

Taxonomic update with DNA barcoding and phylogenetic analysis of Erysiphe sect. Microsphaera (Erysiphaceae, Helotiales) in Iran

H. Darsaraei

S.A. Khodaparast

S. Mousanejad

Department of Plant Protection, Faculty of Agricultural Sciences, University of Guilan, Rasht, Iran

K. Sepahvand

Lorestan Agricultural and Natural Resources Research and Education Center, Agricultural Research, Education and Extension Organization (AREEO), Khorramabad, Iran, and

B. Asgari S. Sajedi

Department of Botany, Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization (AREEO), Tehran, Iran

Abstract: In this study, the phylogeny and taxonomy of Erysiphe sect. Microsphaera was investigated for the first time in Iran. This study was based on morphological examination and rDNA (ITS+ LSU) sequencing. We examined 80 voucher specimens from the Fungus Reference Collection of Herbarium Ministerii Iranici Agriculturae (IRAN) and the University of Guilan Mycological fungarium (including specimens newly collected during 2019-2021). Seventy-nine sequences covering 20 species were generated. E. hyperici was not available for this study. Sequencing of E. begoniicola and E. tortilis failed. Based on our findings, E. coluteae and E. crispula were sequenced for the first time in this study. Records of E. erlangshanensis and E. castaneigena from Iran were rejected. The number of accepted species in sect. Microsphaera increased from 13 in 2009 to 23 in this study. Erysiphe crispula on Astragalus spp. is reported here for the first time, and Syringa vulgaris has been reported as a new host of E. syringae-japonicae in Iran. Furthermore, DNA barcodes, colored plates, digital illustrations, and

identification keys of all *E*. sect. *Microsphaera* in Iran are provided herein.

Keywords: Biodiversity, powdery mildews, rDNA, phylogeny, Taxonomy

INTRODUCTION

Powdery mildews (Erysiphaceae, Helotiales) are plant important pathogens found almost circumglobally (Braun & Cook 2012, Johnston et al. 2019). Erysiphe R. Hedw. ex DC., the largest genus in this family, comprises 5 morphological (but not phylogenetic) sections: Erysiphe sect. Erysiphe (with mycelioid chasmothecial appendages), E. sect. *Microsphaera* (chasmothecial appendages with dichotomously branched tips), E. sect. Uncinula (tips of chasmothecial appendages uncinate-circinate). E. sect. Californiomyces (with no or only a few sparingly developed mycelioid appendages), and E. sect. Typhulochaeta (with special apical cells instead of true appendages) (Braun & Takamatsu 2000, Braun & Cook 2012; Takamatsu et al. 2015). Five species of sect. Californiomyces is limited to Thailand, Taiwan, India, and USA, while sect. Typhulochaeta with three species is limited to China, USA, and Japan (Braun & Cook, 2012).

Section Microsphaera, which previously was considered to be a separate genus (Braun 1987, Braun & Takamatsu 2000), is particularly characterized by having appendage tips that are dichotomously branched (Braun & Cook 2012, Takamatsu et al. 2015). The degree of recurved versus straight appendage tips is the most challenging era in identifying members of the sect. Microsphaera. This characteristic varies from early to late season, under different weather conditions, and at different latitudes (Bradshaw et al. 2021a, Liu et al. 2022); therefore, it is not logical to rely only on this morphological character to distinguish allied species, and taxonomists would need more helpful characteristics for reliable species identification. After the publication of the powdery mildew monograph by Braun and Cook (2012), several attempts have been

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made to discover new species of sect. *Microsphaera* as well, and the molecular evidence has paved the way for species identification to a great extent. Taking advantage of ITS- and 28S-rDNA sequences, some new species have been introduced (Abasova et al. 2018, Bradshaw et al. 2021b, Darsaraei et al. 2022), several varieties upgraded to species level (Bradshaw et al. 2021a), and some previously described species combined as a single species (Liu et al. 2022). However, as mentioned by Liu et al. (2022), sequence data of ITS-rDNA and LSU are not sufficiently discriminating in some cases, such as *Erysiphe* spp. on *Berberidaceae*, and there is an urgent demand for sequencing protein-coding genes to resolve this issue.

Section *Microsphaera* is the largest section in terms of the number of species, followed by sect. *Erysiphe*, sect. *Uncinula*, sect. *Californiomyces*, and sect. *Typhulochaeta* (Braun & Cook, 2012). From approximately 60 species of the genus *Erysiphe* in Iran, *E.* sect. *Microsphaera*, with 23 species, showed the highest diversity in Iran, followed by sect. *Erysiphe* (approximately 22 species), and sect. *Uncinula* (10 species) (Darsaraei 2022).

Having more than 7500 plant species and a diverse climate (Haftlang 2003, Assadi 2019), Iran is located in a good location to find several fungi, including powdery mildew. To the best of our knowledge, members of *E.* sect. *Microsphaera* appear on trees, shrubs, and herbaceous plants as well. Until 2009, only 13 species of the *E.* sect. *Microsphaera* have been reported from Iran (Khodaparast & Abbasi 2009), and no comprehensive study of *Erysiphe* spp. in Iran has been performed since the release of Braun and Cook's monograph of powdery mildews in 2012.

In this study, we re-examined herbarium specimens and newly collected materials to provide a state-of-the-art checklist for *E.* sect. *Microsphaera* in Iran. Meanwhile, DNA barcodes, colored plates, digital illustrations, and identification keys of all *E.* sect. *Microsphaera* in Iran are provided herein.

MATERIALS AND METHODS

Sample collection

Specimens collected from different locations in Iran from 2019 to 2021, as well as voucher specimens obtained from the University of Guilan Mycological fungarium (GUM) and the Fungus Reference Collection of Herbarium Ministerii Iranici Agriculturae (IRAN) (a total of 80) were included in this study.

Morphological examinations

All fungal structures were transferred into a drop of 1:1 glycerin: lactic acid on a microscopic slide, using a sterile needle or a clear adhesive tape. At least 20 fungal structures (sexual or asexual) were examined and measured under a light microscope. 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

Total DNA extraction was performed using Chelex (Walsh et al., 2013, Hirata & Takamatsu 1996) or Thermolysis method (Zhang et al. 2010, Khodaparast et al., 2021).

PCR amplification of the internal transcribed spacer regions, including the intervening 5.8S nuclear ribosomal DNA (ITS) was done using the primers (5'-TCGGACTGGCCYAGGGAGA-3') PMITS1 (Cunnington et al. 2003) /PM11(5'-TACCGCTTC ACTCGCCCGTTA-3') (Bradshaw & Tobin 2020) for the first reaction, and PM10 (5'-GGCCGGAAA GTTGTCCAAAC-3) (Bradshaw & Tobin 2020)/ PM11 for the semi-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'-GKGCTYTMCGCGTAGT) (Takamatsu & Kano2001)/NLP2(5'-GGTCCCAACAGCTATGCTC T-3') (Mori et al. 2000), and the semi-nested reaction using the RPM2 (5-ACCTCAGTAACGGCGAGT GA-3') (Bradshaw & Tobin 2020) / NLP2. PCR components and conditions were in accordance with Darsaraei et al. 2021. The amplicons were then sent to Codon Genetic Group (Tehran, Iran) for sequencing. Newly generated sequences were deposited in GenBank (https://www.ncbi.nlm.nih. gov/genbank/) under the accession numbers written in table 1 (See table S1 for other sequences used in this study). New sequences as well as representative sequences of E. sect. Microsphaera from GenBank were aligned 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). Maximum likelihood (ML) analysis was used to estimate the phylogenetic relationships of combined ITS-rDNA and LSU sequences. The phylogenetic tree was obtained using raxmlGUI (Silvestro & Michalak 2012), under the GTRGAMMA substitution model along with rapid bootstrap analysis of 1000 pseudo-replicates followed by a search for the tree with the highest likelihood.

RESULTS

Phylogenetic analysis

Seventy-nine sequences from 20 species out of 23 species of E. sect. Microsphaera in Iran were generated in this study. Sequencing of E. begoniicola and E. tortilis failed. A total of 127 combined sequences of ITS + LSU rDNA regions were included in the phylogenetic analysis. Phyllactinia moricola (AB080561) and Leveillula taurica (AB667884) were used as the outgroup taxa. The final alignment with 1043 characters was partitioned to partition ITS and partition LSU for the combined analysis. The final ML Optimization Likelihood value was obtained as -4455.098857 for the output tree. The final alignment had 393 distinct alignment patterns. The alignment patterns for partition ITS and partition LSU were 276 and 117, respectively. The alpha parameter was 0.307182 and 0.131950 for partition ITS and partition LSU, respectively. Tree length for partition ITS and

partition LSU was calculated as 1.500832 and 12.449781, respectively. Except for the families Caprifoliaceae, Betulaceae, and Fagaceae, all other host families formed individual clades with high BS support (Fig. 1). Members of E. viburni Duby, E. lonicerae DC. (s. str.), E. symphoricarpi (Howe) U. Braun & S. Takam., E. erlangshanensis (Y.N. Yu) U. Braun & S. Takam., E. viburni-plicati Meeboon & S. Takam., E. lonicerina S. Takam., E. ehrenbergii (Lév.) U. Braun, M. Bradshaw & S. Takam., and E. miurae (U. Braun) U. Braun & S. Takam. from Caprifoliaceae were divided into several clades with 96-100% BS supports. One sequence from the specimen on Viburnum lantana L. (from Iran: OM856008) was placed in the E. viburni clade, while six sequences from the specimens on Lonicera spp. (from Iran: OM855995-OM856000) were placed in the *E. ehrenbergii* clade.

Sequences retrieved from the powdery mildews on the Betulaceae including E. corylacearum U. Braun & S. Takam., E. pseudocorylacearum Meeboon & M. Bradshaw, E. coryli-americanae M. Bradshaw, E. cornutae M. Bradshaw (all from Corylus spp., subfamily Coryloideae) and E. penicillata (Wallr .: Schltdl. (from Alnus spp., subfamily Fr.) Betuloideae), each formed an individual clade with 89-100% BS supports. However, the small subclade comprising E. syringae-japonicae (U. Braun) U. Braun & S. Takam. sequences from *Oleaceae* were also included within the clade of Erysiphe species on Betulaceae. Erysiphe tortilis (Wallr.: Fr.) Link on Cornaceae is a distinct species and formed a separate clade with 100% BS support. Sequences from the species infecting Celastraceae (E. euonymicola U. Braun) formed a clade that is sister to the E. alphitoides (Griff. & Maubl.) U. Braun & S. Takam. clade, and E. quercicola S. Takam. & U. Braun formed a separate clade with 99% BS support. Sequences from E. castaneigena U. Braun & Cunnington, another species infecting Fagaceae, were placed far from other species on Fagaceae and formed an individual, strongly supported clade.

All sequences from the *Berberidaceae* formed a distinct, strongly supported clade. These sequences are rather identical, and there is no significant difference among the morphological varieties of *E. berberidis s. lat.* Sequences retrieved from *Fabaceae*, including *E. trifoliorum* (Wallr.) U. Braun (OP806848 and OP806849), *E. robiniae* Grev. (OP806850), and *E. sesbaniae* Wolcan & U. Braun (OP806847) were placed in the large *E. trifoliorum* complex clade. These sequences are similar and the abovementioned species cannot be distinguished only by ITS + LSU rDNA information.

The small, strongly supported subclade comprising *E. iranica* Darsaraei, Khodap. & Pirnia was also placed within the *E. trifoliorum* complex clade. Sequences assigned to *E. astragali* DC., *E. crispula* (U. Braun) U. Braun & S. Takam., and *E. coluteae* (Kom.) U. Braun & S. Takam. formed a clade with

92% BS support, with subclades of *E. bremeri* U. Braun (79% support) and *E. intermedia* (U. Braun) U. Braun (87% support) within the clade. Another fullysupported clade comprises *E. magnifica* (U. Braun) U. Braun & S. Takam. from *Magnoliaceae* and *Nelumbonaceae*. *Erysiphe platani* (Howe) U. Braun & S. Takam. from *Platanaceae* and *Sapindaceae* formed a distinct clade with 100% BS support. **Taxonomy**

Erysiphe alphitoides (Griff. & Maubl.) U. Braun & S. Takam., Schlechtendalia 4: 5, 2000 Figs. 2–3.

Mycelia epiphyllous, occasionally covers the entire surface of the leaf; conidia cylindrical, ovoid, ellipsoid, sometimes with oil drops, $22-37 \times 12-16$ µm. Chasmothecia epiphyllous, gregarious to scattered, (61-) 70-89 µm; peridium cells conspicuous, irregularly polygonal, 10-25 µm; appendages 5–10, almost equatorial, occasionally with 1 septum near the base, hvaline, pigmented under the septa, length about 1-1.5 times as long as the chasmothecial diam., width 5-7 µm, thin-walled, thicker near the base which decreases towards the tip, rather rough; apices 5-6 times dichotomously branched, primary and secondary branches rather elongated, tips completely recurved; asci 3-4, saccate, globose, almost sessile, $44-50 \times 34-44 \ \mu m$; ascospores (5–) 6–7 (–8), ellipsoid, ovoid, $15-23 \times 9-$ 12 µm.

Host range: Quercus infectoria G. Olivier, Q. macranthera Fisch. & C.A. Mey. ex Hohen. (Fagaceae).

Abbasi et al. (2013) have reported *E. castaneigena* U. Braun & Cunningt. on *Q. macranthera*. We sequenced this specimen (IRAN 14248F), it grouped with *E. alphitoides* and was clearly separated from *E. castaneigena*.

Specimens examined. Iran, West Azerbaijan province, Piranshar-Sardasht road, on *Quercus infectoria*, 2016, K. Sepahvand (GUM 1792); Sardasht- Baneh road, on *Q. infectoria*, Oct. 2016, K. Sepahvand (GUM 1799); Kermanshah province, Gahvareh-Kouzara road, on *Q. infectoria*, Sept. 2017, K. Sepahvand (GUM 1796); Lorestan province, Alashtar (Ghelai), on *Q. infectoria*, K. Sepahvand (GUM 1798, GUM 1800, GUM 1802); East Azerbaijan province, Arasbaran, on *Q. macranthera*, Aug. 2007, M. Donyadost–Chalan (IRAN 14248F). *Erysiphe astragali* DC., FI. franç. 6: 105, 1815 Figs. 4–5.

Asexual state not observed. Chasmothecia globose to depressed globose, hypophyllous or amphigenous, not observed on stems, the number of chasmothecia is obviously fewer than what is expected in *E. caulicola*, scattered to gregarious, 107–156 μ m diam.; peridium cells not very conspicuous, irregularly polygonal,9–30 μ m; appendages 5–25, equatorial or from the upper part of the chasmothecia, long and flexuous, occasionally interwoven with each other, 329–735 μ m (about 1–7.5 times as long as the chasmothecial diam.), occasionally tend to point in one direction, septate, often with 1 septum, pale brown to brown,



— 0.01substitutions/site

Fig. 1. A Maximum-Likelihood consensus tree inferred from the combined ITS and the D1–D2 portion of the LSU ribosomal DNA of members of *Erysiphe* sect. *Microsphaera*. Numbers at the branches indicate bootstrap support above 70 %. The scale bar indicates expected changes per site.



Fig. 2. Erysiphe alphitoides (IRAN 14248F on *Quercus macranthera*). a. Chasmothecia; b. Tips of appendages; c. Acsi in closed chasmothecia; d. Asci. — Scale bars = (a) 50 μ m; (b,c,d) 10 μ m.



Fig. 3. *Erysiphe alphitoides*. a. Chasmothecium; b. Asci; c. Tips of appendages. — Scale bars = (a) 50 μ m; (b,c) 10 μ m.

darker near the base and hyaline towards the tip.

width about 15–25 μ m at the very base, then 5–10 μ m which decreases towards the tip, wall smooth to somewhat rough, thin, somewhat thicker near the base; apices at least dichotomously branched in some appendages, tips rather recurved; asci 5–10, saccate, ellipsoid, short-stalked, 57–82 × 28–46 μ m; ascospores 2–6, ellipsoid, ovoid, 16–28 × 9–17 μ m, colorless.

Host range: Astragalus sp. L., A. glycyphyllos L. (Fabaceae)

Specimens examined. Iran, Zanjan province, Zanjan, on *Astragalus* sp., Aug. 2006, S. A. Khodaparast (GUM 1811, GUM 1895); Golestan province, Golestan National Park, on *A. glycyphyllos*, Sept. 1993, M. A. Tajik Ghanbari (IRAN 9092F); Ardabil province, Ardabil, on *Astragalus* sp., Aug. 2004, S. A. Khodaparast (GUM 1894).



Fig. 4. *Erysiphe astragali* (GUM 1811 on *Astragalus* sp.). a. Chasmothecium with appendages tend to point in one direction; b. Adjacent chasmothecia with interwoven appendages. — Scale bars = (a,b) 50 µm.



Fig. 5. *Erysiphe astragali*. a. Chasmothecium; b. Peridium cells; c. Asci. — Scale bars = (a) 50 μ m; (b,c) 10 μ m.

Erysiphe begoniicola U. Braun & S. Takam., Schlechtendalia 4: 5, 2000

Mycelium amphigenous, mostly epiphyllous, dense or in patches, hyphae slightly sinuous and branched, hyphal cell width 4.8–9.6 μ m; conidiophores erect, 43.2–84 × 7.2–12 μ m; foot-cells cylindrical, 24–52.8 × 7.2–9.6 μ m, followed by 1–2 shorter cell, forming conidia singly, conidia cylindrical, 28.8–60 × 12–19.2 μ m. Sexual state not observed.

Host range: Begonia spp. Hook. (Begoniaceae).

Specimen examined. Iran, Guilan province, Lahijan, on Begonia sp., 15 May 2003, Ghavami (GUM 170); Rasht, 1 July 2004, S. A. Khodaparast (GUM 1930).

The examined specimens included a damaged anamorphic stage, hence were not suitable for morphological studies. The description presented here is based on Sharifi et al., 2013.

Erysiphe berberidis DC., FI. franç. 2: 275, 1805Figs. 6–7

Recently Liu et al. (2022) revisited some *Erysiphe* species on *Berberis* and *Mahonia* spp. including *E. berberidis s. lat., E. berberidicola* (F.L. Tai) U. Braun & S. Takam and *E. multappendicis* (Z.Y. Zhao & Y.N. Yu) U. Braun & S. Takam. They reduced *E.*

berberidicola and *E. multappendicis* (Z.Y. Zhao & Y.N. Yu) U. Braun & S. Takam. to synonyms of *E. berberidis* and accepted three morphological varieties. We follow this decision in the taxonomic treatment of Iranian collections.

Host range: Berberis sp. L., B. vulgaris L., B. thunbergii DC., B. integerrima Bunge, B. aquifolium Pursh (Syn. Mahonia aquifolium (Pursh) Nutt.) (Berberidaceae)

Erysiphe berberidis var. berberidis

Mycelia amphigenous, mostly epiphyllous, sometimes covers the whole surface of the leaves, hyphae branched, hyphal cell width 3-6 µm, hyphal appressoria nipple-shaped, lobed to multi-lobed, solitary or in opposite pairs; conidiophores arising from the middle of the mother cell or rather laterally, straight or somewhat sinuous, $37-68 \times 7-8 \mu m$; footcells cylindrical, $21-31 \times 5-7 \mu m$, followed by 1-2 (-3) other cells, forming conidia singly; conidia cylindrical, ellipsoid, occasionally form a false chain in wet conditions, $24-42 \times 9-13 \mu m$, conidial germination terminal or lateral, germ tube to conidial length ratio 0.31 - 1.8, conidial appressoria multilobed. amphigenous, Chasmothecia mostly epiphyllous, occasionally on stems, gregarious to scattered, 72-146 µm diam.; peridium cells irregularly polygonal to somewhat rounded, not very conspicuous, 7-30 µm; appendages (3-) 5-28, equatorial, stiff, hyaline, occasionally pale brown to brown at the base, septate, with 0-2 septa, about 1-3times as long as the chasmothecial diam., width 5-20 μ m at the very base, then 4–5 μ m, wall smooth to somewhat rough, thicker at the base about 3 µm), then about 1 μ m towards the branchlets; apices 3–6 times dichotomously branched, branching occasionally happens at the base or the middle of the appendage, but often terminal, primary and secondary branches occasionally elongated, tips of mature specimens are straight, or only a single or few tips are somewhat recurved.; asci 3-13, saccate-clavate, ellipsoid to rather globose, short-stalked to almost sessile, 47-86 × 28-55 µm; ascospores (2-) 3-6 (-7), ellispoid, ovoid, rather reniform, (14-) 17–34 × 8–18 μm, colorless.

Specimens examined. Iran, East Azerbaijan province, Arasbaran, on *B. vulgaris*, Oct. 2001, Gh. Tavanaei (GUM 1886); North Khorasan province, Shirvan, on *Berberis* sp., Sept. 1994, Abbasi, Fatehi & Foitzik (IRAN 10545F).

Erysiphe berberidis var. *asiatica* (U. Braun) U. Braun & S. Takam., Schlechtendalia 4: 6, 2000

Appendages tips are similar to var. *berberidis*, but they are uniformly shorter (0.5-1.5 (-2) times as long as the chasmothecial diam.), primary branches are rather elongate, but the apex is rather tight and regular. Tips are straight, rarely with a few recurved tips in mature specimens.

Specimens examined. Iran, Tehran province, Tehran, on *Berberis* sp., Nov. 1998, Abbasi (IRAN 15773F); East Azerbaijan province, on *Berberis* sp., Oct. 1999, Gh. Tavanaei (IRAN 11287F); Guilan province, Damash, on *Berberis* sp., June 2020, S. A. Khodaparast (GUM 1804); Yazd province, Yazd, on *B. integerrima*, July 2007, Esmaeilzadeh-Hosseini (IRAN 13470F).

Erysiphe berberidis var. *dimorpha* (Y.N. Yu & Z.Y. Zhao) L. Liu & U. Braun, Mycoscience 63, 2022

This variety is more similar to var. *berberidis*, but with always recurved tips in mature specimens (or at least a certain number of tips are recurved) and curved, sinuous, or flexuous appendages with various apex branching patterns.

Specimens examined. Iran, Qazvin province, Qazvin, on Berberis sp., June 2019, S. A. Khodaparast (GUM 1803); Guilan province, Deileman-Kalishom road, on *B. vulgaris*, Aug. 1998. S. A. Khodaparast (GUM 73, IRAN 10812F); Rasht, on *B. thunbergii*, May 2021, H. Darsaraei (GUM 1887); Isfahan province, Zarinshahr, on *B. thunbergii*, K. Sharifi (GUM 1715); Alborz province, Karaj, on *B. aquifolium*, Aug. 2011, Tanghatari & Moghimi (IRAN 15601F); Yazd province, Yazd, on *B. integerrima*, June 2010, Esmaeilzadeh-Hosseini (IRAN 15771F); unknown location, on *B. vulgaris*, 1956 (IRAN 2551); on *B. integerrima* (IRAN 2552F).



Fig. 6. Chasmothecia of *Erysiphe beberidis*. a. var. *berberidis* (IRAN 10545F on *Berberis* sp.); b. var. *asiatica* (IRAN 13470F on *B. integerrima*); c. var. *dimorpha* (IRAN 15601F on *B. aquifolium*). — Scale bars = (a,b,c) 50 µm.



Fig. 7. *Erysiphe beberidis s. lat.* a. Chasmothecium; b. Asci; c. Peridium cells; d. Tips of appendages (straight and/or recurved). — Scale bars = (a) 50 μ m; (b,c,d) 10 μ m.

Erysiphe bremeri U. Braun, Mycotaxon 15: 133, 1982 Figs. 8–9

Mycelia branched, hyphal appressoria lobed; conidia ellipsoid, cylindrical, ovoid, 25-40 × 12-17 µm, conidial germination sub-terminal. Chasmothecia amphigenous and caulicolous, gregarious to almost scattered, 120-168 µm diam.; peridium cells irregularly polygonal, 7–20 µm; appendages numerous, almost equatorial or from the lower half, geniculate and sinuous, appendages of the adjacent chasmothecia occasionally interwoven with each other, flexuous, hyaline, sometimes pale brown, with one or more septa rear the base and brown under the septa, length 117–572 µm, (0.5–4.5 times as long as the chasmothecial diam.), width 5-7 µm, thin-walled, somewhat thicker near the base, smooth or verruculose; apices 1-3 times dichotomously branched, primary branches loosely elongated, tips straight or recurved (majority are recurved); asci 7-14, broadly ellipsoid, short to long-stalked or almost sessile, $57-87 \times 23-37 \mu m$; ascospores (2–) 3–6 (–7), ellipsoid, ovoid; $18-25 \times 8-14 \mu m$.

Host range: Alhagi sp. Gagnebin, A. maurorum Medik., Sophora pachycarpa C.A.Mey. (Fabaceae) Specimens examined. Iran, Guilan province, on Alhagi sp., Sept. 2020, S. A. Khodaparast (GUM 1814); Yazd province, Yazd, on A. maurorum, Oct. 2004, Esmaeilzadeh-Hosseini (IRAN 13735F); on *A. maurorum*, Nov. 2010, Javidi (IRAN 15768F); on *Sophora pachycarpa*, June 2007, Esmaeilzadeh-Hosseini (IRAN 13471F).



Fig. 8. Chasmothecia of *Erysiphe bremeri* (IRAN 13471F on *Sophora pachycarpa*). — Scale bar = 50 μ m.

Erysiphe coluteae (Kom.) U. Braun & S. Takam., Schlechtendalia 4: 7, 2000 Figs. 10–11

Asexual state not observed. Chasmothecia 113–161 (–192) μ m diam.; peridium cells irregularly polygonal, 8–26 μ m; appendages 11–20, equatorial, somewhat tend to point to one direction, flexuous, occasionally sinuous near the base, occasionally septate with 1 septa, hyaline to somewhat pale brown, may interwoven with each other, length 392–930 μ m (about 4–9 times as long as the chasmothecial diam.), width 5–8 μ m, thin-walled, somewhat thicker near the base, smooth to rather rough; apices 2–5 times dichotomously and loosely branched, primary branches elongate, tips seem to be straight; asci 6–16, saccate-clavate, ellipsoid, with a short or long stalk, 67–89 × 37–56 μ m; ascospores 4–6, ellipsoid, ovoid, 16–25 × 10–17 μ m, colorless.

Host range: Colutea buhsei (Boiss.) Shap., Colutea sp. L. (Fabaceae)

Specimens examined. Iran, Golestan province, Gilestan National Park, on *Colutea buhsei*, Sept. 1993, M.A. Tajik Ghanbari (IRAN 9105F); Alborz province, on *C. buhsei*, June 1999, Abbasi & Hedjaroud (IRAN 11564 F); Tehran province, Tehran, on *Colutea* sp., Aug. 1993, Abbasi, Fatehi & Foitzik (IRAN 9213F).



Fig. 9. *Erysiphe bremeri*. a. Chasmothecium; b. Asci; c. Conidia; d. Conidial germination; e. Hyphal appressoria. — Scale bars = (a) 50 μ m; (b,c,d,e) 10 μ m.



Fig. 11. *Erysiphe coluteae*. a. Chasmothecium; b. Asci; c. Tips of appendages; d. Peridium cells. — Scale bars = (a) 50 μ m; (b,c,d) 10 μ m.



Mycelia amphigenous, white, scattered or in patches, hyphal appressoria lobed, solitary or in opposite pairs; conidiophores arising from the top of the mother cell, length (40–) 54–160 μ m, foot-cells cylindrical, straight, occasionally somewhat sinuous, 20–50 (–70) × 5–9.5 μ m, followed by 1–2 shorter cells, forming conidia singly; conidia of various shapes, ellipsoid-ovoid, barrel-shape, (19–) 25–42 × (–10) 14–22 μ m, conidial germination terminal, germ tube often short to long, conidial appressoria simple or lobed. Sexual state not observed.

Host range: Corylus avellana L., Corylus sp. L. (Betulaceae)

Specimens examined. Iran, Guilan province, Lahijan, on *Corylus avellana*, May 2017, S. A. Khodaparast (GUM 786); Rasht, on *Corylus* sp., May 2021, H. Darsaraei (GUM 1888).



Fig. 10. Chasmothecia of *Erysiphe coluteae* (IRAN 9105F on *Colutea buhsei*). — Scale bar = $50 \mu m$.



Fig. 12. *Erysiphe corylacearum* (GUM 786 on *Corylus avellana*). a. Conidiophores; b. Conidia; c. Conidial germination. — Scale bars = (a,b,c) 10 µm.

Erysiphe crispula (U. Braun) U. Braun & S. Takam., Schlechtendalia 4: 7, 2000 Figs. 13-14 Asexual state not observed. Chasmothecia amphigenous and caulicolous, gregarious to scattered, 94–182 µm diam.; peridium cells irregularly polygonal, 8-30 µm; appendages 10-15, equatorial or from the lower half, septate, the distribution is rather horizontal and not pointing to one direction, hyaline, occasionally pale brown, septate, with 1 septum near the base or with multiple septa, hardly geniculate, sinuous and twisted, length 60-650 µm (up to about 5.5 times as long as the chasmothecial diam.), with 15-20 µm at the very base, then 5-11 µm which decreases towards the tip, thin-walled, somewhat thicker near the base, smooth to rough or somewhat apices simple verruculose; or 3–6 times dichotomously or sub-dichotomously and loosely branched, tips may recurved at each level; asci 5-15, saccate-clavate, short to long-stalked, 63–89 (-103) \times 31–54 μ m; ascospores 3–61 ellipsoid, ovoid, 17–30 \times 10-17(-19) µm, colorless.

Host range: Astragalus iranicus Bunge, A. ovinus Boiss., A. kahiricus DC., A. basineri Trautv., A. kirrindicus Boiss, Astragalus sp. L. (Fabaceae)

Specimens examined. Iran, Lorestan province, Oshtorankuh, on Astragalus iranicus, K. Sepahvand (GUM 1812); Kamandan village, on A. ovinus, June 2011, K. Sepahvand (GUM 1813); South Khorasan province, Tabas, on A. kahiricus, May 2013, M. Shamszadeh (GUM 798); Guilan province, Deylaman, on Astragalus sp., Aug. 1998, S.A. Khodaparast (IRAN 10811F); Golestan province, Golestan National Park, on A. bassineri, June 1993, M. A. Tajik Ghanbari (IRAN 9104F); Yazd province, Tabas-Robat road, on A. kirrindicus, May 2010, Shamszadeh (IRAN 15063F); Tabas, on A. kirrindicus, May 2009, Shamszadeh (IRAN 15769F).



Fig. 13. *Erysiphe crispula* (GUM 798 on *Astragalus kahiricus*). a. Chasmothecium; b. Asci; c. Tips of an appendage; d. Peridium cell. — Scale bars = (a) 50 μ m; (b,c,d) 10 μ m.



Fig. 14. *Erysiphe crispula* (GUM 1812 on *Astragalus iranicus*). a. Chasmothecium; b. Ascus; c. Peridium cell. — Scale bars = (a) 50 μ m; (b,c) 10 μ m.

Erysiphe ehrenbergii (Lév.) U. Braun, M. Bradshaw & S. Takam., FUSE 7, 2021 Figs. 15-17 Asexual state not observed. Chasmothecia amphigenous and on branches, gregarious to scattered, 67-107 (161) µm diam.; peridium cells irregularly polygonal and conspicuous, 8-31 µm; appendages 4-18, almost equatorial, stiff to flexuous, aseptate or with 1-2 septa, length about 0.15-2 times as long as the chasmothecial diam. (2-4 times in IRAN 10994F and 1-3 times in IRAN 12543F), width 7-10 µm at the very base, then 4-7 µm throughout which decreases at the branches, wall smooth to rough or verruculose, thicker at the base about 12 µm), then thinner towards the tips, hyaline,

brown under the septa, occasionally geniculate; apices 4–5 (–6) times dichotomously branched, primary branches often elongate, tips often recurved the straight/recurved ratio depends on the fungus age or the weather conditions when sampling); asci (2–) 3–4 (3–6 in IRAN 10994F, and 3–7 in IRAN 12543F), saccate-clavate, globose to sub-globose, short-stalked to almost sessile, 46–69 × 30–59 µm; ascospores (2–) 3–6 (mostly 4–5), ellipsoid, ovoid or oblong-ellipsoid, 19–31 × 10–17 µm, colorless.

Host range: *Lonicera iberica* M.Bieb., *L. caucasica* Pall., *L. nummulariifolia* Jaub. & Spach, *Lonicera* sp. L. (*Caprifoliaceae*)

Specimens examined. Iran, East Azerbaijan province, Arasbaran, on Lonicera iberica, Oct. 2001, Gh. Tavanaei (GUM 1890); Aug. 1999, Gh. Tavanaei (IRAN 11014F); Aug. 2007, Donyadost–Chalan (IRAN 14281F); on L. caucasica, Oct. 1999, Gh. Tavanaei (IRAN 10994F); Guilan province, Amarlu, on L. nummulariifolia, Aug. 1998, S. A. Khodaparast (IRAN 10849F); Ardabil province, Ardabil, on Lonicera sp., Aug. 1970, Izadyar (IRAN 12543F).

Erysiphe euonymicola U. Braun, 2012

Fig. 18

Mycelia epiphyllous, in white and dense patches; conidiophores straight, $50-80 \times 7-9 \mu m$; foot-cells cylindrical, straight, $20-50 \times 7-9 \mu m$, followed by 1–2 shorter cells, forming conidia singly; conidia ellipsoid, cylindrical, $24-40 \times 12-18 \mu m$, conidial germination terminal or sub-terminal, germ tube short, conidial appressoria multilobed. Sexual state not observed.

Host range: *Euonymus japonicus* Thunb., *Euonymus* sp. L. (*Celastraceae*)

Specimens examined. Iran, Isfahan province, Isfahan, on *Euonymus* japonicus, K. Sharifi (GUM 1719); Guilan province, Rasht, on *Euonymus* sp., May 2021, H. Darsaraei (GUM 1891).





Fig. 15. *Erysiphe ehrenbergii*. a. Chasmothecium of IRAN 10994F on *Lonicera caucasica*; b. Chasmothecia of GUM 1890 on *L. iberica*; c. Tips of appendages in IRAN 10994F; d. Chasmothecium of IRAN 12543F on *Lonicera* sp. — Scale bars = (a,b,d) 50 μ m; (c) 10 μ m.



Fig. 16. *Erysiphe ehrenbergii*. a. Chasmohecium; b. Asci; c. Peridium cells; d. Tips of appendages. — Scale bars = (a) 50 μ m; (b,c,d) 10 μ m.



Fig. 17. Erysiphe ehrenbergii. a. Chasmohecium; b. Peridium cells; c. Ascospores; d. Asci; e. Tips of appendages. — Scale bars = (a) 50 μ m; (b,c,d,e) 10 μ m.

Conidia ellipsoid, ovoid, cylindrical, occasionally adhering in false chains containing two conidia, 26- $36 \times 10\text{--}16 \ \mu\text{m}$. Conidial germination terminal or sub-terminal. Germ tube up to 150 µm long. amphigenous caulicolous, Chasmothecia and scattered to \pm gregarious, (85–)95–125 µm diam. Peridium cells conspicuous, irregularly polygonal, 8-25 µm diam. Appendages equatorial and somewhat in the lower half, hyaline, ~10-25, mycelioid, occasionally slightly geniculate or angularly bent, sinuous, flexuous, occasionally forked, forming branches near the base or towards the tip, branchlets may be symmetric or not, occasionally with inconspicuous septa, about 0.5-2.5 times as long as the chasmothecial diam., width 12-20 µm at the very base, then 4–5 µm throughout, wall thin, almost equal throughout, smooth to \pm rough. Asci 4–6, saccateclavate, short-stalked to almost sessile, $48-67 \times 27-$ 38 µm, 3-5-spored. Ascospores ellipsoid, with oil drops, $15-23 \times 8-13 \mu m$, colorless or rather faintly vellow.

Host range: Onobrychis caput-galli (L.) Lam. (Fabaceae)

Specimen examined. Iran, Kohkiluyeh & Boyerahmad province, Gachsaran, Khan Ahmad, on *Onobrychis caput-galli*, Apr. 2014, S. Y. Behrooz (GUM 1805).



Fig. 18. *Erysiphe euonymicola* (GUM 1891 on *Euonymus* sp.). a. Conidial germination; b. Conidia. — Scale bars = (a,b) 10 µm.

Erysiphe iranica Darsaraei, Khodap. & Pirnia, Mycotaxon 137: 271-282, 2022 Figs. 19– 20

Mycelium amphigenous, mostly hypophyllous, effuse, hyphal cells 4–6 μ m wide, hyphal appressoria unlobed to lobed, solitary, rarely in opposite pairs. Conidiophores erect, arising centrally from the mother cell, 40–80 μ m long. Foot-cells cylindrical, 32–40 × 6–13 μ m, often sinuous at the basal part, followed by 1–2 shorter cells, forming conidia singly.



Fig. 19. Tips of appendages in *Erysiphe iranica* (GUM 1805 on *Onobrychis caput-galli*). — Scale bars = $10 \mu m$.



Fig. 20. *Erysiphe iranica*. a. Chasmothecium; b. Asci; c. Peridium cells; d. Tips of appendages; e. Conidiophores and hyphal appressoria; f. Conidia; g. Conidial germination. — Scale bars = (a) 50 μ m; (b,e,f,g) 20 μ m; (c,d) 10 μ m.

Erysiphe magnifica (U. Braun) U. Braun & S. Takam., Schlechtendalia 4: 10, 2000 Fig. 21

Mycelia amphigenous, in patches or scattered, covers the entire surface of young leaves and results in deformation; hyphal cells width 2–7 μ m; hyphal appressoria nipple-shaped or multilobed, solitary or in opposite pairs; conidiophores arising from the top of the mother cell, length 45–200 μ m; foot-cells cylindrical and straight, mostly sinuous and flexuous, 25–75 × 5–8.5 μ m followed by 1–2 shorter cells which are obviously wider than the foot–cell, forming conidia singly; conidia ellipsoid, ovoid, barrel-like to ellipsoid-cylindrical, (27–) 33–45 (–50) × 14–18 μ m, germ tube terminal, mostly short, occasionally very long, conidial appressoria simple or often multilobed. Sexual state not observed.

Host range: Magnolia sp. L. (Magnoliaceae)

Specimen examined. Iran, Mazandaran province, Ramsar, on *Magnolia* sp., July 2015, S. A. Khodaparast (GUM 775).



Fig. 21. *Erysiphe magnifica* (GUM 775 on *Magnolia* sp.). a. Conidiophores; b. Conidia; c. Conidial germination. — Scale bars = (a,b,c) 10 µm.

Erysiphe penicillata (Wallr.: Fr.) Schltdl., FI. Berol. 2: 170, 1824 Figs. 22–23

observed. Asexual state not Chasmothecia amphigenous, scattered, 73-99 µm diam.; peridium cells irregularly polygonal, 8-25 µm; appendages 6-11, equatorial, septate, with 1-2 septa, brown under the septa and pale brown or hyaline towards the tip, length 73-130 µm (about 1-1.5 times as long as the chasmothecial diam.), width 6–9 µm at the very base, then 5 μ m throughout which reaches to 10 μ m at the widest parts, wall smooth, somewhat verruculose at least at the lower half, thick-walled, thinner towards the tip; apices 3-6 times dichotomously branched, primary branches always elongate, secondary branches occasionally elongate, tips always recurved; asci 3-5, saccate, globose, short-stalked to almost sessile, $46-65 \times 32-51 \mu m$; as cospores 6-8, ellipsoid, ovoid, $17-22 \times 10-14 \,\mu m$.

Host range: *Alnus subcordata* C.A.Mey. (*Betulaceae*) *Specimen examined*. Iran, on *Alnus* subcordata, Aghapour (GUM 1889).



Fig. 22. Chasmothecium of *Erysiphe penicillata* (GUM 1889 on *Alnus subcordata*). — Scale bar = 50 μ m.



Fig. 23. Erysiphe penicillata. a. Chasmothecium; b. Ascospores; c. Asci; d. Peridium cells; e. Tips of appendages. — Scale bars = (a) 50 μ m; (b,c,d,e) 10 μ m.

Erysiphe platani (Howe) U. Braun & S. Takam., Schlechtendalia 4: 12, 2000 Fig. 24

Mycelia amphigenous, in patches or covers the entire surface of the leaf, results in the deformation of young leaves; conidiophores arising from the top of the mother cell, straight, length 125–300 μ m or even more, width 5–8 μ m; foot-cells cylindrical, about 60 μ m, followed by a cell of the same length and then 1–3 shorter cells, forming conidia singly; conidia ellipsoid, cylindrical, spindle-like, 24–45 \times 12–21 μ m, often with a large oil drop, conidial germination sub-terminal, germ tube length up to 4 times as long as the conidial length, conidial appressoria multilobed. Sexual state not observed.

Host range: *Platanus orientalis* L., *Platanus* sp. L. (*Platanaceae*)

Specimens examined. Iran, Isfahan province, Isfahan, on *Platanus orientalis*, K. Sharifi (GUM 1718); Guilan province, Rasht, on *Platanus* sp., May 2021, H. Darsaarei (GUM 1893); Yazd province, Yazd, on *P. orientalis*, May 2009, Shakibaei (IRAN 14554F).



Fig. 24. *Erysiphe platani* (GUM 1893 on *Platanus* sp.). a. Conidiophore; b. Conidia; c. Conidial germination. — Scale bars = (a) 100 μ m; (b,c) 10 μ m.

Erysiphe quercicola S. Takam. & U. Braun, Mycol. Res. Ill: 819, 2007 Figs. 25–26

Conidia barrel-like, rather ellipsoid, rather cylindrical, $21-32 \times 11-17$ µm. Chasmothecia gregarious or scattered, 96-120 µm diam.; peridium cells conspicuous, irregularly polygonal, 9-29 µm; appendages 7-13 (13-40 in GUM 1795), equatorial. stiff to somewhat flexuous, occasionally with 1 septum near the base, hyaline, pigmented under the septa, length about 0.75-1.5 times as long as the chasmothecial diam., width 5-7 µm which decreases towards the tip, wall thicker near the base, rather rough, apices 4-5 times dichotomously branched, primary and secondary branches occasionally elongated, tips recurved; asci 5-9, saccate-clavate, short-stalked to almost sessile. $60-65 \times 33-42$ um: ascospores 4–6, ellipsoid, ovoid, $17-26 \times 8-17 \mu m$.

Host range: *Quercus infectoria* G.Olivier (*Fagaceae*)

Specimens examined. Iran, West Azerbaijan province, Piranshar, on *Quercus infectoria*, K. Sepahvand (GUM 1794); Kurdestan province, Baneh, on *Q. infectoria*, K. Sepahvand (GUM 1795); Kermanshah province, Javanrood, on *Q. infectoria*, K. Sepahvand (GUM 1797).



Fig. 25. *Erysiphe quercicola* (GUM 1795 on *Qercus* sp.). a. Chasmothecium; b. Tips of an appendage. — Scale bars = (a) 10 μ m; (b) 50 μ m.



Fig. 26. *Erysiphe quercicola*. a. Chasmothecium; b. Asci; c. Tips of appendages. — Scale bars = (a) 50 μ m; (b,c) 10 μ m.

Erysiphe rayssiae (Mayor) U. Braun & S. Takam., Schlechtendalia 4: 13, 2000 Fig. 27

Mycelia amphigenous, white and almost persistent, hyphal cell width 5–7 μ m, hyphal appressoria rather lobed; conidiophores arising from the top of the mother cell, straight, length 45–80 μ m; foot-cells straight to somewhat sinuous, 27–50 × 5–7 μ m, followed by 1–2 shorter for cells, forming conidia singly; conidia ellipsoid–ovoid to cylindrical and barrel-like, 25–38 × 12–18 μ m. Sexual state not observed.

Host range: Spartium junceum L. (Fabaceae) Specimen examined. Iran, Markazi province, Mahalat, on Spartium junceum, K. Sharifi (GUM 1711).

Erysiphe robiniae Grev., Fl. edin.: 460, 1824

Mycelium amphigenous, effuse or in patches, often covering the entire surface of the leaves, persistent or evanescent, hyphae 4–6 μ m wide; conidiophores arising from the upper surface of the mother cell, erect, 45–87.5 μ m long, foot cell cylindrical, straight to slightly sinuous, 30–50.5 × 8.2–10 μ m, followed by 1–2 shorter cells; conidia formed singly, ellipsoid (cylindrical) or doliform, about 27.5–45 × 15–18 μ m; chasmothecia scattered to almost gregarious, depressed globose, 70–130 μ m diam; peridium cells irregularly polygonal, 12– 23 μ m diam; appendages numerous, in the lower half, usually not turning upward, sinuous, but not irregularly shaped, 54.6–730 μ m, 5–9 μ m wide, 1–6 septate, apices mostly simple, dichotomously branched, loose, forked widely, tips straight; asci 4–9, ellipsoid-obovoid, saccate-clavate, 54.6–75 × 31.2–33.8 μ m, sessile or short-stalked, 4–6 spored; ascospores ellipsoid-ovoid, 18.2–25 × 10.4–15.5 μ m, colorless.

Host range: Robinia pseudoacacia L. (Fabaceae)

Specimen examined. Iran, Ardabil province, Ardabil, on *Robinia pseudoacacia*, Oct. 2012, K. Sharifi (FCUMA1003) Isfahan province, Isfahan, on *R. pseudoacacia*, July 2017, K. Sharifi (GUM 1713). The examined specimen (GUM 1713) included a damaged anamorphic stage and was not suitable for morphological studies. The description presented here is based on Sharifi et al., 2014.



Fig. 27. *Erysiphe rayssiae* (GUM 1711 on *Spartieum juncem*). a. Conidiophores; b. Conidia; c. Hyphal appressoria. — Scale bars = (a) 20 μ m; (b,c) 10 μ m.

Erysiphe sesbaniae Wolcan & U. Braun, Mycotaxon 112: 181, 2010 Fig. 28

Mycelia amphigenous, mostly epiphyllous, white and dense, hyphae branched and sinuous, hyphal cell width 4–8 μ m, hyphal appressoria unlobed to somewhat lobed, solitary; conidiophores arising from the middle of the mother cell, straight, 36–134 × 7–10 μ m; foot-cells cylindrical, 14–38 × 5–7 μ m, followed by 1–4 other cells, forming conidia singly; primary conidia ellipsoid to ovoid, secondary conidia cylindrical to cylindrical-ellipsoid, 26–41 × 10–15 μ m, conidial germination terminal to sub-terminal, germ tubes short to long, length reaches to more than 10 times as the conidial length, conidial appressoria swollen and often lobed (longitubus pattern). Sexual state not observed.

Host range: Sesbania punicea (Cav.) Benth. (Fabaceae)

Specimens examined. Iran, Guilan province, Rasht, on Sesbania punicea, July 2011, S. A. Khodaparast

(GUM 777); Pilembera, on *S. punicea*, May 2012, Bujari (IRAN 16115F).



Fig. 28. *Erysiphe sesbaniae* (IRAN 16115F on *Sesbania punicea*). a. Conidia; b. Hyphal appressoria. — Scale bars = (a) 20 μ m; (b) 10 μ m.

Erysiphe syringae-japonicae (U. Braun) U. Braun & S. Takam., Schlechtendalia 4: 14, 2000 Figs. 29–30

Chasmothecia Asexual state observed. not amphigenous, mostly hypophyllous, scattered to gregarious, 75–115 µm diam.; peridium cells irregularly polygonal, 10-28 µm; appendages 4-13, equatorial, septate, with 1-2 septa, brown under the septa, otherwise hyaline, length 12–156 µm (about 12 times as long as the chasmothecial diam.), width 15-20 μ m at the very base, then 5–8 μ m which is equal throughout, thick-walled, smooth to rough; apices 4-5 times dichotomously branched, primary branches often elongated, tips completely recurred; asci (3-) 4-6 (-7), saccate, ellipsoid, short-stalked to almost sessile, $53-66 \times 38-51 \mu m$; ascospores 6–8, ellipsoid, ovoid, $16-24 \times 7-14 \,\mu m$.

Host range: *Syringa vulgaris* L. (*Oleaceae*)

Specimen examined. Iran, Isfahan province, Isfahan, on Syringa vulgaris, K. Sharifi (GUM 1712).



Fig. 29. *Erysiphe syringae-japonicae* (GUM 1712 on *Syringa vulgaris*). a, b. Tips of appendages; c. Base of appendages. — Scale bars = (a,b) 10 µm; (c) 50 µm.



Fig. 30. *Erysiphe syringae-japonicae*. a. Chasmothecium; b. Appendage; c. Ascus. — Scale bars = (a) 50 μ m; (b,c) 10 μ m.

Erysiphe tortilis (Wallr.: Hr.) Link, Sp. pi. 4, 6(1): 111, 1824 Figs. 31–32

Chasmothecia hypophyllous, gregarious to scattered, 84–130 μ m diam.; peridium cells conspicuous, irregularly polygonal, 7–30 μ m; appendages 10–23, from the lower half, flexuous, brown or pale brown which occasionally get hyaline or paler towards the tip, nodulose, long, length at least 5–9 times as long as the chasmothecial diam., even exceeding in the intact appendages, width up to 20 μ m at the very base, then 5–16 μ m, thin-walled, somewhat thicker near the base, smooth or somewhat rough; ask (3) 4 (5), saccate, almost sessile or short-stalked, 50–73 × 39–55 μ m; ascospores 2–57 ellipsoid, ovoid, 18–34 × 10–19 μ m, colorless.

Host range: Cornus sp. L. (Cornaceae)

Specimens examined. Iran, Mazandaran province, Ramsar, on *Cornus* sp., July 2004, S. A. Khodaparast (GUM 1892); West Azerbaijan province, Urmia, on *Cornus* sp., Aug. 2004, S. A. Khodaparast IRAN 4127F.



Fig. 31. Chasmothecium of *Erysiphe tortilis* (GUM 1892 on *Cornus* sp.). — Scale bar = $50 \mu m$.



Fig. 32. *Erysiphe tortilis*. a. Chasmothecium; b. Asci; c. Peridium cells. — Scale bars = (a) 50 μ m; (b) 20 μ m; (c) 10 μ m.

Erysiphe trifoliorum (Wallr.) U. Braun, Mycotaxon 112: 175, 2010 Figs. 33–34

Hyphal cell width $3-5 \mu m$, hyphal appressoria lobed and solitary; conidia ellipsoid, cylindrical, ovoid, 28- $45 \times 10-20 \mu m$, conidial germination sub-terminal, conidial appressoria lobed. Chasmothecia amphigenous and on fruit bodies and stems, scattered to somewhat gregarious, 88-182 µm diam.; peridium cells irregularly polygonal, 10-30 µm; appendages 12-41, flexuous, almost equatorial or from the lower half, septate, with 1(-5) septa, hyaline or pigmented under the septa or at the lower half, geniculate and sinuous, length up to 8 (or 10) times as long as the chasmothecial diam., long appendages mav interwoven with each other, width 9-15 µm at the very base, then 4–7 µm and decreases towards the tip, thin-walled, somewhat thicker near the base, smooth to somewhat rough; apices at least partly 1-3 times dichotomously branched, branching may occur near the base or towards the tip; asci 5-14, saccate-clavate, 46–92 \times 29–53 µm; ascospores 3–6 (–7), ellipsoid, ovoid, $16-26 \times 9-16 \,\mu\text{m}$.

Host range: Sophora alopecuroides L., Trigonella foenum-graecum L., Melilotus indicus (L.) All., cf. Melilotus sp. Mill., Trifolium pratense L., Trifolium sp. L., Trifolium spadiceum L., M. officinalis (Fabaceae)

Specimens examined. Iran, Isfahan province, Isfahan, on Sophora alopecuroides, Aug. 2006, S. A. Khodaparast (GUM 1815); on Melilotus indicus, Aug. 2006, S. A. Khodaparast (GUM 1818); on cf. Melilotus sp., Aug. 2006, S. A. Khodaparast (GUM 1819); on Trifolium sp., 2006, S. A. Khodaparast (GUM 1822, GUM 1823); Hamedan province, Hamedan, on Trigonella foenum-graecum, Oct. 2007, M. Bahador (GUM 1816); unknown host, 2009, M. Bahador (GUM 1817), Sept. 2007, M. Bahador (GUM 1824); Ardabil province, Ardabil, on cf. Melilotus sp., June 2004, S. A. Khodaparast (GUM 1820); East Azerbaijan province, Marand, on Trifolium pretense, Aug. 2004, S. A. Khodaparast (GUM 1821); Kordestan province, Baneh, on T. pretense, Sept. 2015, K. Sepahvand (GUM 1825); Chaharmahal-o-Bakhtiari province, Kuhrang county, on M. officinalis, Aug. 2008, S.A. Khodaparast (IRAN 15776F); Tehran province, Tehran, on T. spadiceum, Aug. 1993, Abbasi & Foizik (IRAN 15774F); Evin, on M. officinalis, Sept. 1968, Dj. Ershad (IRAN 1199F).

Erysiphe viburni Duby, Bot Gall 2:872, 1830 Figs. 35–36

observed. Asexual state not Chasmothecia hypophyllous, scattered, 77-110 µm diam.; peridium cells not very conspicuous, 8-25 µm; appendages 5-8, equatorial, hyaline, sometimes brown under the septa, straight to somewhat flexuous, occasionally septate, length about 70-100 µm, (about the same length as the chasmothecial diam.), width 6-8 µm, thick-walled, about 3 µm, which decreases towards the tip, rather rough to smooth; apices 4-6 times dichotomously branched, primary branches somewhat elongate, tips completely recurved; asci 2-6, saccateclavate, globose, short-stalked to almost sessile, 58- 68×48 – 63μ m; ascospores 3–8, ellipsoid, ovoid, 21– 28×10 –17 µm, colorless.

Host range: Viburnum lantana L. (Adoxaceae)

Specimen examined. Iran, West Azerbaijan province, Arasbaran, on *Viburnum lantana*, Oct. 1999, Gh. Tavanaei (IRAN 11286F).



Fig. 33. Chasmothecia of *Erysiphe trifoliorum*. a. GUM 1815 on *Sophora alopecuroides*; b. IRAN 15776F on *Melilotus officinalis*. — Scale bars = (a,b) 50 μ m.



Fig. 35. *Erysiphe viburni* (IRAN 11286F on *Viburnum lantana*). a, b. Chasmothecia; c, d. Appendages. — Scale bars = (a,b) 50 µm; (c,d) 10 µm.





Fig. 34. *Erysiphe trifoliorum*. a. Chasmothecium; b. Asci; c. Peridium cells; d. Tips of appendages. — Scale bars = (a) 50 μ m; (b,c,d) 10 μ m.



Fig. 36. *Erysiphe viburni*. a. Chasmothecium; b. Asci; c. Peridium cells; d. Tips of appendages. — Scale bars = (a) 50 μm; (b,c,d) 10 μm.

DISCUSSION

Until 2009, there were only 13 records of *Erysiphe* sect. *Microsphaera* in Iran (Khodaparast & Abbasi, 2009). Among all recorded species, *E. hyperici* was not available for this study. Meanwhile, one new species, *E. iranica*, was described (Darsaraei et al. 2022), and the existence of *E. deutziae* (Khodaparast et al. 2021), *E. erlangshanensis*, and *E. castaneigena* in Iran was rejected. Considering all of these taxonomic events, the number of species from sect. *Microsphaera* reached 22 in this study. *Erysiphe crispula* on *Astragalus* spp. is reported here for the first time, and *Syringa vulgaris* is reported as a new host for *E. syringae-japonicae* in Iran.

The specimen IRAN 11286F was previously recorded as a member of *E. hedwigii* (Lev.) U. Braun & S. Takam. with smaller chasmothecium than *E. viburni*. Based on a comprehensive study on *Erysiphe* spp. infecting *Viburnum* species conducted by Bradshaw et al., 2020, it was revealed that available rDNA ITS and 28S sequences from *E. hedwigii* are identical to *E. viburni* type sequences. Therefore, they decided to consider *E. hedwigii* as a synonym of *E. viburni* until the type or epitype sequences of *E. hedwigii* are identical to *E. viburni* type sequences, IRAN 11286F is here recorded as a member of *E. viburni* as well.

According to Liu et al. (2022), collections of E. berberidis s. lat. (Including E. berberidicola, E. dimorpha, E. multappendicis) from Asia, Europe, and North America show a high degree of plasticity in the morphological features of the sexual morph, while their asexual morph is rather uniform. Meanwhile, there is no remarkable difference in the rDNA ITS and 28S sequences, and they all group together within the well-supported clade. Considering the morphology of the sexual state, the authors defined three morphological variety of E. berberidis as follows: E. berberidis var. berberidis (with rather long and stiff appendages with straight tips), E. berberidis var. asiatica (with uniformly short and rather stiff appendages with straight tips), and E. berberidis var. dimorpha (with prevalent recurved tips of appendages). Powdery mildews on Berberis spp. have been previously reported under E. bereridis and E. multappendicis (Z.Y. Zhao & Y.N. Yu) U. Braun & S. Takam. in Iran (Khodaparast & Abbasi 2009).

Sequences from the specimens on *Corylus* spp., subfamily *Coryloideae*, *Betulaceae* (specimens GUM 786 and GUM 1888) that were placed in the *E. corylacearum* clade are easily distinguishable from allied species such as *E. pseudocorylacearum*, *E. cornutae*, and *E. coryli-americanae*. The only sequence from the specimens on *Alnus subcordata*, subfamily *Betuloideae*, *Betulaceae* (specimen GUM 1889) was placed in the clade of *E. penicillata*, the only hitherto recorded species from the sect. *Microsphaera* on *Alnus*.

Before 2021, E. lonicerae that is hard to be morphologically distinguished from \boldsymbol{F} caprifoliacearum, had two varieties: var. lonicerae and var. ehrenbergii (Braun & Cook, 2012, Bradshaw et al. 2021a). According to a comprehensive study on Erysiphe spp. infecting Lonicera spp. by Bradshaw et al. (2021), E. caprifoliacearum was reduced to synonymy with E. lonicerae s. str., and var. ehrenbergii was raised to species status (Bradshaw et 2021a). Furthermore, sequences of E. al. erlangshanensis were provided in that study. The specimens IRAN 10849F, IRAN 14281, IRAN 11014F, and GUM 1890 are morphologically and molecularly corresponded with E. ehrenbergii. Although tips of chasmothecial appendages in IRAN 10849F and IRAN 14281F are relatively more recurved, which brings to mind the similarity with E. erlangshanensis. However, these two species are easily distinguished by rDNA ITS and 28S sequences. Furthermore, the appendages in IRAN 10994F and IRAN 12543F are obviously longer, and the number of asci per chasmothecium is more than in other specimens. Since rDNA ITS sequence of these specimens is similar to E. ehrenbergii (100% identical in IRAN 12543F and with only 1 substitution in IRAN 10994F), we, at the present time, prefer to assign all these specimens to E. ehrenbergii, and conclude that E. ehrenbergii is morphologically diverse in Iran.

Erysiphe euonymicola which usually occurs in the conidial stage is genetically close to *E. alphitoides* complex (Braun and Cook 2012), but morphologically distinct from this species complex. This species occurs in the conidial stage in Iran as well and previously was recorded as *E. euonymijaponici* (Khodaparast & Abbasi 2009).

Efforts for sequencing *E. tortilis* from Iran failed. Therefore, this species is only confirmed by its morphological features.

Sequences representing E. trifoliorum as well as E. astragali complexes are very similar and even identical in some cases. Their host range is somewhat overlapping, viz., there is no significant difference in the anamorphic stage of some species, and the rDNA ITS and 28S sequences are not informative enough to distinguish them. The differentiation of some species such as E. trifoliorum, E. sesbaniae, and E. robiniae, as well as E. astragali, E. crispula, E. coluteae is very difficult. E. bremeri and E. intermedia were placed within the E. astragali complex with 79 and 87% support, respectively. Due to lack of intact type specimens, sometimes it is impossible to distinguish these species even by combining the morphological and molecular data. It seems that the only solution could be obtained by protein-coding sequences from type- or appropriate epitype specimens.

Species infecting *Quercus* spp. in Iran, namely *E. alphitoides* and *E. quercicola* are morphologically indistinguishable, but easy to be differentiated by their rDNA ITS sequences. The same goes for *E. castaneigena*, another species infecting *Fagaceae*.

The specimen IRAN 14248F was previously identified as *E. castaneigena* by its morphology (Abbasi et al. 2013), but the molecular data provided in this study revealed that it belongs to *E. alphitoides*.

According to Braun's description of E. platani, the length of conidiophore in this species is up to 200 µm (Braun & Cook 2012). This characteristic reaches to about 240 µm in other studies (Pastirčáková et al., 2014; Beenken 2017) and even more than 300 µm in Iranian specimens. Despite this difference observed in morphology, all sequences of E. platani formed a single clade with high BS support. Since there is no type sequence nor a sequence from type host (Platanus occidentalis L.) available for E. platani, minor morphological differences were considered here as potential geographical diversity within species, and the decision about probable cryptic species or varieties is postponed for further pieces of evidence. Sequence MW131643 on Koelreuteria paniculata Laxm.. Sapindaceae, with no morphological description from China is the first record of E. platani on a host other than Platanaceae.

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

1a. Only asexual state is present 2 b. The sexual state is present, appendages tips regularly and dichotomously branched 2a. Conidiophore length up to 300 µm, conidia often with a large oil drop, conidial germ tube up to 4 times as long as the conidial length. E. platani b. Conidiophore length less than 200 µm 3 3a. Conidiophore 45-200 µm long, foot-cells mostly sinuous and flexuous, followed by 1-2 shorter cells which are obviously wider, conidia (27-) 33-45 (-50) \times 14–18 µm, causing deformation of young leaves, on Magnolia sp. L. (Magnoliaceae) E. magnifica b. Conidiophore length less than 160 µm 4a. Conidiophore length (40-) 54-160 µm, hyphal appressoria lobed, solitary or in opposite pairs, conidia of various shapes, ellipsoid-ovoid, barrelshape, (19–) 25–42 \times (–10) 14–22 µm, on Corylus spp. (*Betulaceae*) E. corylaceaerum b. Conidiophore length 40–80 µm 5 5a. Primary conidia ellipsoid to ovoid, secondary conidia cylindrical to cylindrical-ellipsoid, conidial germ tube length reaches more than 10 times as the conidial length, hyphae branched and sinuous, on Sesbania punicea (Fabaceae) E. sesbaniae b. Conidia uniform 6a. Foot-cells straight to somewhat sinuous, hyphal appressoria rather lobed, conidiophore length 45-80 μm, on *Spartium jum* (*Fabaceae*) E. rayssiae b. Conidia rather big (24-40 µm long), foot-cells straight, conidial germ tube septate, on Euonymus spp. L. (*Celastraceae*) E. euonymicola 7a. Appendages generally more than 6 times as long as the chasmothecial diam. 8 b. Appendages shorter, rarely reaching 6 times as long as the chasmothecial diam. 11

8a. Appendages brown or pale brown, flexuous, at least 5-9 times as long as the chasmothecial diam., even exceeding in the intact appendages, branched at the end or in the middle of the appendage, with seven septa or more, nodulose, chasmothecia 84-130 µm diam., on *Cornus* sp. L. (*Cornaceae*) E. tortilis b. Appendages shorter (less than 15 times as long as the chasmothecial diam.), on Fabaceae 9 9a. Appendages occasionally tend to point in one direction, up to 7.5 times as long as the chasmothecial diam., chasmothecia 107-156 µm diam., appendages 5-25, apices at least dichotomously branched in some appendages, tips rather recurved, on Astragalus spp. (Fabaceae) E. astragali b. Appendages distribution horizontal, about 4-10 times as long as the chasmothecia diam. 10 10a. Appendages 12–41, up to 8–10 times as long as the chasmothecial diam., geniculate and sinuous, brown under septa, apices at least partly 1-3 times dichotomously branched, asci 5-14, ascospores 3-6 (-7), on Sophora, Melilotus, Trigonella and Trifolium (Fabaceae) E. trifoliorum b. Appendages 11-20, 4-9 times as long as the chasmothecial diam., hyaline or pale brown, branching loose and elongate and occasionally occurs near the base, chasmothecia 113-161 (-192) μm diam., asci 6-16, ascospores 4-6, on Colutea (*Fabaceae*) E. coluteae 11a. Appendages up to 5.5 times as long as the chasmothecial diam., geniculate or sinuous, tips simple or rarely dichotomously branched 12 b. Appendages may be shorter and/ or tips are obviously branched dichotomously 13 12a. Appendages numerous, about 0.5-4.5 times as long as the chasmothecial diam., geniculate and sinuous, apices 1-3 times dichotomously branched, primary branches loose and elongate, chasmothecia 120-168 µm diam., on Alhagi and Sophora (Fabaceae) E. bremeri b. Appendages up to 5.5 times as long as the chasmothecial diam., hyaline or pale brown, apices 3-6 times dichotomously branched, may be recurved at different levels, hardly geniculate, sinuous and twisted, chasmothecia 94-182 µm diam., asci 5-15, on Astragalus spp. (Fabaceae) E. crispula 13a. Appendages about 0.5-2.5 times as long as the chasmothecial diam., hyaline, mycelioid, geniculate or angularly bent, with symmetric or asymmetric branching near the base or towards the tip, aseptate or with inconspicuous septa, on Onobrychis caput-galli (Fabaceae) E. iranica b. Apices specifically dichotomously branched 14 14a. Appendages 5-8, length about the chasmothecial diam., apices 4-6 times dichotomously branched, primary branches occasionally elongate, tips totally recurved, asci 2-6, ascospores 3-8, on Viburnum *lantana* (*Adoxaceae*) E. viburni b. Appendages more than 8, and/or longer than chasmothecial diam. 15 15a. Tips of ultimate branches at least partly recurved (mix of straight and recurved) 16

b. Tips of ultimate branches always totally recurved 17

16a. Appendages 0.5-3 times as long as the chasmothecial diam., straight to rather flexuous, hyaline, occasionally pale brown to brown near the base, apices 3-6 times dichotomously branched, branching may occur near the base or from the middle of the appendage, but often is terminal, primary or secondary branches occasionally elongate, tips straight, but at least partly recurved, asci 3-13, ascospores (2–) 3–6 (–7), on Berberis spp. E. berberidis s. lat. (Berberidaceae) b. Appendages 0.75–2 (or up to 3 and 4) times as long as the chasmothecial diam., straight to flexuous, hyaline, brown under the septa, occasionally geniculate, apices 4-5 (-6) times dichotomously branched, primary branches generally elongate, tips generally recurved, asci 3-4, ascospores (2-) 3-6 (mostly 4–5), chasmothecia 67–107 (–161) um diam., on *Lonicera* spp. (*Caprifoliaceae*) E. ehrenbergii 17a. Ascospores 6-8 per ascus 18 b. As cospores 4-7(-8) per ascus 19

18a. Chasmothecia 73–99 μ m diam., appendages 6– 11, 1–1.5 times as long as the chasmothecial diam., with 1–2 septa, brown under septa and pale brown to hyaline towards the tip, apices 3–6 times dichotomously branched, primary branches always elongate, secondary branches occasionally elongate, tips always recurved, asci 3–5, on *Alnus subcordata* (*Betulaceae*) *E. penicillata*

b. Chasmothecia 75-115 µm diam., appendages 4-13, 1-2 times as long as the chasmothecial diam., with 1-2 septa, brown under septa, otherwise hyaline, apices 4-5 times dichotomously branched, primary branches generally elongate, tips totally recurved, asci (3-) 4-6 (-7), on *Syringa vulgaris* E. syringae-japonicae 19a. Chasmothecia (61-) 70-89 µm diam., appendages 5-10, about 1-1.5 times as long as the chasmothecial diam., hyaline, brown under septa, apices 5-6 times dichotomously branched, primary and secondary branches rather elongate, tips totally recurved, asci 3-4, ascospores (5-) 6-7 (-8), on E. alphitoides Quercus spp. (Fagaceae) b. Chasmothecia 96-120 µm diam., appendages 7-13 (or 13-40), 0.75-1.5 times as long as the chasmothecial diam., straight to somewhat flexuous, hyaline, brown under septa, apices 4-5 times dichotomously branched, primary and secondary branches occasionally elongate, tips recurved, asci 5-9, ascospores 4-6, sequencing ITS rDNA necessary to distinguish from E. alphitoides, on Quercus infectoria (Fagaceae) E. quercicola

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DNA بازبینی تاکسونومیکی به کمک تجزیه و تحلیل فیلوژنتیک و خطشناسه گذاری Erysiphe sect. Microsphaera (Erysiphaceae, Helotiales) گونههای (

حميده دارسرائي'، سيد اكبر خداپرست*'، صديقه موسى نژاد'، كرم سپه وند'، بيتا عسگرى''، سپيده ساجدى''

۱-گروه گیاه پزشکی دانشکده علوم کشاورزی دانشگاه گیلان ۲-مرکز تحقیقات و آموزش کشاورزی و منابع طبیعی استان لرستان، سازمان تحقیقات، آموزش و ترویج کشاورزی، تهران، ایران ۳-بخش تحقیقات رستنیها، مؤسسه تحقیقات گیاه پزشکی ایران، سازمان تحقیقات، آموزش و ترویج کشاورزی، تهران، ایران

كلمات كليدى: تنوع زيستى، سفيدكهاى پودرى، rDNA، تبارشناسى، آرايەشناسى

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