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A taxonomic revision of *Erysiphe* sect. *Uncinula* (*Erysiphaceae*, *Helotiales*) in Iran

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ABSTRACT: Since the publication of the latest monograph of powdery mildews by Braun and Cook in 2012, no comprehensive revision has been done to check the accuracy of the hitherto recorded species of the genus *Erysiphe* in Iran. In this study, we present a taxonomic revision of *Erysiphe* sect. *Uncinula* in Iran using morphological traits of voucher specimens and ITS-LSU rDNA sequence analysis. Thirty-eight voucher specimens were obtained from the University of Guilan Mycological herbarium (fungarium, GUM) and the Fungus Reference Collection of Herbarium Ministerii Iranici Agriculturae (IRAN), as well as newly collected specimens during 2019–2021, were examined morphologically. The ITS sequences were generated for 26 selected specimens, and the LSU sequences were generated for 16 specimens. Two ITS sequences of *E. paradoxa* (OM574846 and OM574845), as well as ITS and LSU sequences of *E. celtidis* (OM574855 and OM574834, respectively), were sequenced for the first time in this study. Precise morphological observations and molecular analyses of Iranian specimens changed the number of accepted species of *Erysiphe* sect. *Uncinula* from six taxa in 2009 to 10 taxa in 2021. All species identified from Iran are here described and illustrated. A key to species of *Erysiphe* sect. *Uncinula* in Iran is also provided.

KEYWORDS: Biodiversity, phylogeny, Taxonomy, rDNA

INTRODUCTION

The genus *Erysiphe* R. Hedw. ex DC., belonging to the family *Erysiphaceae* (*Ascomycota*: *Helotiales*), accommodates species that are the causal agents of powdery mildew on many plant species. Before taxonomic revision by Braun and Takamatsu (2000), most powdery mildew species with more or less cylindrical to doliiform and non-catenate conidia were traditionally classified into three major genera based on the type of appendages of chasmothecia viz., *Erysiphe* (with mycelioid appendages), *Uncinula* Lév. (with uncinate appendages) and *Microsphaera* Lév. (with regular dichotomously branched appendages). However, based on the results of rDNA phylogenetic analysis, Braun and Takamatsu (2000) and subsequently Braun and Cook (2012) merged all these species into a single genus, *Erysiphe*, and divided it into five sections viz., *E.* sect. *Erysiphe*, *E.* sect. *Microsphaera*, *E.* sect. *Uncinula*, *E.* sect. *Typhulochaeta* and *E.* sect. *Californiomyces*. Phylogenetic analyses using rDNA sequences (Hirata and Takamatsu 1996, Takamatsu et al. 1998, Mori et al. 2000a, Mori et al. 2000b, Cunnington et al. 2003, Takamatsu 2004, Khodaparast et al. 2005, Niinomi et al. 2008, Takamatsu 2013a, Takamatsu 2013b, Takamatsu et al. 2015a, Takamatsu et al. 2015b, Khodaparast 2016, Siahaan et al. 2018) have created a new window for classification of these important plant pathogenic fungi.

Members of *Erysiphe* sect. *Uncinula* are usually characterized by having a single uniform type of uncinuloid appendages (Braun and Cook 2012). These fungi are distributed globally, although the number of defined species is more in East Asia (Takamatsu et al. 2015b). Most species of *E.* sect. *Uncinula* infect trees and shrubs (Takamatsu et al. 2015b). Until 2012, 146 species and varieties of sect. *Uncinula* were described (Braun and Cook 2012). Now, having about 150 species (Meeboon and Takamatsu 2013a, Meeboon et al. 2013, Darsaraei et al. 2021, Qiu et al. 2019; Kirschner et al. 2020; Yamaguchi et al. 2021), this section consists of about 35% of species in the genus. Since then, taking advantage of molecular studies, several new species, varieties, and combinations have been introduced. For example, morphological and phylogenetic analysis of *E.* sect. *Uncinula* on *Carpinus* L. species

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revealed that it consists of at least five distinct species on this plant (Braun et al. 2006, Meeboon & Takamatsu 2013b). Similar studies on *Erysiphe* species (sect. *Uncinula*) occurring on ash trees (*Fraxinus* L.), *Celtis* L., *Deutzia* Thunb., *Nothofagus* Blume, and *Ulmus* L. led to the introduction of several new taxa on these plants (Meeboon and Takamatsu 2013a, 2017; Meeboon et al. 2013; Qiu et al. 2019; Kirschner et al. 2020; Yamaguchi et al. 2021). In one of the most recent publications, *E. adunca* complex infecting Salicaceae was revisited (Darsaraei et al. 2021). They reestablished *E. salicis* DC. (on *Salix* spp.) and introduced the new combination *Erysiphe salicis* var. *salicis–gracilistylae* (Homma) Darsaraei, Khodaparast, S. Takam. & U. Braun.

It is estimated that more than 7500 plant species grow in Iran (Assadi 2019). The country's vastness and diversity in the ecosystems have made Iran one of the most important countries for biodiversity conservation in the Middle East and West Asia. Located in the center of the Palearctic Ecological Zone, Iran is like a bridge between Southeast Asia, Central Asia, Saudi Arabia, and Europe, and is the source of many genetic resources (Makhdoum 1990). Such conditions provide a suitable substrate for fungal diversity. During the last decades, several new species of powdery mildew fungi have been recorded from Iran. From which, the nomenclature of some species has been changed over time, mainly owing to the molecular studies (Khodaparast et al. 2000, Khodaparast et al. 2005, Khodaparast and Abbasi 2009, Sharifi et al. 2013, Abbasi et al. 2013, Khodaparast 2016, Arzanlou and Torbati 2016). Since the release of Braun and Cook's monograph of powdery mildews in 2012, no comprehensive revision of *Erysiphe* spp. in Iran has been performed. It is for the first time that morphological surveys, along with molecular studies, come together to form a state–of–the–art checklist of *E.* sect. *Uncinula* in Iran, and to produce their DNA barcodes based on rDNA sequences. We also present an identification key to all species included in *E.* sect. *Uncinula* in Iran.

MATERIALS AND METHODS

Sample collection

Thirty-eight voucher specimens were obtained from the University of Guilan Mycological herbarium (fungarium, GUM) and the Fungus Reference Collection of Herbarium Ministerii Iranici Agriculturae (IRAN), as well as newly collected specimens during 2019–2021, were examined (Table S1).

Morphological examinations

Fungal structures of infected leaves were mounted using a clean needle or clear adhesive tape and transferred into a drop of 1:1 lactic acid and glycerin on a microscope slide. At least 20 chasmothecia, appendages, asci, ascospores, conidiophores, and conidia were examined for each specimen. All photos were taken using a Leica DM 100 microscope (Wetzlar, Germany) equipped with a Canon camera (Tokyo, Japan). All digital illustrations were done with Adobe Fresco (Version 3.4 for iPad OS).

Molecular phylogeny

DNA extraction was performed using either 20–30 ascomata or a piece of mycelia with the Chelex method (Walsh et al. 1991, Hirata and Takamatsu 1996, Khodaparast et al. 2020). PCR amplification of the internal transcribed spacer regions 1 and 2 including the intervening 5.8S nuclear ribosomal DNA (ITS) was done using the primers PMITS1 (5'–TCGGACTGGCCYAGGG AGA–3') (Cunnington et al. 2003)/PM11(5'–TACCGCTTCACTCGCC G TTA–3') (Bradshaw and Tobin 2020) for the first reaction, and PM10 (5'–GGCCGGAAAGTTGTCC A AAC–3)(Bradshaw and Tobin 2020)/PMITS2 (5'–TCACTCGCCGTTCTGAGGT–3') Cunnington et al. 2003) for the nested reaction. For the D1/D2 domains of the partial nuclear 28S ribosomal DNA (LSU), the first reaction was done using the primers PM3 (5'–GKGCTYTMCG CGTAGT) (Takamatsu and Kano 2001)/NLP2 (5'–GGTCCCAACAGCT ATGCTCT–3') (Bradshaw and Tobin 2020), and the nested reaction using the RPM2 (5–ACCTCAG TAACGGCGAGTGA–3') (Bradshaw and Tobin 2020) / NLP2. PCR components and conditions were in accord with the method described in Ellingham et al. (2019). The amplicons were sent to Codon Genetic Group (Tehran, Iran) for sequencing. in one direction. New sequences generated in this study were deposited in GenBank under the accession numbers of OM530243, OM530246–8, OM574832–41, and OM574844–55.

New sequences generated in this study were aligned against sequences of members of the *Erysiphe* sect. *Uncinula* retrieved from GenBank (Table S1) using MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/index.html) (Katoh et al. 2002), and manually optimized with MEGA 7 (Kumar et al. 2016). Several sequences (preferably type or reference sequences, if available) from GenBank were selected for phylogenetic analyses. Sequences of the ITS region and partial LSU were combined, and Maximum likelihood (ML) analysis was used to estimate phylogenetic relationships using raxmlGUI (Silvestro and Michalak 2012), under the GTRGAMMA substitution model along with rapid bootstrap analysis of 1000 pseudoreplicates followed by a search for the tree with the highest likelihood.

RESULTS

Phylogenetic analysis

42 sequences of ITS and LSU rDNA were obtained from 10 species of *E.* sect. *Uncinula* in this study. A total of 88 taxa, including *Leveillula taurica* (AB667884) and *Phyllactinia moricola* (AB080561) as outgroups, were included in the phylogenetic analysis (Fig. 1). The final alignment was partitioned to partition 0 (ITS) and partition 1 (28S) for the combined analysis.

The final ML Optimization Likelihood value was obtained as -7178.756221. The alignment had 572 distinct alignment patterns.

The alignment patterns for partition 0 (ITS) and partition 1 (28S) were 396 and 176, respectively. Alpha parameter for partition 0 (ITS) and partition 1 (28S) were 0.363946 and 0.186646, respectively. Tree length for partition 0 (ITS) and partition 1 (28S) was calculated as 3.205769 and 35.098034, respectively. The 86 ingroup taxa were divided into seven well-supported clades and subclades (more than 95% in bootstrap analysis). Most of these clades are rather specific to the host plant family, so those species recovered from *Cannabaceae*, *Betulaceae* (except for *E. arcuata* U. Braun, S. Takam. & Heluta, and *E. carpini-cordata* (Tanda & Y. Nomura) U. Braun & S. Takam.), *Lythraceae*, *Salicaceae* and *Ulmaceae* made single clades. *Erysiphe necator* Schwein. represents a polyphagous powdery mildew as the sequences retrieved from different host plants, including *Anacardium occidentale* L. (*Anacardiaceae*), *Carica papaya* L. (*Caricaceae*), and *Hevea brasiliensis* (Willd. Ex A. Juss.) Müll. Arg. (*Euphorbiaceae*) were included in this clade in addition to the *Vitis vinifera* L. (*Vitaceae*), which is a common host for this species (Fonseca et al. 2019). Sequences retrieved from powdery mildew on *Rosaceae* viz., *E. prunastri* DC. and *E. simulans* (E.S. Salmon) U. Braun & S. Takam. were clustered in one unsupported clade. Two varieties of *E. prunastri*, viz., *prunastri* (bootstrap= 94%) and *japonica* (bootstrap= 100%), formed a sister clade with 100% support. Powdery mildew occurring on *Carpinus* spp. L. (*Betulaceae*) comprised of five distinctly supported species (bootstrap= 100%) viz. *E. arcuata*, *E. carpini-cordatae*, *E. carpinicola* (Hara) U. Braun & S. Takam., *E. paracarpinicola* and *E. carpini-laxiflorae* U. Braun, S. Takam. & Heluta, from which only *E. arcuata* was identified in Iran. However, these species were divided into three supported clades. Two sequences generated from *Acer* L. (*Sapindaceae*) in Iran that were morphologically identified as *E. paradoxa* (S. Simonyan) U. Braun & S. Takam., formed an unsupported clade with *Erysiphe ljubarskii* (Golovin) U. Braun & S. Takam., another species from *Acer* spp. However, *E. flexuosa* (Peck) U. Braun & S. Takam. which also infects the *Sapindaceae* was not included in this clade.

Powdery mildew infecting *Ulmaceae* and *Cannabaceae* were clustered together. The *Ulmaceae* clade (bootstrap= 95%) consists of three subclades, viz. *E. kenjiana* (Homma) U. Braun & S. Takam., *E. ulmi* var. *ulmi* Castagne and *E. parvifoliae* R. Kirschner. Sequences retrieved from *Salix* and *Populus* (*Salicaceae*), formed a clade with 100% support. This clade consists of *E. adunca* (Wallr.) Link on *Populus* L., *E. capreae* DC. ex Duby on *Salix* L., two varieties of *E. salicis* DC. on *Salix*, and *E. mandshurica* (Miura) U. Braun on *Populus*. Finally, *E. australiana* (McAlp.) U. Braun & S. Takam. that is occurring on *Lagerstroemia* L. (*Lythraceae*) formed a distinct clade with 100% support.

Taxonomy

Erysiphe adunca (Wallr.) Link, emend. Darsaraei *et al.* Mycological Progress 20: 521 (2021) Figs. 2–3

Chasmothecia scattered to somewhat gregarious, 130–153 µm diam.; peridium cells irregularly polygonal, 9–18 µm diam.; appendages 40–60 per chasmothecium, ± equatorial, 2–3 times as long as the chasmothecial diam., width 12–20 µm at the base, 3–6 µm at the narrower parts, 1–2 septate, occasionally forked into 2–3 branches, flexuous, with constrictions and swellings, occasionally folded or somewhat twisted, hyaline; apices uncinate–circinate; asci 11–12, obovoid, saccate–clavate, 60–73 × 41–56 µm diam., short–stalked to somewhat sessile, 4–6–spored; ascospores ellipsoid-ovoid to somewhat reniform, 22–28 × 11–16 µm, colorless.

Host range: *Populus* sp. (*Salicaceae*)

Specimen examined. Iran, Hamedan province, Hamedan, on *Populus* sp., Oct. 2007, M. Bahador (GUM 1753).

Erysiphe arcuata U. Braun, S. Takam. & Heluta, Schlechtendalia 16: 99 (2007) Fig. 4

Mycelium epiphyllous, forming patches or effuse; hyphae 4––6 µm wide, hyaline, smooth, thin-walled; hyphal appressoria strongly lobed in opposite pairs or nipple-shaped; conidiophores arising centrally from mother cell, erect, straight or almost so, 47–63(–73) × 6–8 µm; foot–cells cylindrical, 24–39 × 6–8 µm, basal septum occasionally elevated up to 7 µm from the mother cell, followed by l–2(–3) shorter cells, forming conidia singly; conidia ellipsoid, cylindrical, hyaline, 27–37(–50) × 13–17 µm.

Host range: *Carpinus betulus* L. (*Betulaceae*)

Specimen examined. Iran, Golestan province, on *Carpinus betulus*, May 2015, Heidari (IRAN 16841F).

Fig. 1. Phylogenetic analysis of combined data of the ITS and the 5'-end of the LSU rDNA (including domains D1 and D2) region for 86 sequences from *Erysiphe* sect. *Uncinula* and two outgroup sequences. Horizontal branch lengths are proportional to the number of substitutions. BS (> 70%) values by the maximum likelihood (ML) method are shown on the branches.

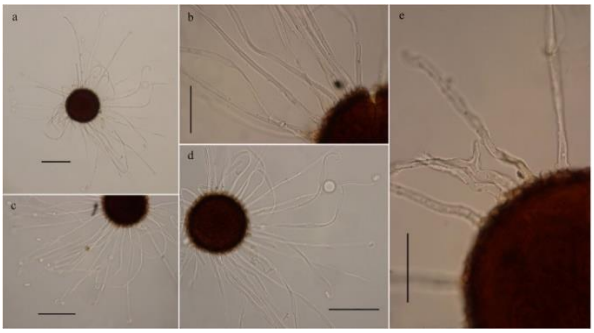

Fig. 2. *Erysiphe adunca* (GUM 1753, on *Populus* sp.). a,c,d. Chasmothecia; b. a close-up of basal appendages; e. basal appendage with short branchlet. — Scale bars = (a,c,d) 100 µm; (b,e) 50 µm.

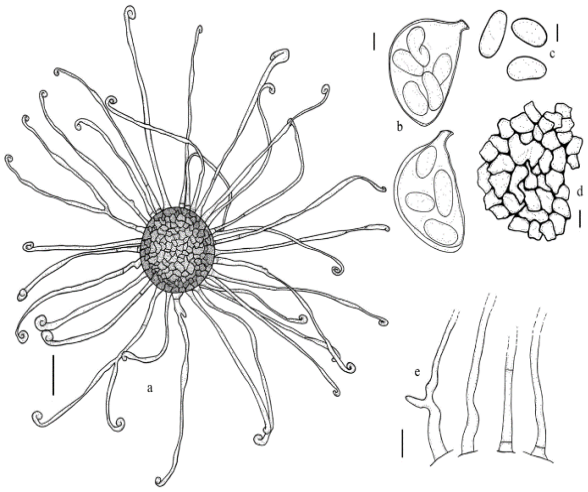

Fig. 3. *Erysiphe adunca* (GUM 1753, on *Populus* sp.). a. Chasmothecium; b. Asci; c. Ascospores; d. Peridium cells; e. Basal parts of appendages (outlines and appendage with a short branchlet). — Scale bars = (a) 50 µm; (b,c,d,e) 10 µm.

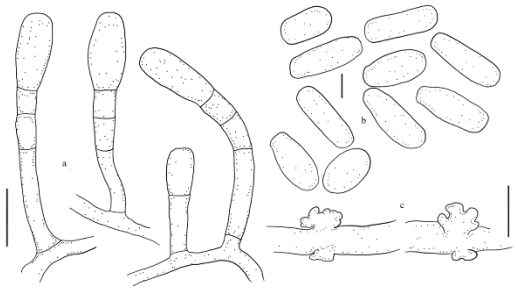

Fig. 4. *Erysiphe arcuata* (IRAN 16841F on *Carpinus* sp.). a. Conidiophores; b. conidia; c. Hyphal appressoria. — Scale bars = (a) 30 µm; (b,c) 10 µm.

Erysiphe australiana (McAlp.) U. Braun & S. Takam., Schlechtendalia 4: 17 (2000).Fig. 5

Mycelium amphigenous, white and dense; hyphal cells width 4–7 µm; hyphal appressoria lobed to multilobed, mostly solitary; conidiophores erect, 40–72 × 7–10 µm; foot cells cylindrical, 15–48 × 7–9 µm, followed by 1–2 shorter cells, forming conidia singly; conidia cylindrical, 21–41 × 10–17 µm, conidial germination from Pseudoidium type, germ tubes terminal to sub–terminal, conidial appressoria multilobed.

Host range: *Lagerstroemia indica* L. (*Lythraceae*)

Specimens examined. Iran, Isfahan province, Isfahan, on *Lagerstroemia indica*, K. Sharifi (GUM 1716); Guilan province, Rasht, 7 Sept. 2010, A. Khodaparast (GUM 782); Guilan province, Rasht, 30 May 2021, H. Darsaraei (GUM 1902).

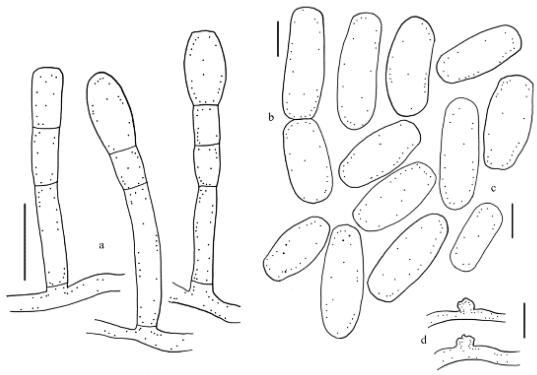

Fig. 5. *Erysiphe australiana* (GUM 1716, on *Lagerstroemia indica)*. a. Conidiophores; b. Conidia forming false chain; c. Conidia; d. Hyphal appressoria. — Scale bars = (a) 30 µm; (b,c,d) 10 µm.

Erysiphe capreae DC. ex Duby, Botanicon gallicum 2: 871 (1830). Figs. 6–8

Chasmothecia gregarious or scattered, (112–)117–187 µm diam.; peridium cells irregularly polygonal, 6–21 µm diam.; appendages 33–102 per chasmothecium, ± equatorial, straight to somewhat curved, stiff to flexuous, 1–1.5 times as long as the chasmothecial diam., width 4–8 µm throughout, almost equal throughout, aseptate, hyaline, walls thin throughout, smooth, somewhat thicker at the base; apices uncinate-circinate, tip sometimes enlarged or slightly narrowed towards the tip; asci 6–15, ellipsoid-obovoid, saccate-clavate, 46–81 × 31–52 µm, short–stalked, sometimes almost sessile, 3–6–spored; ascospores ellipsoid–ovoid to somewhat reniform, 20–30 × 12–17 µm, colorless.

Host range: *Salix aegyptiaca* L., *Salix* sp. L. (*Salicaceae*)

Specimens examined. Iran, East Azerbaijan province, Kaleybar, on *Salix aegyptiaca*, 2007, M. Donyadost–Chalan (GUM 1754); East Azerbaijan province, Kaleybar, on *Salix* sp., 2009, M. Donyadost–Chalan (GUM 1755); Guilan province, Shafarod, on *Salix* sp., 1991, Danesh (IRAN 8127F); East Azerbaijan province, Arasbaran, on *Salix aegyptiaca*, Oct. 2001, Gh. Tavanaei (GUM 1752); Mazandaran province, Abbas Abad, on *Salix aegyptiaca*, 1971, Mostofi (IRAN 5841F); on *Salix* cf. *aegyptiaca* (IRAN 15062F).

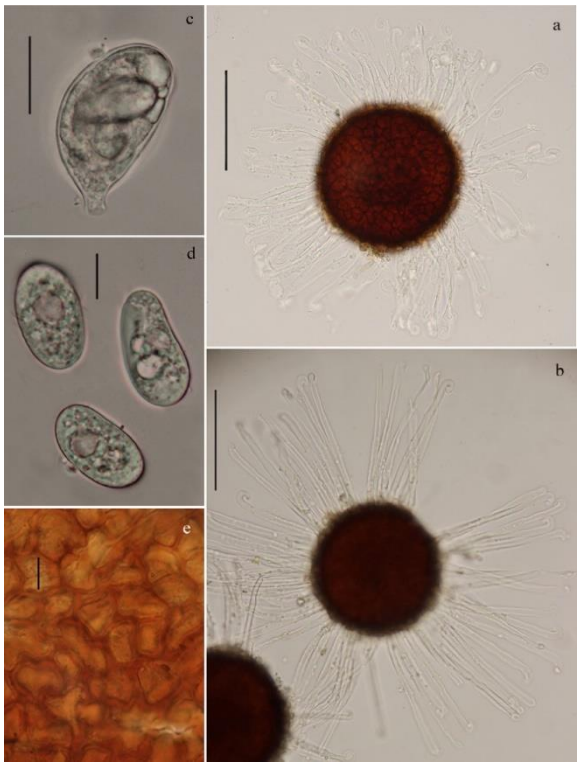

Fig. 6. *Erysiphe capreae* a. (IRAN 8127F, on *Salix* sp.) and b. (GUM 1754, on *Salix aegyptiaca*) chasmothecia; c. Asci; d. Ascospores; e. Peridium cells. — Scale bars = (a,b) 100 µm, (c) 50 µm, (d,e) 10 µm.

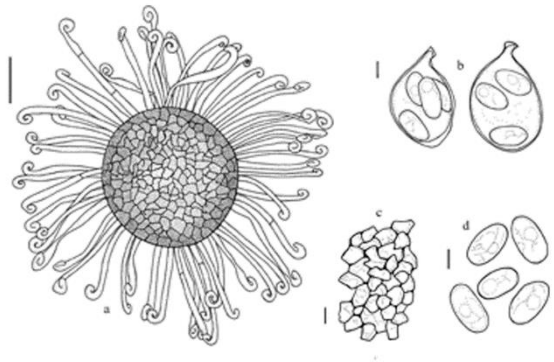

Fig. 7. *Erysiphe capreae* (IRAN 8127F, *Salix* sp.). a. Chasmothecium; b. Acsi; c. Peridium cells; d. Ascospores. — Scale bars = (a) 50 µm; (b,c,d) 10 µm.

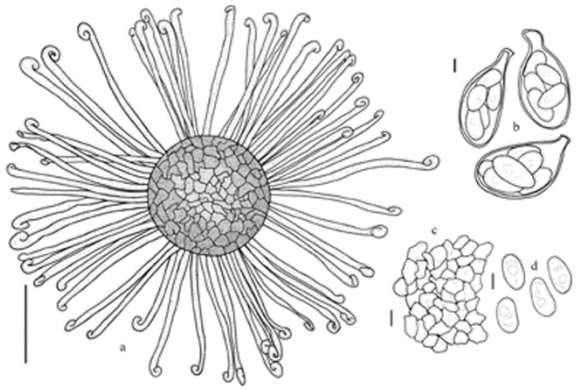

Fig. 8. *Erysiphe capreae* (GUM 1754, *Salix aegyptiaca*). a. Chasmothecia; b. Asci; c. Peridium cells; d. Ascospores. — Scale bars = (a) 50 µm; (b,c,d) 10 µm.

Erysiphe celtidis (Shvartsman & Kusnezowa) U. Braun & S. Takam., Schlechtendalia 4: 18 (2000).Figs. 9–10

Chasmothecia scattered to gregarious, 83–107 µm diam.; peridium cells irregularly polygonal, 10–25 µm diam.; appendages 9–21, equatorial, stiff to flexuous, occasionally sinuous, 1–2 times as long as the chasmothecial diam., rarely forked, width up to 13 µm at the base, 4–5 µm throughout, width increases towards the tip, especially near the apices (up to 10 µm), aseptate, hyaline, thin-walled, thicker at the base, verruculose, especially at the lower half; apices uncinate-circinate, (sub-helicoid); asci 3–5, saccate, ellipsoid-obovoid, 46–61 × 35–45 µm, sessile to short–stalked, 4–6–spored; ascospores ellipsoid, ovoid, 17–28 × 11–15 µm, colorless.

Host range: *Celtis australis* subsp. *caucasica* (Willd.) C.C.Towns. (Syn. *Celtis caucasica* L.) (*Cannabaceae*)
Specimen examined. Iran, East Azerbaijan province, Arasbaran, on *Celtis australis* subsp. *caucasica*, Oct. 2001, Gh. Tavanaei (GUM 1770).

Fig. 9. *Erysiphe celtidis* (GUM 1770, *Celtis caucasica*). a. Chasmothecium; b. Acsi; c,d. Appendage outline. — Scale bars = (a) 50 µm; (b,c,d) 10 µm.

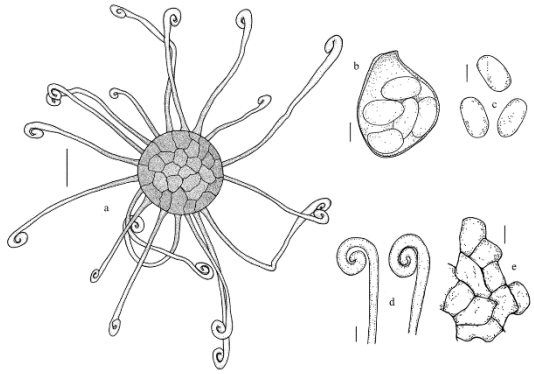

Fig. 10. *Erysiphe celtidis* (GUM 1770, *Celtis caucasica*). a. Chasmothecia; b. Asci; c. Ascospores; d. Appendage tip; e. Peridium cells. — Scale bars = (a) 50 µm; (b,c,d,e) 10 µm.

Erysiphe necator Schwein., Transactions of the American Philosophical Society 4(2): 270 (1834), **var.*necator***. Figs. 11–12
Chasmothecia scattered to somewhat gregarious, 101–138 µm diam.; peridium cells irregularly polygonal to almost globose, 8–22 µm diam.; appendages 17–24, equatorial, long and flexuous, sometimes forked, 1–4 times as the chasmothecial diam., width variable, 5–7 µm, or uniform throughout, septate, 2–5 septa, ± brown in the lower half, paler or hyaline in the upper part walls thin, somewhat thicker at the base; apices uncinated–circinate; asci 4–5, saccate–clavate, globose, obovoid, 47–70 × 42–52 µm, sessile and short–stalked, 4–5–spored; ascospores ellipsoid, ovoid, 17–26 × 10–14 µm, colorless.

Host range: *Vitis vinifera* L. (*Vitaceae*)
Specimens examined. Iran, Hamedan province, Hamedan, on *Vitis vinifera*, Nov. 2001, M. Bahador (GUM 1768); Fars province, Shiraz, on *V. vinifera*, June 2002, V. Bahrami (GUM 1779); Chaharmahal and Bakhtiari province, Babaheidar, on *V. vinifera*, Oct. 2013, S.A. Hashemi (GUM 1780); East Azerbaijan province, Maragheh, on *V. vinifera*, Oct. 2010, M. Damadi (GUM 1781).

Fig. 11. *Erysiphe necator* var. *necator* (GUM 1768, *Vitis vinifera*). Chasmothecium. — Scale bars = 50 µm.

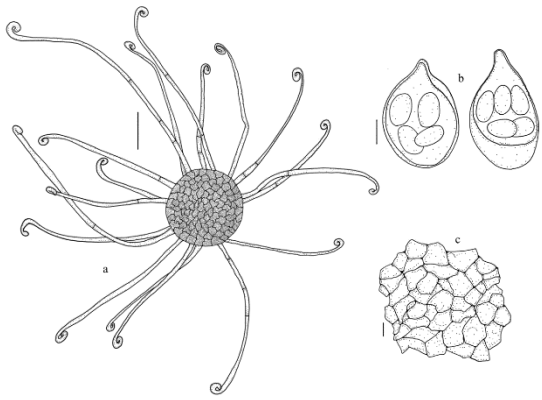

Fig. 12. *Erysiphe necator* var. *necator* (GUM 1768, *Vitis vinifera*). a. Chasmothecia; b. Asci; c. Peridium cells. — Scale bars: (a) 50 µm; (b,c) 10 µm.

Erysiphe paradoxa (S. Simonyan) U. Braun & S. Takam., Schlechtendalia 4: 22 (2000).Figs. 13–14
Chasmothecia scattered to gregarious, 143–177 µm diam.; peridium cells obscure, 5–13 µm diam.; appendages 40–68, equatorial, flexuous-curved, on aggregated chasmothecia often densely interwoven with each other, widely or loosely curved, sinuous or twisted, length variable, up to 7 times as long as the chasmothecial diam, width 11–23 µm at the very base, about 4–5 µm throughout, up to 1–2 µm at the tip, aseptate, hyaline, walls thin, 1–3 µm width, with a slight decrease towards the tip, smooth; apices

very widely and loosely uncinate or forming very irregular and loose spirals; asci 8–15(–20), easily visible in mature, still closed chasmothecia, ellipsoid–ovoid, 60–75 × 30–45 µm, short–stalked, 4–7–spored; ascospores ellipsoid, ovoid, sub-cylindrical to cylindrical, 22–27 × 11–15 µm, colorless.

Host range: *Acer hyrcanum* Fisch. & C.A.Mey., *Acer monspessulanum* L. (*Sapindaceae*)

Specimens examined. Iran, East Azerbaijan province, Arasbaran, on *Acer hyrcanum*, Aug. 1999, Gh. Tavanaei (GUM 1764); East Azerbaijan province, Arasbaran, on *A. monspessulanum*, Gh. Tavanaei (GUM 1767); Golestan province, Golestan National Park, on *A. monspessulanum*, Sept. 1993, M.A. Tajik Ghanbari (IRAN 9109F); East Azerbaijan province, Tabriz, on *A. hyrcanum*, 1998, Gh. Tavanaei (IRAN 10574F).

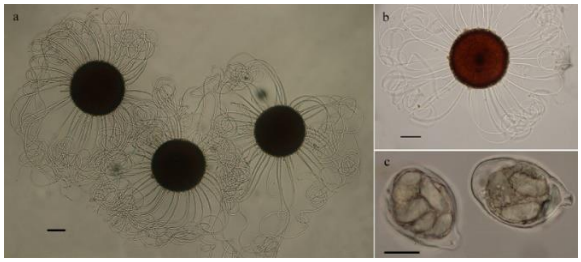

Fig. 13. *Erysiphe paradoxa* (GUM 1764, *Acer hyrcanum*). a. Appendages of aggregated chasmothecia interwoven with each other; b. Asci that are visible in still closed mature chasmothecium; c. Asci. — Scale bars = (a.b) 50 µm; (c) 20 µm.

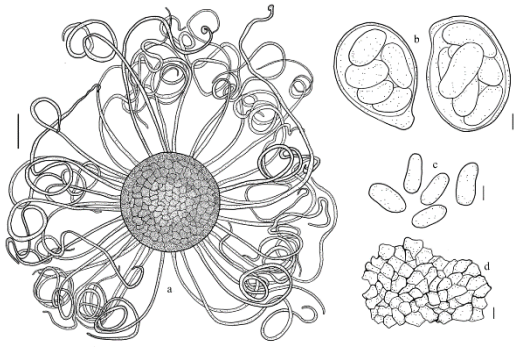

Fig. 14. *Erysiphe paradoxa* (GUM 1764, *Acer hyrcanum*). a. Chasmothecia; b. Asci; c. Ascospores; d. Peridium cells. — Scale bars = (a) 50 µm; (b,c,d) 10 µm.

Erysiphe prunastri DC., Flore française 6: 108, 1815, **var. *prunastri***.Figs. 15–16

Chasmothecia almost always gregarious to ±scattered, 80–138 µm diam.; peridium cells not very conspicuous, irregularly polygonal, 7–19 µm diam.; appendages dimorphic, either long and uncinoloid or short and bristle-like, uncinoloid appendages 16–35, equatorial, ± stiff to flexuous, occasionally geniculate, 0.75–2.5 times as the chasmothecial diam., width 7–17 µm at the base, 3–4 µm throughout, somewhat increasing up to 6–7 µm near the apices, aseptate, occasionally with a single septum, hyaline, walls thicker (about 2 µm) at least at the lower half, but thin-walled towards the tip, verruculose; apices uncinate-circinate, helicoid; bristle-like appendages numerous in young chasmothecia, less numerous or almost lacking in mature chasmothecia, from the upper half of the chasmothecia, aseptate, hyaline, 10–25 × 3–5 µm; asci 8–23, ellipsoid, obovoid, saccate-clavate, 40–63 × 20–42 µm, short-stalked, 4–7(–10)–spored; ascospores ellipsoid–ovoid, 11–21 × 8–11, colorless.

Host range: *Prunus cerasus* L., *P. cerasifera* Ehrh. (Syn. *P. divaricate* Ledeb.), *P. spinosa* L., *Prunus* sp. L. (*Rosaceae*)

Specimens examined. Iran, Khorasan Razavi province, on *Prunus cerasus*, Karimi (GUM 1765); Guilan province, Rasht, on *P. cerasifera*, Oct. 2004, S.A. Khodaparast (GUM 1766); East Azerbaijan province, Arasbaran, on *P. ceracifera*, Oct. 2001, Gh. Tavanaei (GUM 1771); Mazandaran province, on *P. spinosa*, Oct. 1994, Abbasi and Moini (IRAN 9210F); Guilan province, Masooleh, on *Prunus* sp., June 1997, S.A. Khodaparast (IRAN 10828F); East Azerbaijan province, Arasbaran, on *Prunus* sp., Sept. 1999, Gh. Tavanaei (IRAN 10993F); Golestan province, Golestan National Park, on *P. ceracifera*, July 1993, M.A. Tajik Ghanbari (IRAN 9110F); Guilan province, Amarlu, on *P. ceracifera*, Oct. 1998, S.A. Khodaparast (IRAN 10829F); Mazandaran province, on *P. ceracifera*, Oct. 2004, Abbasi and Zare (IRAN 12343F).

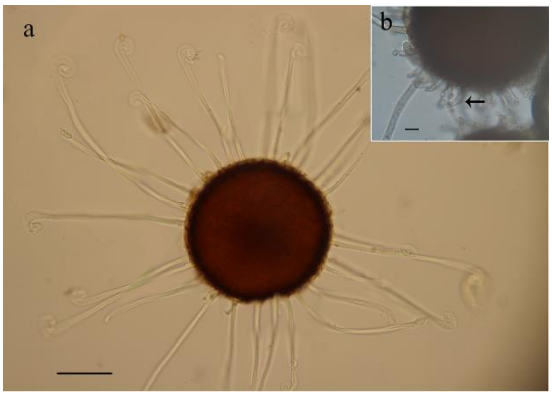

Fig. 15. *Erysiphe prunastri* var. *prunastri* (IRAN 10993F, *Prunus* sp.). a. Chasmothecium; b. Anchor hyphae. — Scale bars = (a) 50 µm; (b) 10 µm.

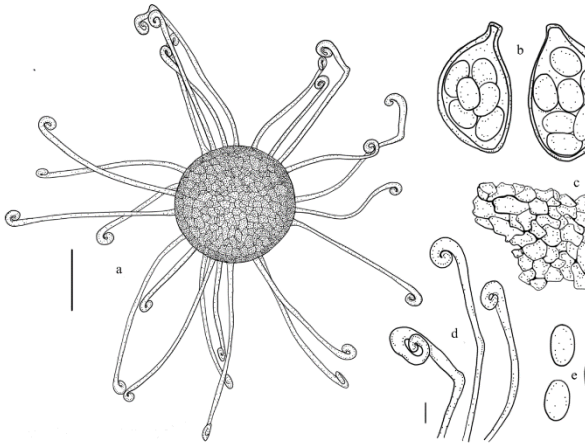

Fig. 16. *Erysiphe prunastri* var. *prunastri* (GUM 1766, *Prunus divaricata*). a. Chasmothecia; b. Asci; c. Peridium cells; d. Appendage tip; e. Ascospores. — Scale bars: (a) 50 µm; (b,c,d,e) 10 µm.

Erysiphe salicis DC., Flore française 2: 273 (1805), **var. *salicis***.Figs. 17–18

Chasmothecia gregarious or scattered, 122–172 µm diam.; peridium cells irregularly polygonal, 6–15 µm diam.; appendages 25–56 per chasmothecium, ± equatorial, flexuous, 0.5 to 3 times as long as chasmothecial diam., width about 4–7 µm around the base, up to 6–9 µm towards the tip, occasionally with a septum at the base, hyaline, walls thin throughout, somewhat thicker at the base, smooth, irregular outline, with constrictions and swellings, ± folded to twisted; apices uncinate-circinate; asci 8–17, ellipsoid-obovoid, saccate-clavate, 41–80 × 30–52 µm, short–stalked, sometimes almost sessile, 3–5–spored; ascospores ellipsoid–ovoid, 20–29 × 10–16 µm, colorless.

Host range: *Salix* sp. (*Salicaceae*)

Specimens examined. Iran, Isfahan province, Kashan, on *Salix* sp., 1950, Safavi (IRAN 5842F); Hamedan province, Hamedan, on *Salix* sp., Oct. 2015, M. Bahador (IRAN16921F); Chaharmahal and Bakhtiari province, Babaheidar, on *Salix* sp., S.A. Hashemi (GUM 1774F).

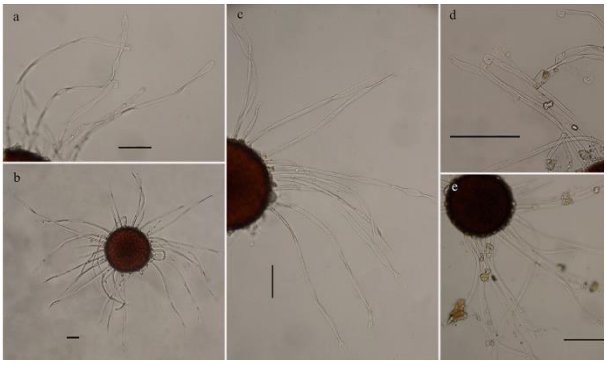

Fig. 17. *Erysiphe salicis* var. *salicis* (IRAN 16921F, on *Salix excelsa*). A,c,d,e. Close-up of appendages; b. Chasmothecium. — Scale bars = (a,b,c) 50 µm; (d,e) 100 µm.

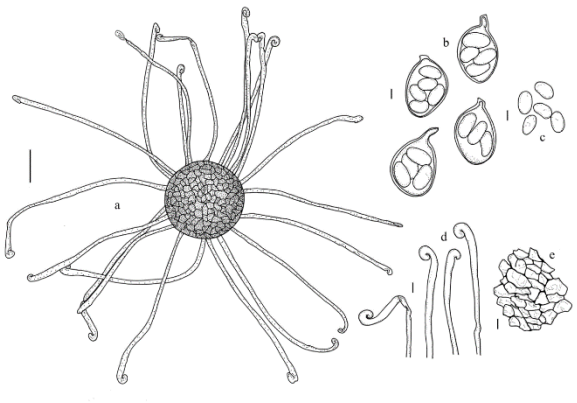

Fig. 18. *Erysiphe salicis* var. *salicis* on *Salix excelsa* (IRAN 16921F). a. Chasmothecia; b. Asci; c. Ascospores; d. Upper part of appendages; e. peridium cells. — Scale bars = (a) 50 µm, (b,c,d,e) 10 µm.

Erysiphe ulmi Castagne, Catalogue des plantes qui croissent naturellement aux environs de Marseille 492 (1845), **var. *ulmi***.Figs. 19–23

Chasmothecia scattered to ± gregarious, 70–99(–105) µm diam.; peridium cells irregularly polygonal, 7–23 µm diam.; appendages 6–26, equatorial, stiff to ± flexuous, occasionally curved around the chasmothecia, sometimes geniculate, 0.5–2 times as long as the chasmothecial diam, width 10–12 µm at the very base, 4–9 µm at the lower half, increase up to 6–12 µm towards the tip, aseptate, occasionally with a single septum near the base or in the lower half, hyaline, walls verruculose, thick–walled, width about 1–2 µm at the base, then decrease towards the tip; apices uncinate, circinate, often enlarged, occasionally 1–1.5 times coiled into a helix; asci (2–)3–7, often 3–6, sometimes they are countable in still closed mature chasmothecia, broadly ellipsoid-obovoid to globose, 40–62 × 32–50 µm, sessile to short-stalked, usually immediately split by water absorption, (1–)2–(3)–spored, mostly 2; ascospores large, ellipsoid-ovoid, 25–40 × 15–29 µm, colorless.

Host range: *Ulmus glabra* Huds. (Syn. *U. campestris*), *U. minor* Mill., *Ulmus* sp. L. (*Ulmaceae*)

Specimens examined. Iran, East Azerbaijan province, Arasbaran, on *Ulmus glabra*, Oct. 2001, Gh. Tavanaei (GUM 1769); Guilan province, Rasht, on *Ulmus* sp., 2019, H. Darsaraei (GUM 1772); Hamedan province, on *Ulmus* sp., Oct. 2015 (GUM 1773); Guilan province, Manjil, on *Ulmus* sp., Sept. 2020, S.A. Khodaparast (GUM 1775); Alborz province, Karaj, on *U. minor*, 1954, Mohammadi Doostdar (IRAN 11585F); Guilan province, Sumesara, on *Ulmus* sp., Aug. 1997, S.A. Khodaparast (IRAN 10826F); Guilan province, Amarlu, on *Ulmus* sp., Aug. 1998, S.A. Khodaparast (IRAN 10827F); Guilan province, Rasht, on *Ulmus* sp., 2020, H. Darsaraei (GUM 1776).

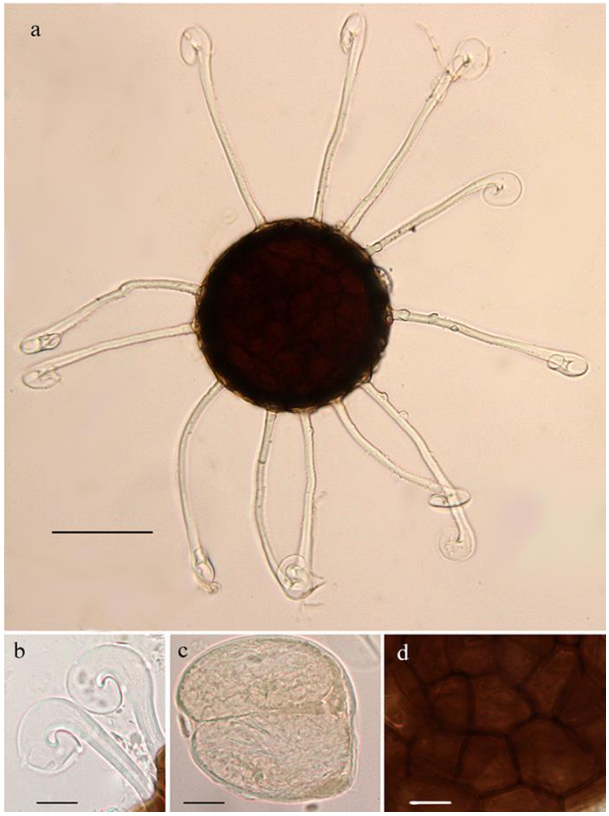

Fig. 19. *Erysiphe ulmi* var. *ulmi* (GUM 1769, on *Ulmus glabra*). a. Chasmothecium; b. Appendage tip; c. Asci; d. Perridium cells. — Scale bars = (a) 50 µm; (b,c,d) 10 µm.

Fig. 21. *Erysiphe ulmi* var. *ulmi* (IRAN 10826F, on *Ulmus* sp.). a,b. Chasmothecium; c. Asci; d. Close-up of appendages. — Scale bars = (a,b) 50 µm; (c,d) 10 µm.

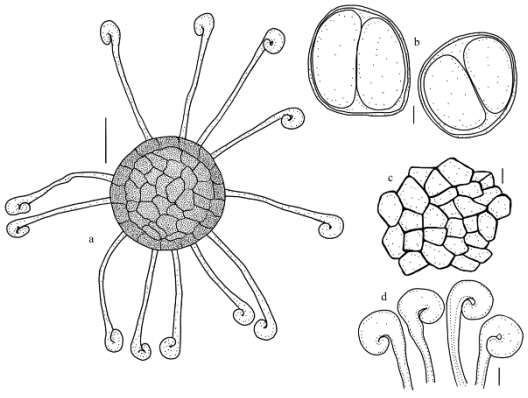

Fig. 20. *Erysiphe ulmi* var. *ulmi* (GUM 1769, on *Ulmus glabra*). a. Chasmothecia; b. Asci; c. Peridium cells; d. Appendage tip. — Scale bars = (a) 50 µm, (b,c,d) 10 µm.

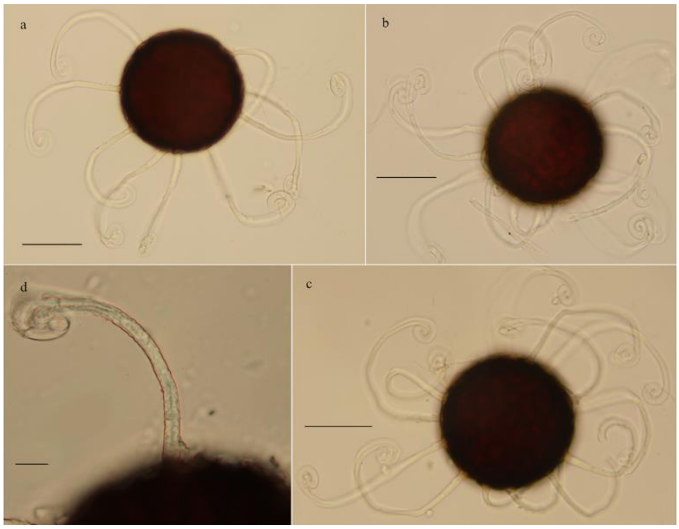

Fig. 22. *Erysiphe ulmi* var. *ulmi* (GUM 1776, on *Ulmus* sp.). a,b,c. Chasmothecium; d. Close-up of an appendage. — Scale bars = (a,b,c) 50 µm; (d) 10 µm.

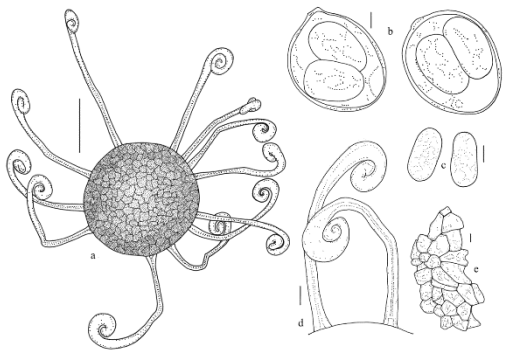

Fig. 23. *Erysiphe ulmi* var. *ulmi* (IRAN 10826F, on *Ulmus* sp.). a. Chasmothecium; b. Asci; c. Ascospores; d. Appendages; e. Perridium cells. — Scale bars = (a) 50 µm; (b,c,d,e) 10 µm.

DISCUSSION

We included 42 sequences of ITS and LSU rDNA generated from 26 Iranian specimens belonging to *E.* sect. *Uncinula* in our phylogenetic analyses (Fig. 1). These specimens were from eight plant families including *Betulaceae*, *Cannabaceae*, *Lythraceae*, *Rosaceae*, *Salicaceae*, *Sapindaceae*, *Ulmaceae*, and *Vitaceae*. In our analysis, most of sequences of powdery mildew species from a single plant family more or less clustered in a clade or related subclades. Powdery mildew fungi are a group of obligate plant pathogens that have evolved closely related with their host plants (Matsuda and Takamatsu 2002). Therefore, according to our findings, it can be suggested that species belonging to *E.* sect. *Uncinula* have also diverged in accordance with their host plants with exception of some powdery mildew species on *Carpinus* spp. that show different phylogeny. These findings have previously been shown by Takamatsu et al. (2015b) in a more comprehensive work on *E.* sect. *Uncinula* from Japan.

Sequences of *E. arcuata*, *E. australiana*, and *E. nacator* var. *necator* generated in this study perfectly matched the representative sequences of the same species in GenBank. Although there was a variation in *E. necator* sequences, we identified the Iranian specimens precisely using morphological features. The sequences available for *E. necator* on *Anacardium* (MK240383), on *Carica* (LC228619), and on *Hevea* (MT182958), have 5, 1, and 2 bases differences in ITS region compared with other sequences on *Vitis*, respectively. Hence, sequences of more genes should be provided to determine if this species is polyphagous or not. Two sequences from the ITS region of *E. paradoxa* are generated in this study for the first time. Morphological characteristics of our collection are largely concordant with Braun and Cook (2012) description. Hence, we propose this sequence as reference sequence for *E. paradoxa* until type material sequenced.

Four powdery mildew species infecting *Salix* and *Populus* species were included in our analyses. A full discussion concerns to *E.* sect. *Uncinula* species on Salicaceae is available in Darsaraei et al. (2021). *Erysiphe adunca s. lat.* is a common powdery mildew species on *Populus* and *Salix* species. Darsaraei et al. (2021) showed that *E. adunca* is a species complex comprising at least four species viz., *E. adunca s. str.* (on *Populus* spp.), *E. capreae*, (on *Salix* spp.), *E. salicis* (on *Salix* spp.), and *E. mandshurica* (on *Populus* spp.). This finding was confirmed by this study as all these species formed a single lineage with high bootstrap support (100%). The status of powdery mildew species occurring on Cannabaceae is rather ambiguous. Except for *E. aphananthes* that formed a well–supported clade, other species infecting *Celtis* spp., viz., *E. kusanoi*, *E. michikoae*, *E. celtidis* and four unspecified *Erysiphe* species, along with *E. zelkowae* on *Zelkova*, clustered together. Therefore, we need sequences from type material and more genes to answer if these species are conspecific or belong to different species. The Iranian specimen that we identified as *E. celtidis* (GUM 1770, OM574855) has appendages occasionally forked into branches, the character that was not mentioned in Braun's description, and its appendages wall are verruculose compared to the distinctly verrucose appendages in Braun's description. Besides, the sequence from Iranian specimen is clearly different from other species recorded on *Cannabaceae*. However, since no sequences of type or any other specimens of *E. celtidis* are available in GenBank, we preferred to ignore these morphological differences, and to assign this specimen to *E. celtidis*.

Powdery mildew specimens on *Ulmus* spp. from Iran showed some minor morphological differences with *E. ulmi* (according to Braun and Cook, 2012) in having smaller chasmothecia (70–99 µm vs. 75–110 µm), less number of appendages (6–26 vs. 9–40), 0–1–septate appendages with occasionally helicoid apices, and larger asci and ascospores. Nevertheless, the sequences from Iranian specimens have only one base different from sequences retrieved from Germany in which the type specimen originated. Moreover, there is no type sequence from *E. ulmi* still recorded in GenBank. Recently, Kirschner et al. (2020) segregated a new species from *E. ulmi* complex in Taiwan, namely *E. parvifoliae*. This species is well distinguished from other allied species in *E. ulmi* complex by the ITS sequences. With all these have in mind, we preferred to assign our specimen to *E. ulmi* var. *ulmi*.

Key to the species of *Erysiphe* sect. *Uncinula* in Iran

1a. Only asexual state is present 2
b. The sexual state is present 3
2a. Hyphal appressoria strongly lobed in opposite pairs or nipple–shaped; conidiophores 47–63(–73) ×

6–8 µm, foot–cells cylindrical, 24–39 × 6–8 µm, basal septum occasionally elevated up to 7 µm from the mother cell, followed by l–2(–3) shorter cells, on *Carpinus betulus* (*Betulaceae*) ***E. arcuata***

b. Hyphal appressoria lobed to multilobed, solitary, conidiophores 40–72 × 7–10 µm, foot cells cylindrical, 15–48 × 7–9 µm, followed by 1–2 shorter cells, on *Lagerstroemia indica* (*Lythraceae*) - ***E. australiana***

3a. Appendages widely or loosely uncinate, flexuous–curved, up to 8 times as long as the chasmothecial diam., on *Acer* (*Aceraceae*) - ***E. paradoxa***

b. Appendages typically uncinoloid 4

4a. Appendages dimorphic, uncinoloid and bristle–like, bristle–like appendages less numerous or even lacking in mature chasmothecia, uncinoloid appendages occasionally geniculate, 0.75–2.5 times as long as the chasmothecial diam., asci 9–18 (–23) in number, ascospores 4–7 per ascus, on *Prunus* spp. (*Rosaceae*) ***E. prunastri* var. *prunastri***

b. Appendages not dimorphic, only uncinoloid 5

5a. Appendages more than 25 per chasmothecium 6

b. Appendages less than 25 8

6a. Chasmothecia 117–187 µm diam., appendages numerous, 70–105 per chasmothecium, ± equatorial, (0.5–) 1–2 times as long as the chasmothecial diam., on *Salix* spp. (*Salicaceae*) ***E. capreae***

b. Appendages length up to 3 times as long as the chasmothecial diam. 7

7a. Chasmothecia 130–150 µm diam., appendages 40–60, occasionally forked into 2–3 branches, flexuous, irregular outline, with constrictions and swellings, asci 11–12 per chasmothecium, ascospores 4–6 per ascus, on *Populus* (Salicaceae) - ***E. adunca s. str.***

b. Chasmothecia 122–172 µm diam., appendages 25–56 per chasmothecium, with constrictions and swellings, asci 8–17 per chasmothecium, 3–5–spored, on *Salix* (*Salicaceae)* ***E. salicis* var. *salicis***

8a. Appendages 1–4 times as long as the chasmothecial diam., flexuous, multi–septate, brown at least at the lower half, asci 4–5–spored, on *Vitis vinifera* (*Vitaceae*) ***E. necator* var. *necator***

b. Appendage up to 2 times as long as the chasmothecia diam., width increases near the apex 9

9a. Chasmothecia 83–107 µm diam., appendages 9–21 per chasmothecium, wall verruculose, asci 3–5 per chasmothecium, 4–6–spored, on *Celtis australis* subsp. *caucasica* (*Cannabaceae*) ***E. celtidis***

b. Chasmothecia 78–105 µm diam., appendages 6–26 per chasmothecium, wall verruculose, asci 3–7 per chasmothecium, 2 (–3)–spored, on *Ulmus* spp. (*Ulmaceae*) ***E. ulmi* var. *ulmi***

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بازبینی تاکسونومیکی گونه‌های *Erysiphe* sect. *Uncinula* (*Erysiphaceae, Helotiales*) در ایران

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چکیده— پس از انتشار آخرین تک‌نگاره‌ی سفیدک‌های پودری توسط براون در سال ۲۰۱۲، بررسی جامعی روی گونه‌های از پیش گزارش‌شده‌ی جنس *Erysiphe* در ایران انجام نگرفته است. در مطالعه‌ی حاضر، با استفاده از ویژگی‌های ریخت‌شناختی و نیز توالی نواحی ITS و LSU (rDNA)، بازبینی تاکسونومیکی گونه‌های *Erysiphe* sect. *Uncinula* در ایران انجام پذیرفت. تعداد ۳۸ نمونه‌ی تهیه شده از هرباریوم قارچ‌شناسی دانشگاه گیلان (GUM) و مجموعه مرجع قارچ‌های وزارت جهاد کشاورزی (IRAN) و نمونه‌های تازه جمع‌آوری شده طی سال‌های ۱۴۰۰–۱۳۹۸ از نظر ریخت‌شناختی مورد بررسی قرار گرفتند. از این میان، ۲۶ نمونه برای مطالعه‌ی مولکولی انتخاب شد. برای هر ۲۶ نمونه توالی ITS و برای ۱۶ نمونه نیز توالی LSU تهیه شد. دو توالی از ناحیه‌ی ITS گونه‌ی *E. paradoxa* (OM574846 و OM574845) و نیز توالی نواحی ITS و LSU گونه‌ی *E. celtidis* (به ترتیب OM574855 و OM574834) سابقه‌ای در بانک ژن نداشتند و برای اولین بار در دنیا در این مطالعه تهیه شدند. بررسی‌های دقیق ریخت‌شناختی در کنار مطالعات مولکولی، تعداد گونه‌های *Erysiphe* sect. *Uncinula* در ایران را از ۶ گونه در سال ۱۳۸۸ به ۱۰ گونه در سال ۱۴۰۰ تغییر داد که در این مقاله تمامی این گونه‌ها با استفاده از تصاویر و ترسیم‌های دیجیتالی به طور دقیق توصیف می‌شوند. کلید شناسایی گونه‌های *Erysiphe* sect. *Uncinula* در ایران نیز در این مقاله آورده شده است.

کلمات کلیدی: تنوع زیستی، تبارشناسی، تاکسونومی، rDNA.

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