved in planning and supervised the work; Jing Feng performed DNA sequencing and color photos; Susumu Takamatsu, Michael Bradshaw, and Seyed Akbar Khodaparast performed phylogenetic analysis; Timur Bulgakov, Guan-Xiu Guan, Feng-Yun Zhao, and Shu-Rong Tang provided part of powdery mildew specimens. All authors reviewed the manuscript and commented on the manuscript.

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**Data availability** The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request. Moreover, alignments were deposited in TreeBASE (http://www.treebase.org/) under the accession number S28710.

**Declarations**

**Competing interests** The authors declare no competing interests.

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