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

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Abstract: Taxonomy and phylogeny of *Erysiphe* sect. *Erysiphe* (*Erysiphaceae*, *Helotiales*) in Iran was revised. One hundred samples from the University of Guilan Mycological Fungarium (GUM) and the fungal reference collection of the Ministry of Jihad-e Agriculture (IRAN), as well as newly collected specimens during 2019–2021, were investigated using morphology and ITS-LSU rDNA sequence analysis. Based on our findings, *Erysiphe* sect. *Erysiphe* has 23 accepted and two unknown species in Iran *viz*.: *E. aquilegiae, E. betae, E. buhrii, E. caulicola, E. circaeae, E. convolvuli, E. cruchetiana, E. cruciferarum, E. heraclei, E. howeana, E. limonii, E. lycopsidis, E. malvae, E. mayorii, E. medicaginis*, *E. neolycopersici*, *E. paeoniae, E. pisi, E. polygoni, E. punicae, E. rumicicola, E. sedi, E. urticae. E. sedi* and *E. paeoniae* are new records for the funga of Iran. In addition, *Mesostemma kotschyana* (*Caryophyllaceae*) is reported as a new host for *E. buhrii.* The occurrence of potential cryptic species on *Urtica* spp. is discussed as well.

Keywords: Biodiversity, Phylogeny, Powdery mildews, Ribosomal DNA, Taxonomy.

INTRODUCTION

Powdery mildews (*Erysiphaceae*, *Helotiales*) are important plant pathogens that can infect about 10000 flowering plants (Rogerson 1987, Braun & Cook 2012). The white cover visible on different structures of the host plant is a remarkable symptom of the powdery mildews. *Erysiphe* R. Hedw. ex DC., with five morphological (but not phylogenetical) sections and more than 400 known species, is the largest genus within the *Erysiphaceae* family (Braun & Cook 2012). Among them, *ca.* 60 species from three sections, *i.e.* sect. *Erysiphe*, sect. *Microsphaera*, and sect. *Uncinula* is confirmed to exist in Iran (Darsaraei 2022). Members of sect. *Erysiphe* mainly infects herbaceous hosts, while two other sections can also be found on trees and shrubs. Most species in sect. *Erysiphe* are believed to infect several genera within a given plant family (Braun & Cook 2012). Considering the biotrophic nature of powdery mildews, it is necessary to determine whether they are truly polyphagous or consist of several species that should be classified separately. Some species of *Erysiphe* are important pathogens of cultivated plants. Plants such as sugar beet and tomato, legumes like peas, and alfalfa are important agricultural hosts that are infected by species of this genus. Powdery mildews of the above-mentioned plants are especially damaging in areas where conditions such as plant susceptibility, weather, and cultural practices favor disease development (Francis 2002). Recently, reports of *E. neolycopersici* on tomatoes have increased in Europe, Africa, North and South America, and Asia (Kiss et al. 2001, Hsiao et al. 2022). A few years ago, this species was also reported in Iran (Davari et al. 2015). *Erysiphe pisi* is another invasive species that causes severe infection in legumes. This species has been reported from almost all over the world and recently it has been investigated in Iran (Darsaraei et al. 2023c). In this study, some of the ambiguities about the species taxonomy have been resolved. Takamatsu et al. (2002) have shown that at least two species have been associated with the outbreak of soybean powdery mildew in Eastern Asia, one of which was *Erysiphe glycines*, belonging to the *E*. sect. *Erysiphe*. To better identification of the less-known species and understand the biodiversity of species of *E*. sect. *Erysiphe* in Japan, Meeboon & Takamatsu (2014) determined the nucleotide sequences of the 28S rRNA gene and the internal transcribed spacer (ITS) regions. They reported *E. aquilegiae*, *E. huayinensis*, *E. liriodendra*, *E. mayorii*, *E. sedi*, *E. trifoliorum,* and *Pseudoidium* cf. *neolycopersici* (=*E. neolycopersici*) and eight new hosts of powdery mildews in Japan. Furthermore, during recent years some new species have been described in *E*. sect. *Erysiphe* such as *E. celosiae* (Tanda 2000), *E. baptisiicola* (Braun et al.

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2010), *E. asiatica* and *E. monoperidiata* (Divarangkoon 2011), *E. javanica* (Meeboon et al. 2012), *E. lupini* (Bradshaw et al. 2022) and *E. ruyongzhengiana* (Liu et al. 2022b).

From the point of view of plant pathologists, in several cases, more than one species is involved as the causal agent of powdery mildew on a single host such as powdery mildew species on tomatoes, cucurbits, and sunflowers (Braun &Cook 2012). In such cases, accurate species identification is crucial in the breeding strategy for resistant cultivars (Kiss et al. 2001). This becomes more important when the species is seen in asexual form. Recently, using the ITS sequence has become highly useful for the accurate identification of powdery mildews, although, it is not sufficient for closely related species (Kiss et al. 2001, Davari et al. 2015, Shin et al. 2019, Hsiao 2022, Liu et al. 2022a, Khodaparast et al. 2021).

Following the previous studies on *Uncinula* and *Microsphaera* sections (Darsaraei et al. 2021b, 2023b), species of *Erysiphe* sect. *Erysiphe* in Iran was studied to achieve the following goals: DNA barcodes for species, color plates, digital illustrations, and a key to all species of *E*. sect. *Erysiphe* in the country.

MATERIALS AND METHODS

Sample collection

One hundred powdery mildew specimens covering all species, including herbarium vouchers from the University of Guilan Mycological Fungarium (GUM) and the fungal reference collection of the Ministry of Jihad-e Agriculture (IRAN), as well as newly collected specimens during 2019–2021 were investigated in the current study.

Morphological examinations

Fungal structures were transferred from infected host plants into a drop of 1:1 glycerin: lactic acid on a microscopic slide using a sterile needle or a clear piece of adhesive tape. For each specimen, at least 20 repetitions of various structures, including conidiophores, conidia, chasmothecia, appendages, asci, and ascospores were measured. The photos were taken using a Canon camera (Tokyo, Japan) on a Leica DM 100 microscope (Wetzlar, Germany). All digital illustrations were done with Adobe Fresco (Version 3.4 for iPad OS).

Molecular studies

Total DNA was extracted from mycelia or chasmothecia using the thermolysis method (Zhang et al. 2010, Khodaparast et al. 2021) or Chelex-100 medium (Walsh et al. 2013). Two rounds of PCR were carried out to amplify the internal transcribed spacers and 28S rDNA (LSU) regions. Amplification of ITS regions (ITS1 and ITS2) including the intervening 5.8S nuclear ribosomal DNA (nrDNA) was done using the primer pairs PMITS1 (Cunnington et al. 2003) and PM11 (Bradshaw & Tobin 2020) for the first reaction. Primers PM10 (Bradshaw &Tobin 2020) and PM11 were also used for the second PCR reaction. For the D1/D2 domains of the 28S rDNA, the first PCR reaction was done using the primers PM3/NLP2 (Mori et al. 2000), and the second PCR was carried out using the RPM2 (Bradshaw &Tobin 2020) /NLP2. PCR components and conditions were in accord with the method described in Darsaraei et al. (2021a). All PCR amplicons were sent to Codon Genetic Group (Tehran, Iran) for sequencing. New sequences generated in this study were deposited in GenBank (Table S1).

Newly generated sequences were aligned against type (if available) or authentic sequences of *E*. sect. *Erysiphe* retrieved from GenBank 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). Afterward, Maximum likelihood (ML) analysis was used to estimate phylogenetic relationships of combined sequences of the ITS and LSU regions using raxmlGUI (Silvestro &Michalak 2012), under the GTR+GAMMA substitution model along with rapid bootstrap analysis of 1000 pseudoreplicates followed by a search for the tree with the highest likelihood.

RESULTS

Molecular and phylogenetic analysis

A total of 100 ingroup as well as two outgroup taxa, *Phyllactinia moricola* (AB080561) and *Leveillula taurica* (AB667884) were included in the final ML tree conferred from combined sequences of ITS-LSU rDNA regions (Fig. 1). The final alignment with 392 distinct alignment patterns was partitioned to ITS and LSU, of which 284 and 108 alignment patterns were for ITS and LSU, respectively. The Final ML Optimization Likelihood was calculated as -4687.220574. The alpha parameter was calculated as 0.316451 and 0.171337 for ITS and LSU, respectively.

Members of *E*. sect. *Erysiphe* fell into 10 clades (Fig. 1). Clade 1 with 87% bootstrap (BS) support, consists of *E. aquilegiae*, *E. asclepiadis*, *E. circaeae*, *E. neolycopersici*, and *E. sedi*. *Erysiphe medicaginis* formed a distinct clade with 100% BS support (Clade 2). Several sequences retrieved from *Amaranthaceae*, *Apiaceae*, *Caryophyllaceae*, *Malvaceae,* and *Polygonaceae* were included in the Clade 3 with 86% support. This clade includes several subclades with or without support such as those of *E. polygoni* complex, *E. buhrii*, and *E. heraclei/E. betae* complex.

Erysiphe viciae-unijugae and *E. cruchetiana* on fabaceous hosts formed Clade 4 with 73% bootstrap support. *Erysiphe lupini*, *E. convolvuli*, and *E.*

limonii, each formed a separate, highly supported subclade within the Clade 5 (no BS support). *Erysiphe caulicola* was placed in this clade too.

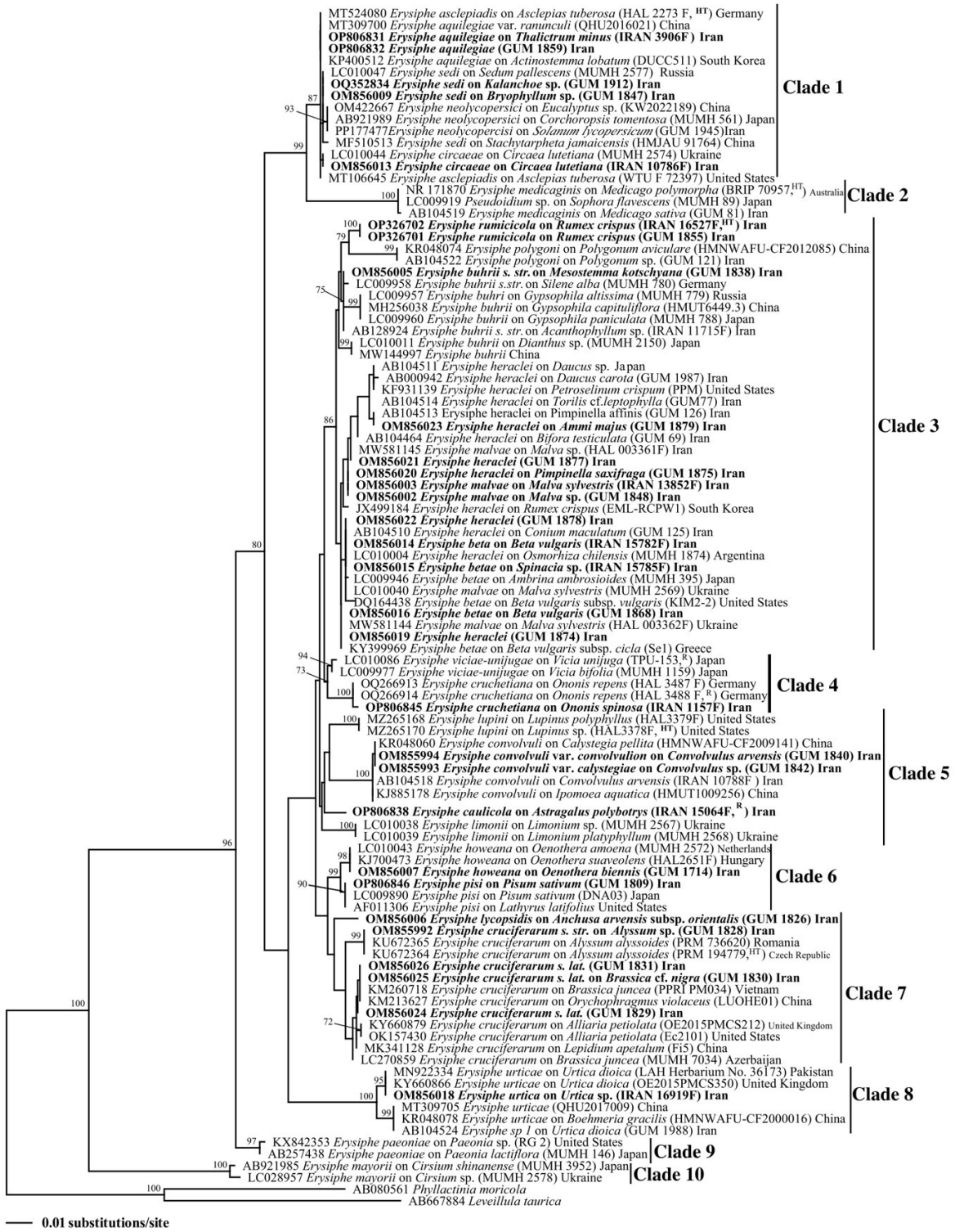

Fig. 1. Maximum-Likelihood consensus tree inferred from the combined ITS and the D1–D2 domains of the LSU ribosomal DNA of members of *Erysiphe* sect. *Erysiphe*. Numbers at the branches indicate bootstrap support above 70 %. Sequences generated in this study are indicated in bold font. The scale bar indicates expected changes per site. The tree was rooted with *Phyllactinia moricola* (AB080561) and *Leveillula taurica* (AB667884) as outgroup taxa. GenBank accession numbers (ITS) are followed by species names, host taxa, specimen vouchers, and collection locality. HT and R show sequences from holotype, and reference materials, respectively.

Erysiphe howeana with 98% and *E. pisi* with 90% BS support formed the well-supported Clade 6. Clade 7 includes *Erysiphe lycopsidis* and *E. cruciferarum s. lat.* The subclade of *E. cruciferarum s. lat.* consists of two groups of sequences: one from type material on *Alyssum alyssoides* and the second from different genera of *Brassicaceae*. The remaining clades, *i.e.,* Clades 8, 9 and 10, included *E. urticae*, *E. paeoniae*, and *E. mayorii*, respectively.

Taxonomy

According to our study, *Erysiphe* sect. *Erysiphe* includes 23 accepted and two unknown species in Iran, of which *E. sedi* and *E. paeoniae* are new records for the funga of Iran. Additionally, *Mesostemma kotschyana* (*Caryophyllaceae*) is also reported as a new host for *E. buhrii*.

Erysiphe aquilegiae DC., FI. franç. 6: 105, 1815 **var. *aquilegiae*** Fig. 2, 4

Chasmothecia amphigenous and caulicolous, scattered to almost gregarious, 69–137 µm diam.; peridium cells irregularly polygonal, 9–29 µm; appendages 11–26, myceloid, irregularly branched, from the lower half, brown, hyaline towards the tip, or pale brown, septate with 0–5 septa, length more than four times as long as the chasmothecial diam., width 4–7 µm, thin-walled, smooth to rough; asci (2) 3–9, saccate-clavate, rather long or short-stalked, 58–91 × 30–49 µm; ascospores 3–6, ellipsoid, ovoid, 18–26 (29) × 9–16 µm.

Host range: *Aquilegia vulgaris* L., *Ranunculus* sp. (*Ranunculaceae*).

Specimens examined: Iran, Chaharmahal and Bakhtiari Province, Babaheidar, on *Ranunculaceae*, July 2007, S.A. Hashemi (GUM 1859); Kuhrang, on *Ranunculus* sp., Aug. 2008, S.A. Khodaparast (IRAN 15420F); Alborz Province, Karaj, on *Aquilegia vulgaris*, Jan. 1970, Shahidi (IRAN 1128F); Hamedan Province, Hamedan, on *A. vulgaris*, Jan. 2015, M. Bahador (IRAN 16922F).

Erysiphe aquilegiae **var. *ranunculi*** (Grev.) R.Y. Zheng & G.Q. Chen, Sydowia 34: 302, 1981 Fig.3–4

This variety differs from var. *aquilegiae* in having shorter appendages which rarely reach to 4 times as long as the chasmothecial diam. Moreover, the chasmothecia are surrounded by appendages of unequal length, which are often unbranded.

Host range: *Aquilegia vulgaris* L., *Ranunculus* sp., *Thalictrum minus* L. (*Ranunculaceae*).

Specimens examined: Iran, Hamedan Province, Hamedan, on *A. vulgaris*, Oct. 2015, M. Bahador (GUM 1860); Guilan Province, Masuleh, on *Ranunculus* sp., May 2019, S. Nazari (GUM 1861); Zanjan Province, Zanjan, on *Ranunculaceae*, Aug. 2004, S.A. Khodaparast (GUM 1862); Ardabil Province, Meshkinshahr-Ahar old road, on *Thalictrum minus*, Aug. 2004, S.A. Khodaparast (IRAN 3906F); Golestan Province, Golestan National Park, on *T. minus*, July 1993, M.A. Tajik Ghanbari (IRAN 9090F).

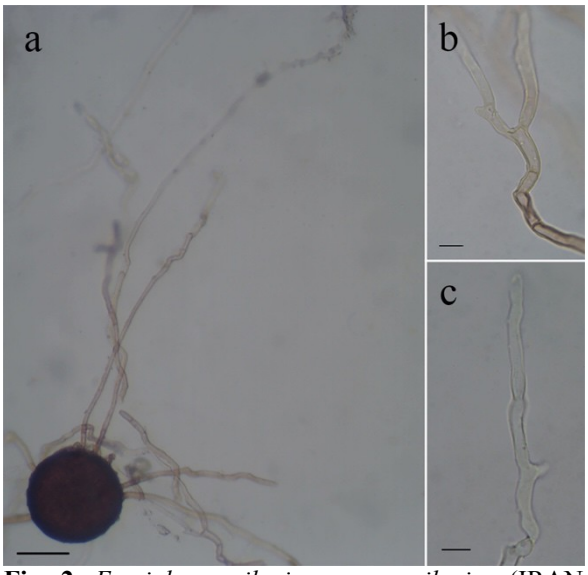

Fig. 2. *Erysiphe aquilegiae* var. *aquilegiae* (IRAN 16922F). a. chasmothecium; b, c. a close-up of appendages. — Scale bars = (a) 50 µm; (b, c) 10 µm.

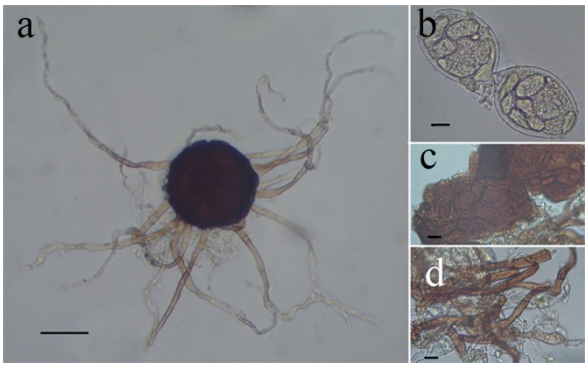

Fig. 3. *Erysiphe aquilegiae* var. *ranunculi* (IRAN 3906F). a. chasmothecium; b. asci; c. peridium cells; d. brown and septate appendages. — Scale bars = (a) 50 µm; (b–d) 10 µm.

Erysiphe betae (Vaňha) Weltzien, Phytopathol. Z. 47: 127, 1963 Fig. 5–6

Mycelia amphigenous, sometimes covers the whole surface of the leaves; hyphal width 3–6 µm; hyphal appressoria lobed to multilobed, solitary or in opposite pairs; conidiophores arising from the top of the mother cell, 65–105 µm long; foot-cells cylindrical, erect, sometimes sinuous, 21–42 × 6–10 µm, followed by a cell of approximately the same length or a longer cell, or 1–2 shorter cells, forming conidia singly; conidia ellipsoid, cylindrical, 21–55 × 10–17 (20) µm; conidial germination (on the natural

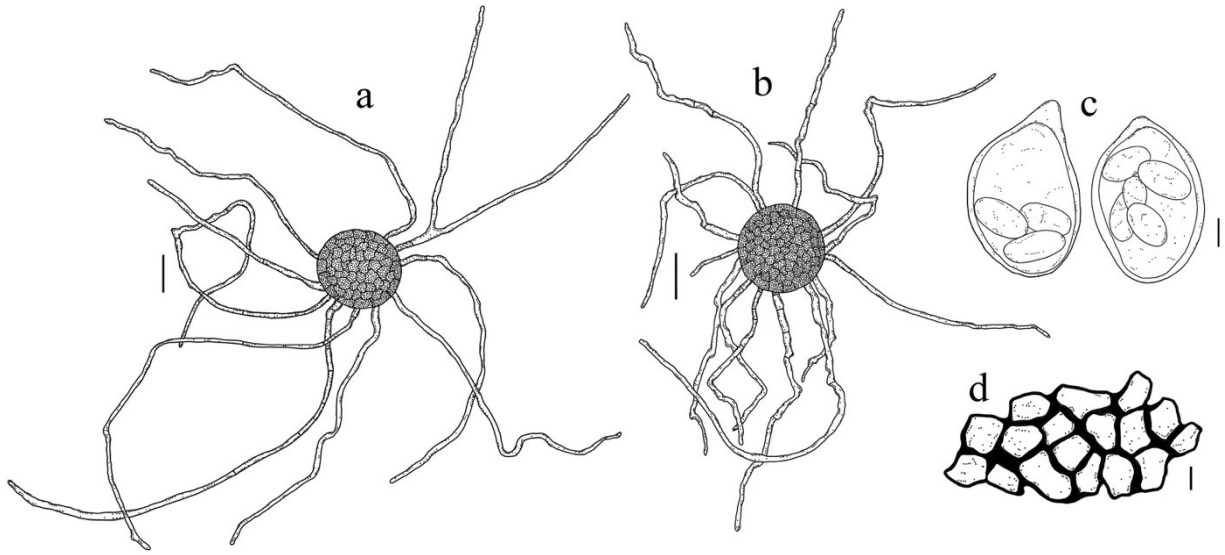

Fig. 4. An illustration of *Erysiphe aquilegiae*. a. var. *aquilegiae*; b. var. *ranunculi*; c. asci; d. peridium cells. — Scale bars = (a, b) 50 µm; (c, d) 10 µm.

substrate) sub-terminal; about 15–54 µm (0.5–1 times as long as the conidial length), with a single septum at the base; conidial appressoria lobed to multilobed. Chasmothecia amphigenous, gregarious to rather scattered, (95) 101–132 (140) µm diam.; peridium cells irregularly polygonal, 8–30 µm diam.; appendages numerous, mycelioid, simple or with irregular branches, almost equatorial or from the lower half, septate, hyaline, brown when mature, 50–150 µm long, often about the chasmothecial diam. or shorter, width 4–8 µm, wall thin, smooth to rather rough; asci 4–7, saccate-clavate, short-stalked to almost sessile, 45–71 (85) × 31–46 µm; ascospores (2) 3–5, ellipsoid, ovoid, almost globular, 15–23 × 9–18 µm.

Host range: *Beta vulgaris* L., *Spinacia* sp. (*Amaranthaceae*).

Specimens examined: Iran, Kermanshah Province, Kermanshah, on *Beta vulgaris*, Oct. 2012, Safaei (GUM 1863); 2021 (GUM 1868); Chaharmahal and Bakhtiari Province, Shahrekord, Taherian (GUM 1864); Hamedan Province, Asad Abad, on *B. vulgaris*, Oct. 2008, M. Bahador (GUM 1865); Unknown location, Aug. 2007, V. Shiri (GUM 1866); Yazd Province, Yazd, Nov. 2009, Esmailzadeh-Hosseini (IRAN 14569F); Eqlid-Yazd Road, May. 2010, Javadi (IRAN 15780F); Banadak Sadat, Aug. 2010, Esmailzadeh-Hosseini (IRAN 15781F); Taft, May. 2010, Ardeshiri (IRAN 15782F); Eqlid-Yazd Road, Oct. 2010, Yazdanian (IRAN 15783F); Taft, May. 2010, Dehghan (IRAN 15784F); Yazd, on *Spinacia* sp., Apr. 2011, Nateghi (IRAN 15785F).

Erysiphe buhrii U. Braun, Česka Mykol. 32(2): 80, 1978 Fig. 7–8

Chasmothecia amphigenous and caulicolous, mostly hypophyllous, (86) 98–149 µm diam.; peridium cells irregularly polygonal, 7–25 µm; appendages numerous, about 20–40, from the lower half, myceloid and with irregular branching, hyaline, sometimes pale brown, short and interlaced with each other, 0.5–15 times as long as the chasmothecial diam., width 5–7 µm which is almost equal throughout, septate, with 0–2 septa, thin-walled, smooth to somewhat rough; asci (3) 4–9, ellipsoid-obovoid, saccate, stalked, 65–86 (94) × 32–52 µm; ascospores (2) 3–5, ellipsoid, ovoid, 21–25 (35) × 10–18 (23) µm.

Host range: *Mesostemma kotschyana* (Fenzl ex Boiss.) Vved., *Silene latifolia* Poir., *Aconthophyllum* cf. *mucronatum* C.A.Mey. (Syn. *A. microcephalum* Boiss.) (*Caryophyllaceae*).

Specimens examined: Iran, Lorestan Province, Oshtorankuh, on *Mesostemma kotschyana*, June 2014, K. Sepahvand (GUM 1838); Alborz Province, Karaj, on *Aconthophyllum* cf. *mucronatum*, Aug. 1996 (IRAN 10904F); Ardabil Province, Ardabil, on *Silene latifolia*, Aug. 2004, S.A. Khodaparast (GUM 1839).

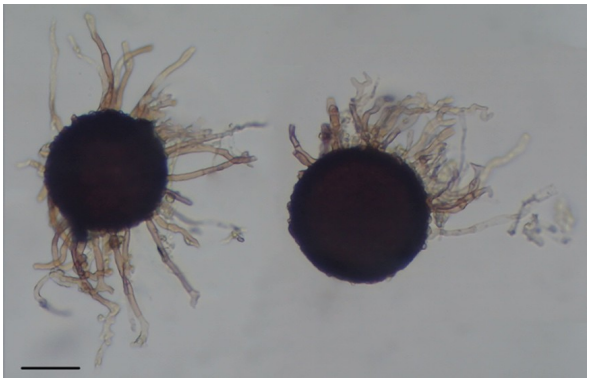

Fig. 5. Chasmothecia of *Erysiphe betae* (IRAN 15784F). — Scale bar = 50 µm.

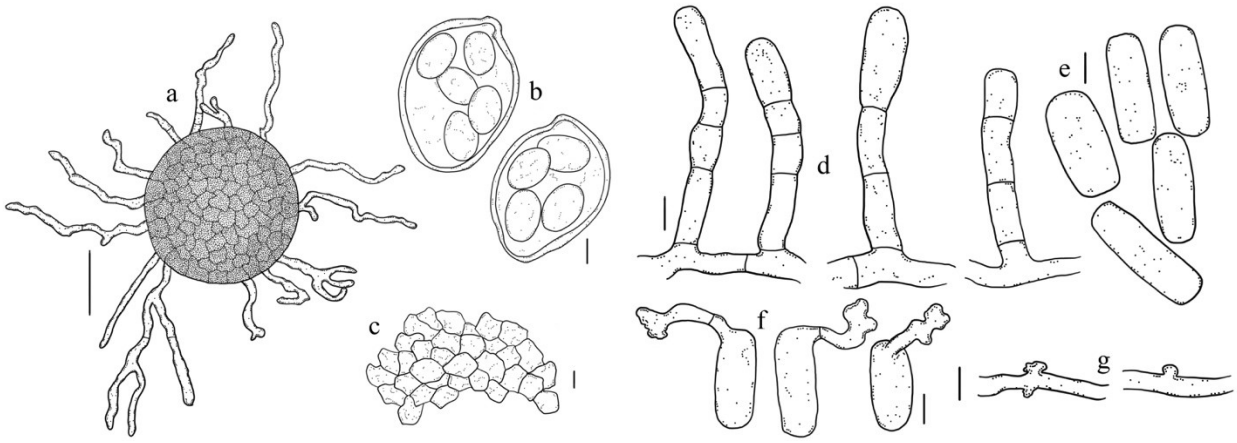

Fig. 6. An illustration of *Erysiphe betae*. a. chasmothecium; b. asci; c. peridium cells; d. conidiophores; e. conidia; f. germination of conidia; g. hyphal appressoria. — Scale bars = (a) 50 µm; (b–g) 10 µm.

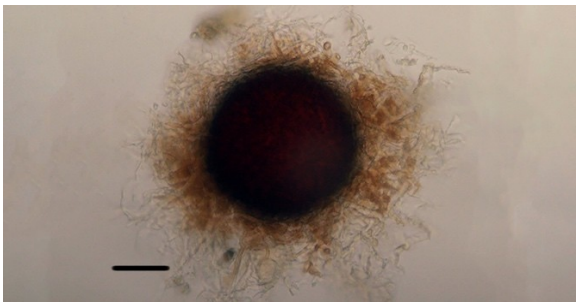

Fig. 7. Chasmothecia of *Erysiphe buhrii* (GUM 1838). — Scale bar = 50 µm.

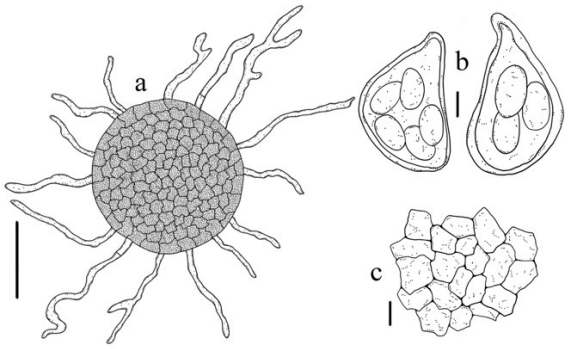

Fig. 8. An illustration of *Erysiphe buhrii*. a. chasmothecium; b. asci; c. peridium cells. — Scale bars = (a) 50 µm; (b, c) 10 µm.

Erysiphe caulicola (Petr.) U. Braun, Mycotaxon 15: 135, 1982

This species has recently been described in Darsaraei et al. (2023c).

For detailed description, host range, and distribution, as well as color plates and digital illustrations, see Darsaraei et al. (2023c).

Erysiphe circaeae L. Junell, Sv. Bot. Tidskr. 61(1): 224, 1967 Fig. 9

Mycelia semi-persistent, amphigenous and on petioles, stem and fruits; hyphal width (3) 4–6 (7) µm; hyphal appressoria unlobed to lobed; conidiophores straight to somewhat sinuous which arising from the middle of the mother cell; foot-cells cylindrical, 18–35 (46) × 6–8 µm, followed by 1–2 other cells, forming conidia singly; conidia ellipsoid, cylindrical, (26) 28–39 (43) × (10) 12–18 (20) µm; conidial germination (on natural substrate) almost terminal; conidial appressoria lobed to multilobed. Chasmothecia amphigenous and on petioles and stems, scattered to gregarious, (71) 85–105 (118) µm diam.; peridium cells irregularly polygonal, 8–17 µm; appendages less than 20, myceloid, sometimes forked into branches near the base or towards the tip, straight or geniculate and sinuous with numerous swellings, with multiple conspicuous septa, hyaline, completely or majorly brown when mature, length about 0.9–2.4 times as long as the chasmothecial diam., width 5–9 µm; asci 3–5, ellipsoid, ovoid or almost clavate, short-stalked to almost sessile, 49–67 × 31–45 µm; ascospores (2) 3–4, ellipsoid, ovoid, or with irregular shapes, (17) 18–23 (25.5) × (9) 11–13 µm.

Host range: *Circaea lutetiana* L. (*Onagraceae*).

Specimen examined: Iran, Guilan Province, Talesh, on *Circaea lutetiana*, Aug. 1998, S.A. Khodaparast (IRAN 10786F).

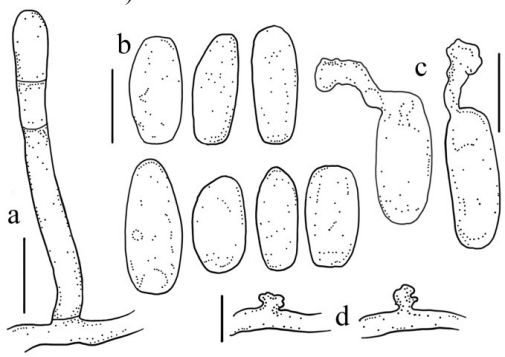

Fig. 9. An illustration of *Erysiphe circaeae* (IRAN 10786F). a. conidiophore; b. conidia; c. conidial germination; d. hyphal appressoria. — Scale bars = (a, c, d) 10 µm; (b) 20 µm.

Erysiphe convolvuli DC., FI. franç. 2: 274, 1805 **var. *convolvuli*** Fig. 10–11

Mycelia occasionally sinuous, width 4–7 µm, hyphal appressoria unlobed to multilobed, solitary or in opposite pairs; conidiophores arising from top of the mother cell, 42–75 µm; foot-cells cylindrical, straight, sometimes almost sinuous, 18–35 × 5–7 µm, followed by a cell of the same length or a little longer and sometimes swollen, or by two shorter cells, forming conidia singly; conidia cylindrical, rather rectangular, ellipsoid, 31–47 × 11–15 µm, conidial germination (on natural substrate) terminal or sub-terminal. Chasmothecia amphigenous and caulicolous, scattered to gregarious, 104–146 µm; peridium cells irregularly polygonal, 10–26 µm; appendages numerous, myceloid, from the lower half, mostly 1–2 times irregularly branched, septate, hyaline or brown at least at the lower half, length 96–288 µm (about 0.75–3 times as long as the chasmothecial diam.), width about 14 µm at the very base, then 4–7 µm which decreases towards the branches, thin-walled, smooth to somewhat rough; asci 4–7, saccate-clavate, short-stalked, 61–93 × 33–50 µm; ascospores 3–5, ellipsoid, ovoid, colorless, with a large oil drop, 19–30 × 10–16 µm.

Host range: *Convolvulus* spp. L. (*Convolvulaceae*).

Specimens examined: Iran, Hamedan Province, Hamedan, on *Convolvulus arvensis* L., Nov. 2010, M. Bahador (GUM 1840); Zanjan Province, Zanjan, on *Convolvulus* sp., Oct. 1990, Pashapoor (GUM 1841).

Erysiphe convolvuli* var. *calystegiae U. Braun, Nova Hedwigia 34: 691, 1981 Fig. 10–11

Chasmothecia amphigenous and caulicolous 99–151 µm diam.; peridium cells irregularly polygonal, 8–30 µm; appendages numerous, myceloid, from the lower half, mostly 1–2 times irregularly branched, septate, hyaline or brown at least at the lower half, length 52–442 µm (about 0.5–4 times as long as the chasmothecial diam.), width about 9–20 µm at the very base, then 3–8 µm, thin-walled, smooth to somewhat rough; asci 4–11, saccate-clavate, short-stalked, 56–87 × 32–58 m; ascospores 3–6 (7), ellipsoid, ovoid, colorless, with a large oil drop, 19–31 × 10–19 µm.

Host range: *Convolvulus* spp. L., cf. *Calystegia sepium* (L.) R. Br. (*Convolvulaceae*).

Specimens examined: Iran, Khorasan Razavi Province, Nishapur, on *Convolvulus* sp., Sep. 2019, M. Ghadamyari (GUM 1842); Kerman Province, Jiroft, on cf. *Calystegia sepium*, Dec. 2007, A.R. Amirmijani (GUM 1843); East Azerbaijan Province, Maragheh, on *Convolvulus* sp., Sep.2010, M. Damadi (GUM 1844); Tehran Province, Tehran, on *Convolvulus* sp., Oct. 1987, La'linia (GUM 1845); Varamin, on *Convolvulus* sp., Oct. 1989, Boorboor (GUM 1846).

Erysiphe cruchetiana S. Blumer, Beitr. Krypt.-Fl. Schweiz 7(1): 193, 1933

This species has recently been described in Darsaraei et al. (2023c).

For detailed description, host range, and distribution, as well as color plates and digital illustrations, see Darsaraei et al. Darsaraei et al. (2023c).

Erysiphe cruciferarum s. str. Opiz ex L. Junell, Sv. Bot. Tidskr. 61(1): 217, 1967 Fig. 12–13

Chasmothecia on stem and fruit bodies, gregarious to scattered, 103–130 µm diam.; peridium cells not very conspicuous, irregularly polygonal, 11–30 µm; appendages form the lower half, myceloid, sometimes 1–2 times dichotomously branched, septate, hyaline, sometimes pale brown at the lower half, occasionally geniculate, interlaced with each other, length up to 3 times as long as the chasmothecial diam., width about 17 µm at the very base, then 6–10 µm, wall smooth to somewhat rough, wall width about 2–3 µm; asci (3) 4–10, saccate-clavate, ellipsoid, short-stalked, 58–89 × 31–52 µm; ascospores 4–7, rather globose, ellipsoid, ovoid, 17–24 × 10–16 µm.

Host range: *Descurainia sophia* (L.) Webb ex Prantl, *Alyssum* sp. L. (*Brassicaceae*).

Specimens examined: Iran, Ardabil Province, Ardabil, on *Descurainia Sophia*, Aug. 2004, S.A. Khodaparast (GUM 1827); Zanjan Province, Zanjan, on *Alyssum* sp., Aug. 2004, S.A. Khodaparast (GUM 1828).

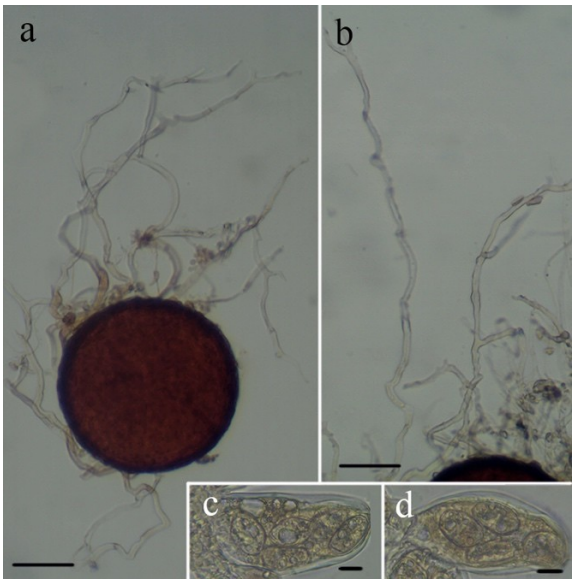

Fig. 10. *Erysiphe convolvuli*. a. chasmothecium; b. appendages; c. ascus with 5 ascospores in var. *calystegiae* (GUM 1842); d. asci with 4 ascospores in var. *convolvuli* (GUM 1840). Scale bars = (a) 50 µm; (b) 20 µm; (c, d) 10 µm.

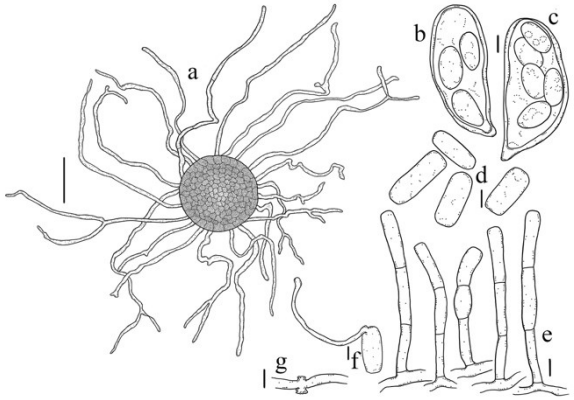

Fig. 11. An illustration of *Erysiphe convolvuli*. a. chasmothecium; b. ascus with 3 ascospores in var. *convolvuli*; c. asci with 5 ascospores in var. *calystegiae*; d. conidia; e. conidiophores; f. conidial germination; g. hyphal appressoria. Scale bars = (a) 50 µm; (b–g) 10 µm.

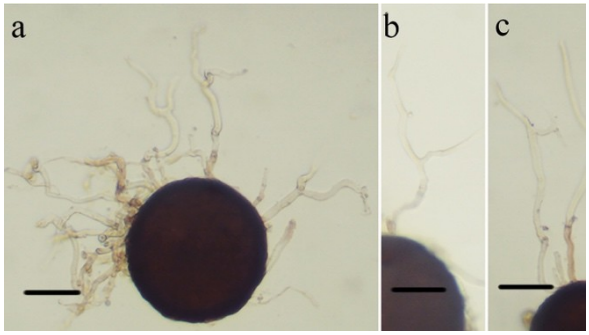

Fig. 12. *Erysiphe cruciferarum s. str.* (GUM 1827). a. chasmothecia; b, c. appendages. — Scale bars = 50 µm.

Erysiphe cruciferarum s. lat. Fig. 13

Chasmothecia amphigenous and caulicolous, gregarious to somewhat scattered, 86–150 µm diam.; peridium cells not very conspicuous, irregularly polygonal, 8–28 µm; appendages myceloid, occasionally branched, sometimes geniculate, relatively flexuous, from the lower half, sometimes sinuous and with irregular outline, septate, with 0–2 septa, pale brown to brown when mature, length 0.5–3 times as long as the chasmothecial diam., width about 10–16 µm at the very base, then 4–8 µm, thin-walled, smooth to somewhat rough; asci 3–7, saccate-clavate, short-stalked to almost sessile, 58–87 × 31–58 µm; ascospores 3–6, ellipsoid, ovoid, 18–32 × 10–19 µm, colorless.

Host range: *Barbarea* sp., *Brassica nigra* (L.) K. Koch (Syn. *Sinapis nigra*), *Lepidium draba* L. (Syn. *Cardaria draba*), *Rapistrum rugosum* (L.) All., *Lepidium* sp. L., *Brassica* sp. L. (*Brassicaceae*).

Specimens examined: Iran, Fars Province, Sepidan, on *Barbarea* sp., August 2006, E. Ghasemi (GUM 1571); Guilan Province, Bararud, on cf. *Brassica nigra*, June 2020, S.A. Khodaparast (GUM 1830); Damash, on *Brassicaceae*, June 2020, S.A. Khodaparast (GUM 1831); Dasht-e Veyl, on *Brassicaceae*, June 2020, S.A. Khodaparast (GUM 1832); Harzevil, on *Brassicaceae*, June 2020, S.A. Khodaparast (GUM 1829); Zanjan Province, Zanjan, on *Lepidium draba*, Aug. 2006, S.A. Khodaparast (GUM 1833); West Azerbaijan Province, Urmia, on *Rapistrum rugosum*, Aug. 2004, S.A. Khodaparast (GUM 1834); Unknown location, on *Lepidium* sp. (GUM 1835); Markazi Province, Arak, on *Brassica* sp., Oct. 2008, M. Bahador (GUM 1836).

Erysiphe heraclei DC., FI. franco 6:107,1815 Fig. 14–15

Chasmothecia on both sides of leaves and stems, gregarious to somewhat scattered, 77–143 µm diam.; peridium cells not very conspicuous, irregularly polygonal, 8–28 µm; appendages numerous, myceloid, simple or frequently irregularly branched, often in a coral-like manner, hyaline to somewhat pale brown, septate, appendages of adjacent chasmothecia sometimes interwoven with each other, 0.5–2 (3) times as long as the chasmothecial diam., width 12–18 µm at the very base, then 2–10 µm throughout, wall thin, smooth, somewhat verruculose; asci 3–8, saccate-clavate, short-stalked to almost sessile, 42–89 × 30–58 µm; ascospores 2–5, ellipsoid, ovoid, 15–35 × 9–19 µm, colorless.

Host range: *Falcaria vulgaris* Bernh., *Turgenia latifolia* (L.) Hoffm., *Eryngium* sp., *Daucus carota* L., *Pimpinella saxifraga* L., *Pimpinella peregrina* L. (Syn. *Pimpinella affinis*), *Ammi majus* L., *Bunium* sp., *Heracleum persicum* Desf. ex Fisch., C.A. Mey. & Avé-Lall. (*Apiaceae*).

Specimens examined: Iran, Kurdistan Province, Marivan, on *Falcaria vulgaris*, July 2015, K. Sepahvand (GUM 1869); Hamedan Province, Hamedan, on *Turgenia latifolia*, July 2009, M. Bahador (GUM 1870); Ardabil Province, Ardabil, on *Eryngium* sp., Aug. 2004, S.A. Khodaparast (GUM 1871); West Azerbaijan Province, Urmia, on *Daucus carota*, Aug. 2004, S.A. Khodaparast (GUM 1872); Guilan Province, Harzevil, on *Apiaceae*, June 2020, S.A. Khodaparast (GUM 1873); Bararud, on *Apiaceae*, June 2020, S.A. Khodaparast (GUM 1874); Amarlu, on *Pimpinella saxifraga*, June 2020, S.A. Khodaparast (GUM 1875); on *Apiaceae*, June 2020, S.A. Khodaparast (GUM 1877); Damash, on *Apiaceae*, June 2020, S.A. Khodaparast (GUM 1878); Dasht-e Veyl, on *Ammi majus*, June 2020, S.A. Khodaparast (GUM 1879); East Azerbaijan Province, Sufiyan-Shabestar Road, on *Pimpinella peregrina*, Aug. 2004, S.A. Khodaparast (GUM 1876); South Khorasan Province, Birjand, Fourteen Falls, on *Bunium* sp., May 2009, Jahani (GUM 1880); Zanjan Province, Zanjan, on *Heracleum persicum*, Aug. 2006, S.A. Khodaparast (GUM 1881); on *Apiaceae*, Aug. 2006, S.A. Khodaparast (GUM 1882).

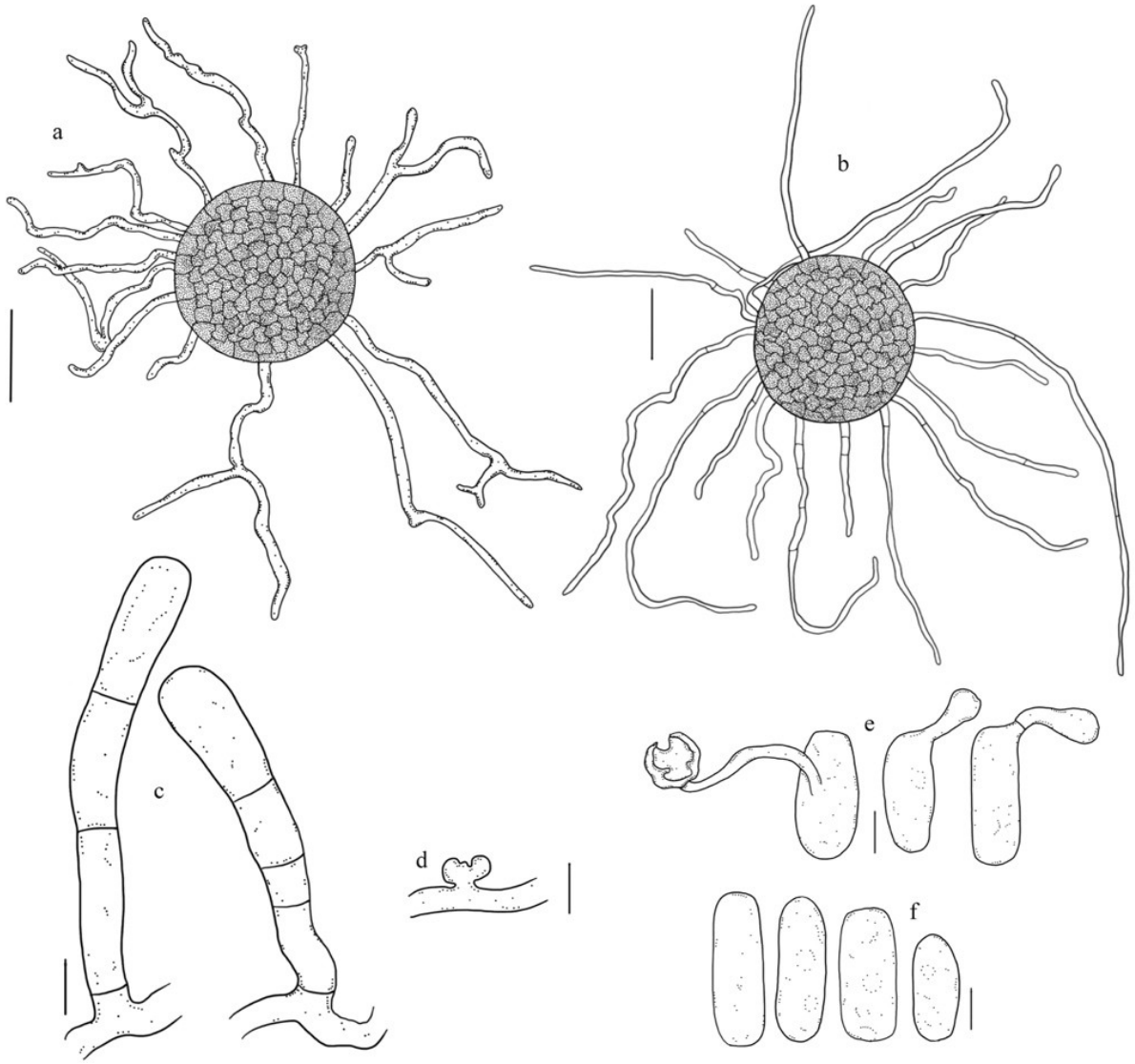

Fig. 13. An illustration of *Erysiphe cruciferarum*. a. chasmothecium in *E. cruciferarum s. str.*; b–f. *E. cruciferarum s. lat.*; b. chasmothecium; c. conidiophores; d. hyphal appressorium; e. conidial germination; f. conidia. — Scale bars = (a, b) 50 µm; (c–f) 10 µm.

Erysiphe howeana U. Braun, Mycotaxon 14(1): 373, 1982 Fig. 16

Mycelia compact and white, occasionally covers the entire surface of the leaves; hyphal width 5–7 µm; conidiophores arising towards one end of the mother cell, erect, 41–74 µm; foot-cells cylindrical, straight, 22–46 × 7–10 µm, followed by 1–2 cells of the same length or shorter cells, forming conidia singly; conidia ellipsoid, ovoid, almost barrel-shaped to somewhat cylindrical, 24–38 × 10–19 µm; conidial germination terminal or sum-terminal; conidial appressoria lobed. Sexual state not seen.
Host range: *Oenothera biennis* L. (*Onagraceae*)
Specimen examined: Iran, Isfahan Province, Isfahan, on *Oenothera biennis*, Unknown date, K. Sharifi (GUM 1714).

Erysiphe limonii L. Junell, Sv. Bot. Tidskr. 61(1): 225, 1967 Fig. 17–18

Chasmothecia amphigenous, almost gregarious to scattered, 94–132 µm diam.; peridium cells not very conspicuous, irregularly polygonal, 10–27 µm; appendages numerous, myceloid, simple or somewhat irregularly branched, from the lower half, hyaline, sometimes brown, septate, length 72–168 µm, width 4–6 µm, thin-walled, smooth to rough; asci 3–5, saccate-clavate, short-stalked to almost sessile, 63–79 × 36–49 µm; ascospores (2) 3–4 (5), elisposid, ovoid, 21–31 × 10–17 µm.
Host range: *Limonium meyeri* (Boiss.) Kuntze (*Plumbaginaceae*).
Specimen examined: Iran, East Azerbaijan Province, Tabriz, on *Limonium meyeri*, Oct. 2002, Gh. Tavanaei (GUM 1858).

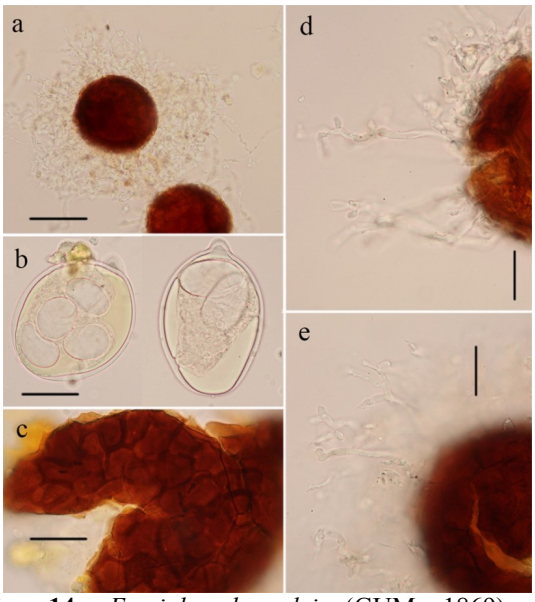

Fig. 14. *Erysiphe heraclei* (GUM 1869). a. chasmothecium; b. asci; c. peridium cells; d, e. outline of appendages. — Scale bars = (a) 100 µm; (b, c) 20 µm; (d, e) 50 µm.

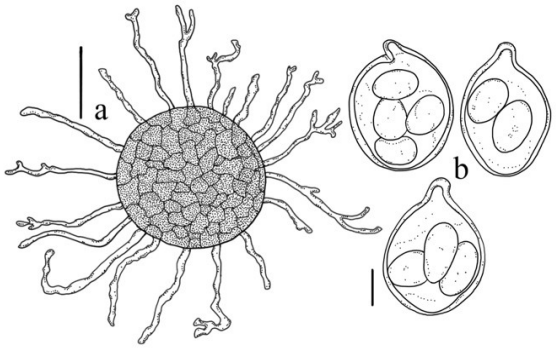

Fig. 15. An illustration of *Erysiphe heraclei*. a. chasmothecium; b. asci. — Scale bars = (a) 50 µm; (b) 10 µm.

Erysiphe lycopsidis R.Y. Zheng & G.Q. Chen, Sydowia 34: 234, 1981 Fig. 19–20

Chasmothecia gregarious to almost scattered, 101–132 µm; peridium cells irregularly polygonal, 7–25 µm, appendages myceloid, simple or with irregular branching, geniculate-sinuous, hyaline or brown, in the lower half, 43–168 µm (about 0.5–1.5 times as long as the chasmothecial diam.), width 5–7 µm, thin-walled, rather rough; asci 4–6, short-stalked to almost sessile, saccate-clavate, ellipsoid, 62–89 × 43–60 µm; ascospores 3–5(6), ellipsoid, 21–27 × 11–18 µm. Host range: *Anchusa arvensis* subsp. *Orientalis* (L.) Nordh. (Syn. *Anchusa ovata*) (*Boraginaceae*). *Specimens examined*: Iran, Ardabil Province, Ardabil, on *Anchusa arvensis* subsp. *Orientalis*, Aug. 2004, S.A. Khodaparast (GUM 1826); Guilan Province, Amarlu, Aug. 1998, S.A. Khodaparast (IRAN 10802F).

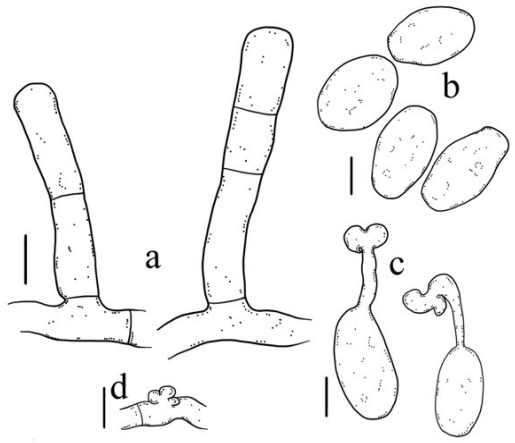

Fig. 16. An illustration of *Erysiphe howeana* (GUM 1714). a. conidiophores; b. conidia; c. conidial germination; d. hyphal appressorium. — Scale bars = 10 µm.

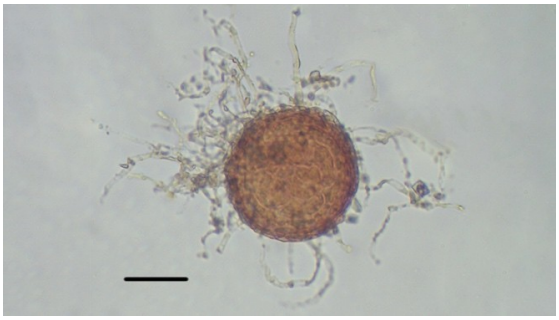

Fig. 17. Chasmothecium of *Erysiphe limonii* (GUM 1858). — Scale bar = 50 µm.

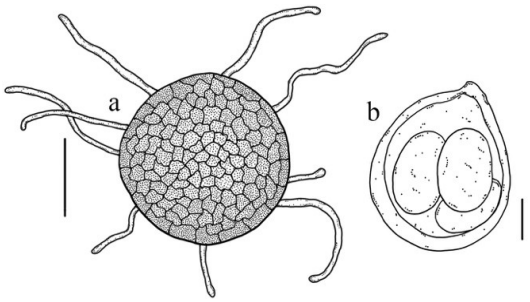

Fig. 18. An illustration of *Erysiphe limonii*. a. chasmothecium; b. ascus. — Scale bars = (a) 50 µm; (b) 10 µm.

Erysiphe malvae Heluta, Ukrayins'k. Bot. Zhum 47(4): 75, 1990 Fig. 21–22

Mycelia amphigenous and caulicolous; hyphal width 4–6 µm; hyphal appressoria nipple-shaped to lobed and multilobed, solitary or in opposite pairs; conidiophores arising from the top of the mother cell, straight or sinuous, (52) 70–135 µm; foot-cells cylindrical, straight or sinuous, 28–65 × 6–10 µm, followed by a cell of the same length and a shorter cell, or two shorter cells, width of these cells sometimes increases towards the tip, basal septum of the foot-cells sometimes distance a few µm from the

mother cell; conidia single, ellipsoid, cylindrical, ovoid, 31–47 × 10–17 µm; conidial terminal or sub-terminal; conidial appressoria lobed to multilobed. Chasmothecia amphigenous and caulicolous, scattered to gregarious, 81–120 µm diam.; peridium cells irregularly polygonal, 7–30 µm; appendages numerous, myceloid, irregularly branched or with multiple short branchlets, hyaline or brown at the lower parts, septate, from the lower half, sometimes interlaced with the appendages of other chasmothecia, length 39–168 µm (about 0.5–2 times as long as the chasmothecial diam.), width about 17 µm at the very base, then 3–7 µm, thin-walled, smooth to somewhat rough; asci 4–6, saccate, ellipsoid, short-stalked to almost sessile, 52–84 × 35–55 µm; ascospores 3–6 (mostly 4–5), colorless, broadly ellipsoid, 18–25 × 10–17 µm.

Host range: *Malva sylvestris* L., *Malva* sp. (*Malvaceae*).

Specimens examined: Iran, Guilan Province, Manjil, on *Malva sylvestris*, 25 July 2007, S.A. Khodaparast (GUM 1943); Rudbar, on *Malva* sp., June 2020, S.A. Khodaparast (GUM 1848); Yazd Province, Yazd, on *M. sylvestris*, July 2008, Esmailzadeh Hosseini (IRAN 13937F); Aug. 2007 (IRAN 13466F); Nov. 2007, Soltani (IRAN 13852F); Tehran Province, Tehran, on *Malva* sp., Aug. 2012, Abbasi (IRAN 15984F).

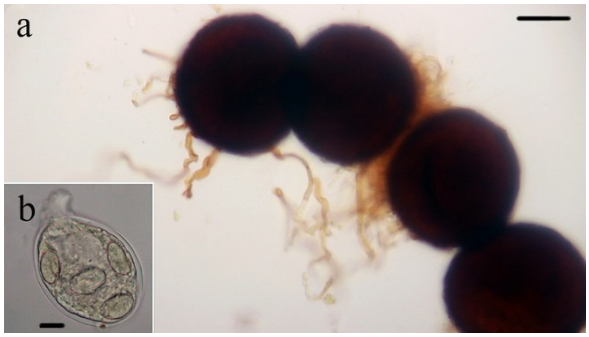

Fig. 19. *Erysiphe lycopsidis* (GUM 1826). a. chasmothecium; b. ascus. — Scale bars = (a) 50 µm; (b) 10 µm.

Erysiphe mayorii* var. *japonica U. Braun & Y. Nomura, Mycotaxon 20: 497, 1984 Fig. 23–24

Mycelia epiphyllous, forming patches or covering the whole surface of the leaves, hyaline, smooth. Chasmothecia amphigenous, scattered, 89–119 µm; peridium cells not very conspicuous, irregularly polygonal, 8–15 µm; appendages numerous, rather equatorial, sometimes interwoven with the hyphae, with irregular branching, septate, firstly hyaline, then become yellow and pale brown, completely brown when mature, short and about the length of the chasmothecial diam., often shorter, width 3–7 µm, thin-walled, rather smooth; asci 7–12 and even more, saccate-clavate, broadly ellipsoid, stalked, 61–70 × 21–32 µm; ascospores (4) 5–7, ellipsoid and ovoid, 16–22 × 8–13 µm.

Host range: *Lactuca macrophylla* (Willd.) A. Gray (Syn. *Mulgedium cacaliifolium* (M.Bieb.) DC.) (*Asteraceae*).

Specimens examined: Iran, Guilan Province, Asalem, on *Lactuca macrophylla*, Aug. 1970, Izadyar (IRAN 1201F).

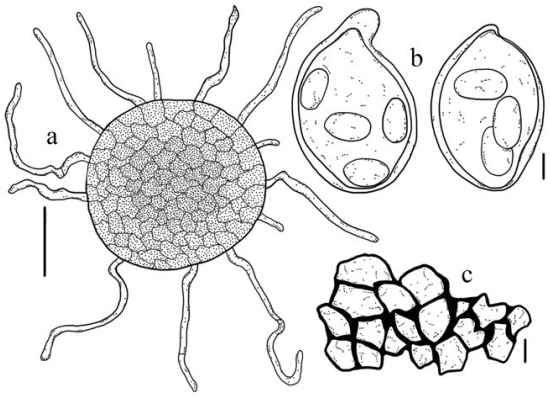

Fig. 20. An illustration of *Erysiphe lycopsidis*. a. chasmothecium; b. asci; c. peridium cells. — Scale bars = (a) 50 µm; (b, c) 10 µm.

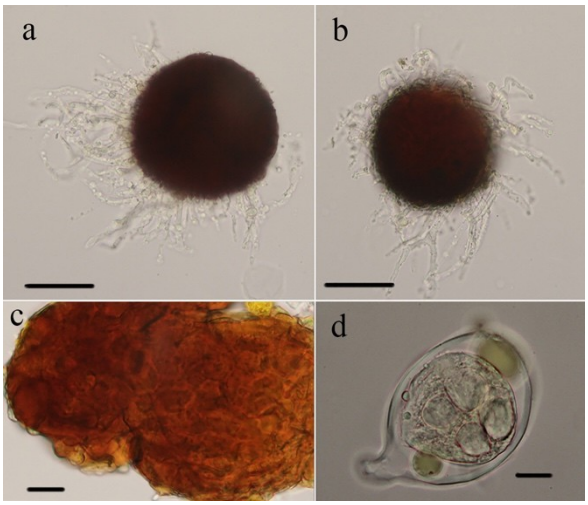

Fig. 21. *Erysiphe malvae* (GUM 1848). a, b. chasmothecia; c. peridium cells; d. ascus. — Scale bars = (a, b) 50 µm; (c, d) 10 µm.

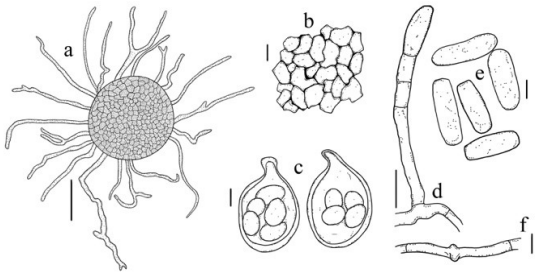

Fig. 22. An illustration of *Erysiphe malvae*. a. chasmothecium; b. peridium cells; c. asci; d. conidiophore; e. conidia; f. hyphal appressoria. — Scale bars = (a) 50 µm; (d) 20 µm; (b, c, e, f) 10 µm.

Fig. 23. A chasmothecium of *Erysiphe mayorii* var. *japonica* (IRAN 1201F). — Scale bar = 50 µm.

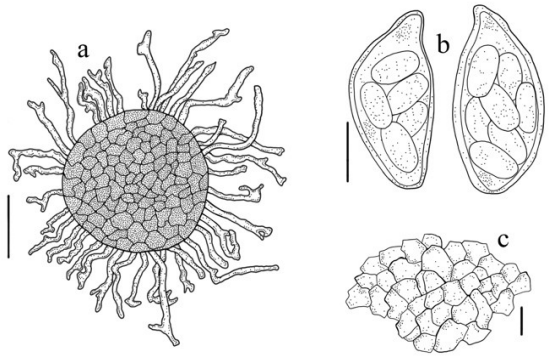

Fig. 24. An illustration of *Erysiphe mayorii* var. *japonica*. a. chasmothecium; b. asci; c. peridium cells. — Scale bars = (a) 50 µm; (b) 20 µm; (c) 10 µm.

Erysiphe medicaginis L. Kiss, L. Kelly & Vaghefi, Persoonia 44: 389, 2020

This species has recently been described in Darsaraei et al. (2023c).

For detailed description, host range, and distribution, as well as color plates and digital illustrations, see Darsaraei et al. Darsaraei et al. (2023c).

Erysiphe neolycopersici (L. Kiss) H.Y. Hsiao & Y.M. Shen, in Hsiao, Ariyawansa, Hsu, Wang & Shen, Diversity 14(3, no. 204), 14 (2022)

Mycelia white, dense or in scattered patches, mostly epiphyllous, caulicolous, width 4.8–7.2 µm, hyphal appressoria nipple shaped and lobed, conidiophores erect, arising towards one end of the mother cell, 45.6–110.4 × 4.8–7.2 µm, forming conidia singly, foot cells cylindrical, rarely swollen in the middle and constricted at the base, 26.4–57.6 × 4.8–7.2 µm, followed by 1–3 shorter cells, conidia ellipsoid-ovoid, sub-cylindrical, 21.6–40.8 × 12–16.8 µm. Sexual state not seen.

Host range: *Solanum lycopersicum* L. (syn. *Lycopersicon esculentum* Mill.) (*Solanaceae*).

Specimen examined: Iran, Ardabil Province, Ardabil, on *Solanum lycopersicum* (GUM 1945).

The examined specimens had a damaged asexual state and hence were not suitable for morphological studies. The description presented here is based on Davari et al. (2015).

Erysiphe paeoniae R.Y. Zheng & G.Q. Chen, Sydowia 34: 300, 1981 Fig. 25–26

Chasmothecia amphigenous and caulicolous, scattered, 95–119 (–140) µm diam.; peridium cells conspicuous, irregularly polygonal, 10–25 µm; appendages numerous, almost equatorial or from the lower half, first hyaline and then brown, septate, irregularly branched or with coral-like branchlets, length less than chasmothecial diam., rarely exceeds, width 5–7 µm, thin-walled, smooth to rough; asci 5–9, saccate-clavate, ellipsoid, often short-stalked, 59–72 × 34–43 µm; ascospores 3–6, ellipsoid, ovoid, 18–26 × 9–14 µm.

Host range: *Paeonia* sp. (*Paeoniaceae*).

Specimen examined: Iran, Ardabil Province, Heroabad, on *Paeonia* sp., Aug. 1970, Izadyar (IRAN 1328F).

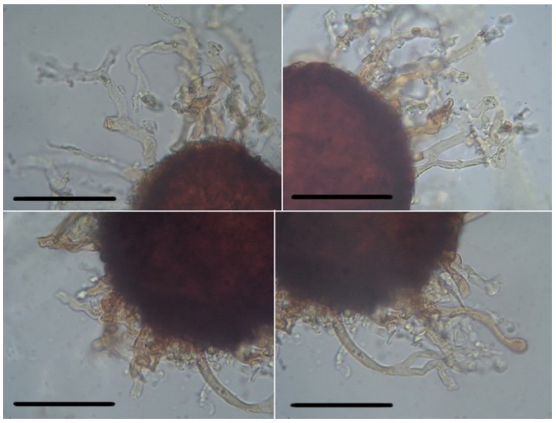

Fig. 25. Appendages arising from chasmothecia of *Erysiphe paeoniae* (IRAN 1328F). — Scale bars = 50 µm.

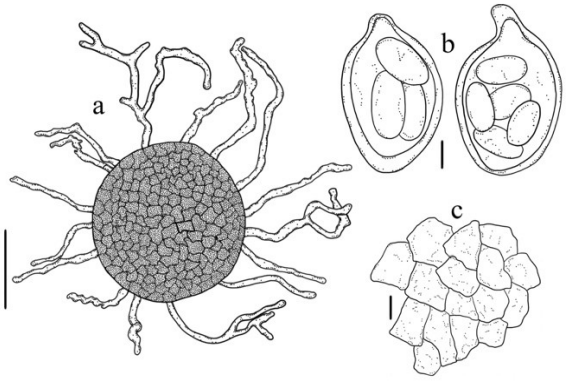

Fig. 26. An illustration of *Erysiphe paeoniae*. a. chasmothecium; b. asci; c. peridium cells. — Scale bars = (a) 50 µm; (b, c) 10 µm.

Erysiphe pisi DC., FI. franc. 2: 274, 1805

This species has recently been described in Darsaraei et al. (2023c).

For detailed description, host range, and distribution, as well as color plates and digital illustrations, see Darsaraei et al. Darsaraei et al. (2023c).

Erysiphe polygoni DC., FI. franc. 2: 273, 1805

This species has recently been described in Darsaraei et al. (2023a).

For detailed description, host range, and distribution, as well as color plates and digital illustrations, see Darsaraei et al. (2023a).

Erysiphe punicae T.M. Achundov, Novosti Sist. Nizsh. Rast. 24: 95, 1987

Mycelia epiphyllous, almost cover some or the whole surface of the leaves uniformly, finely, and sparsely; conidia single, ellipsoid, cylindrical, (23) 25–35 × 10–15 µm, germ tubes short, conidial appressoria multilobed. Chasmothecia scattered (70) 85–113 µm diam.; peridium cells irregularly polygonal, 10–21 µm; appendages 9–13, from the lower half or equatorial, myceloid, septate, flexuous and long, first hyaline and thin-walled, then brown and thick-walled, pale brown towards the tip, length 130–680 µm (about 1.5–7.7 times as long as the chasmothecial diam.), width 5–9 µm; asci 2–4, ovoid to almost globose, sessile, 42–75 × 30–44 µm; ascospores ellipsoid to ovoid, 20–24 × 12–13 µm.

Host range: *Punica granatum* L. (*Lythraceae*).

Specimen examined: Iran, Guilan Province, Rudbar, on *Punica granatum*, Oct. 1997 and Nov. 1998, S.A. Khodaparast (IRAN 10851F).

Erysiphe rumicicola Darsaraei, Khodap., Afshan & U. Braun. Sydowia 75, 2023

This species has recently been described in Darsaraei et al. (2023a).

For detailed description, host range, and distribution, as well as color plates and digital illustrations, see Darsaraei et al. (2023a).

Erysiphe sedi U. Braun, Feddes Repert. 92(7–8): 502, 1981 Fig. 27–28

Mycelia amphigenous, in white patches, hyphal appressoria multilobed, solitary or in opposite pairs; conidiophores arising from the top of the mother cell, often straight, 44–90 × 7–10 µm; foot-cells cylindrical, 25–42 × 7–10 µm, followed by 1–2 other cells, forming conidia singly; conidia cylindrical, ellipsoid, (29) 37–46 × 13–18 (21) µm. Sexual state not seen.

Host range: *Bryophyllum* sp., *Kalanchoe* sp. (*Crassulaceae*).

Specimens examined: Iran, Guilan Province, Rasht, on *Bryophyllum* sp., March 2021, S.A. Khodaparast (GUM 1847); on *Kalanchoe* sp. Oct. 2022, S.A. Khodaparast (GUM 1912).

Erysiphe urticae (Wallr.) S: Blumer, Beitr. Krypt.-Fl. Schweiz 7(1): 224, 1933 Fig. 29–30

Mycelia amphigenous, white, in patches, confluent; hyphal cell width 3–7 µm; hyphal appressoria lobed, solitary or in opposite pairs; conidiophores arising from the top of the mother cell, straight, length about 50–70 µm; foot-cells straight to sinuous, cylindrical, 32–56 × 7–9 µm, followed by 1–2 other cells, basal septa of the foot-cell often located 5–6 µm upper then the mother cell's surface, forming conidia singly; conidia ellipsoid, cylindrical, ovoid, 25–46 × 11–17 µm. Chasmothecia amphigenous, scattered, immersed in hyphal patches, 83–114 µm diam.; peridium cells not very conspicuous, irregularly polygonal, 10–35 µm; appendages from the lower half, myceloid, simple or with irregular branchlets, length shorter than or equals to the chasmothecial diam., slender, width 3–5 µm, aseptate or with a few septa, thin-walled, smooth to somewhat rough, hyaline, sometimes brown at the base; asci 4–11, saccate, broadly ellipsoid-ovoid, 46–81 × 25–53 µm; ascospores 4–5, ellipsoid, somewhat ovoid, 16–26 × 9–15 µm, colorless.

Host range: *Urtica* sp. (*Urticaceae*).

Specimen examined: Iran, Hamedan Province, Hamedan, on *Urtica* sp., 2015, M. Bahador (IRAN 16919F and GUM 1898).

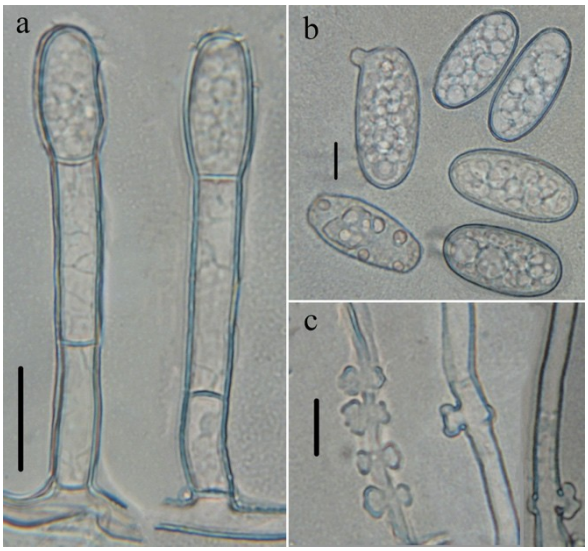

Fig. 27. *Erysiphe sedi* (GUM 1912). a. conidiophores; b. conidia; c. hyphal appressoria. — Scale bars = (a) 20 µm; (b, c) 10 µm.

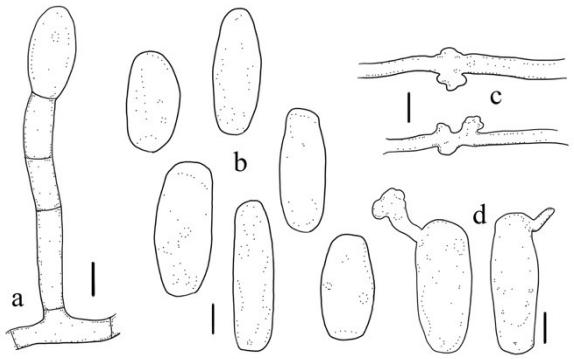

Fig. 28. An illustration of *Erysiphe sedi*. a. conidiophores; b. conidia; c. hyphal appressoria; d. conidial germination. — Scale bars = 10 µm.

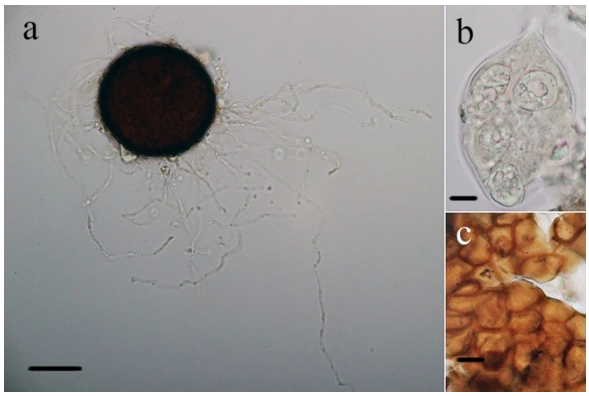

Fig. 29. *Erysiphe urticae* (GUM 1898). a. chasmothecium; b. ascus; c. peridium cells. — Scale bars = (a) 50 µm; (b, c) 10 µm.

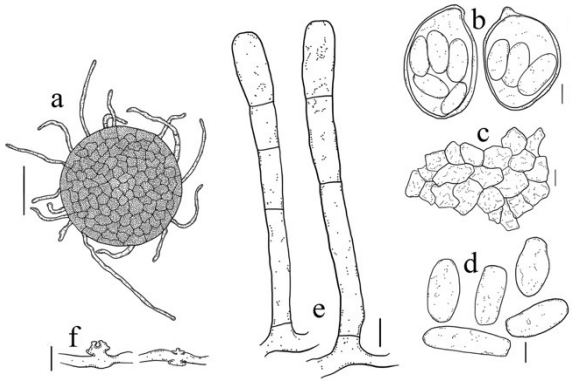

Fig. 30. An illustration of *Erysiphe urticae* (GUM 1898). a. chasmothecium; b. asci; c. peridium cells; d. conidia; e. conidiophores; f. hyphal appressoria. — Scale bars = (a) 50 µm; (b–f) 10 µm.

***Erysiphe* sp. 1** Fig. 31–32

Mycelia amphigenous, persistent, scattered or in white patches; foot-cells cylindrical, 25–35 × 6–9 µm, followed by 1–2 shorter or with the same length cells; conidia ellipsoid, cylindrical, 25–50 × 10–17 µm. Chasmothecia mostly hypophyllous, immersed in mycelial patches, scattered, 91–120 µm diam.; peridium cells irregularly polygonal, 10–30 µm; appendages from the lower half, few to numerous, myceloid, length often shorter than or sometimes equal to the chasmothecial diam., slender, width 2–3 µm which are hyaline towards the tip, but wider and brown at the base, aseptate or with a few inconspicuous septa, thin-walled, rough; asci 4–6, saccate, short-stalked to almost sessile, 60–80 × 39–48 µm; ascospores 4–7, ellipsoid, almost globose, colorless, 18–21 (25) × 11–18 µm.

Host range: *Urtica dioica* L. (*Urticaceae*).

Specimen examined: Iran, Guilan Province, Amarlu, on *Urtica dioica*, Oct. 1997, S.A. Khodaparast (IRAN 10808F).

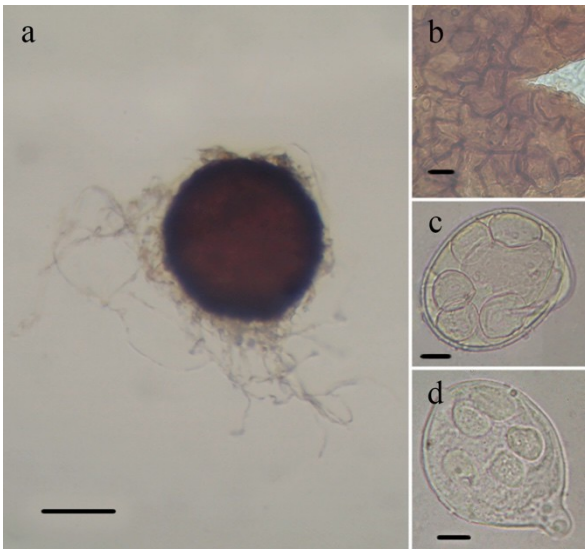

Fig. 31. *Erysiphe* sp. 1 (IRAN 10808F). a. chasmothecium; b. peridium cells ascus; c, d. asci — Scale bars = (a) 50 µm; (b–d) 10 µm.

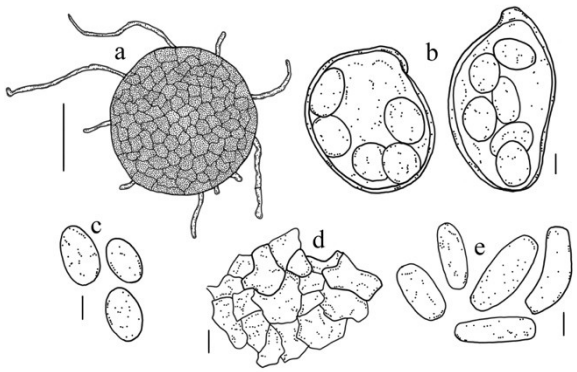

Fig. 32. An illustration of *Erysiphe* sp. 1 (IRAN 10808F). a. chasmothecium; b. asci; c. ascospores; d. peridium cells; e. conidia. — Scale bars = (a) 50 µm; (b–e) 10 µm.

***Erysiphe* sp. 2** Fig. 33–34

Chasmothecia amphigenous, (87) 93–112 µm diam.; peridium cells irregularly polygonal, 18–30 µm; appendages 8–12, myeloid and simple, almost equatorial, occasionally irregularly branched, brown, pale brown towards the tip, or at least brown at the base, long and flexuous, length 120–530 µm (up to 5 times as long as the chasmothecial diam.), width 5–10 µm, septate with 1–2 septa, wall smooth to rough, thick, sometimes the thickness decreases towards the tip; asci 3–5, saccate, clavate, short-stalked, 52–65 × 36–43 µm; ascospores 3–4 (5), ellipsoid, ovoid, 18–25 × 11–15 µm.

Host range: cf. *Potentilla* sp. L. (*Rosaceae*).

Specimen examined: Iran, Isfahan Province, Isfahan, on cf. *Potentilla* sp., Aug. 2006, N. Panahi (GUM 1885).

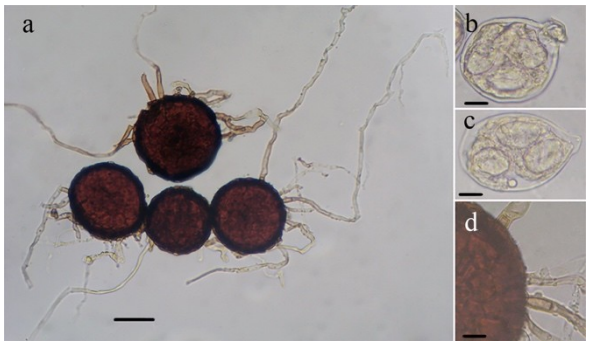

Fig. 33. *Erysiphe* sp. 2 (GUM 1885). a. chasmothecium; b, c. asci; d. basal septum of appendages. — Scale bars = (a) 50 µm; (b–d) 10 µm.

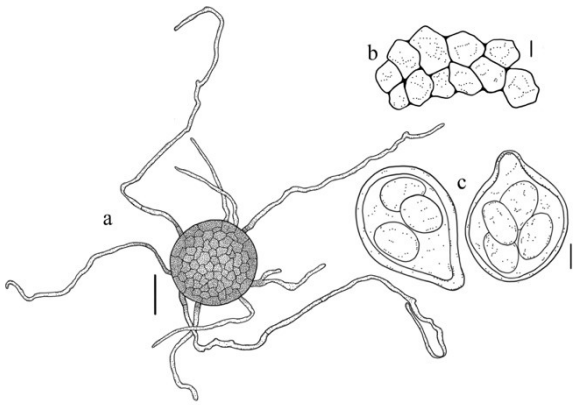

Fig. 34. An illustration of *Erysiphe* sp. 2 (GUM 1885). a. chasmothecium; b. peridium cells; c. asci. — Scale bars = (a) 50 µm; (b, c) 10 µm.

DISCUSSION

Within the framework of taxonomic update and DNA barcoding of the genus *Erysiphe*, we examined collections of the *Erysiphe* sect. *Erysiphe* and conducted a phylogenetic analysis based on rDNA sequences. Twenty species (of 23 species) occurring in Iran, were included in phylogenetic analysis. The majority of species formed their own clade along with representative sequences from GenBank. However, some clades require more attention. Clade 1 (including *E. aquilegiae* and some phylogenetically closely related species) is homogeneous, as previously indicated by Takamatsu et al.)2015(, which includes sequences from several species on a wide range of plant families. Members of this group *i.e.*, *E. aquilegiae*, *E. circaeae*, *E. sedi*, *E. asclepiadis*, and *E. neolycopersici*, can infect plants in different families. As emphasized by Takamatsu et al.)2015(, we here note that taxonomic and phylogenetic re-evaluation of this clade using more gene sequencing of type materials and wide host range examination is necessary. Undoubtedly, consistent with previous morphological and molecular studies (Davari et al. 2015, Meeboon & Takamatsu 2014, Takamatsu et al. 2015, Hsiao et al. 2022, Kashimoto et al. 2003, Shin et al. 2019), this group might include closely related taxa that still overlap in the host range, or some may belong to the same species. However, phylogenetic analysis of such a group of taxa, based solely on sequences of ITS does not often yield the necessary resolutions (Takamatsu et al. 2015, Liu et al. 2022a).

Erysiphe medicaginis (Clade 2) is a newly described species on *Medicago polymorpha* (Crous et al. 2020). The ITS sequence of powdery mildew obtained from *M. sativa* (AB104519, voucher GUM 81, IRAN 10803F) that was previously assigned to *E. pisi* by Khodaparast et al. (2000) is identical to the holotype of *E. medicaginis* (NR 171870, voucher BRIP 70957). Khodaparast et al. (2000) reported this species based on characteristics of asexual and sexual states, however, the original description of *E. medicaginis* was based on asexual state (Crous et al. 2020). Furthermore, *E. pisi* and *E. medicaginis* are morphologically very similar, hence the ITS sequence studied here was helpful to assign this fungus to correct taxonomic placement. *Erysiphe polygoni* which is supposed to infect various host genera of *Polygonaceae* (Braun &Cook 2012), was recently restricted to *Polygonum aviculare*, and *E. rumicicola* was introduced as a species infecting some species of *Rumex*, *Fagopyrum*, and *Rheum* (Darsaraei et al. 2023a). The family *Caryophyllaceae* is infected by *E. buhrii* (Braun &Cook 2012). Sequences obtained from *Erysiphe* on *M. kotschyana* and *Acanthophyllum* sp. (OM856005 and AB128924, respectively) in Iran have only one substitution against the type sequence of *E. buhrii* (LC009958, on *Silene alba* from Germany). Sequences from *Erysiphe* species on *Gypsophila* and *Dianthus*, other genera of *Caryophyllaceae*, show four and five bases substitutions against the ITS sequence of the type material and form small subclades with 99% BS support. This brings to mind that *E. buhrii* needs more precise morphological and molecular investigations to see whether the species has intraspecific variations or should be segregated into more species.

The largest clade with no BS support in the middle of the tree (Clade 3) contains sequences from *E. betae*, *E. heraclei*, and *E. malvae*. These species are rather morphologically similar, but infect different plant host families, *i.e.*, *Amaranthaceae*, *Apiaceae*, and *Malvaceae*, respectively. The ITS rDNA performs poorly as a DNA barcode marker for these species. The most essential requirement in such cases is to obtain sequences from protein-coding genes that might have a better resolution to segregate closely related species. For now, these species should be treated as separate species based on their hosts until further information is provided. The sequences obtained from *E. cruciferarum* (Clade 7) fell into two subclades (see Results). The sequence from this fungus on *Alyssum* sp. (OM855992, voucher: GUM

1828) clustered with the type sequence of *E. cruciferarum* on *Alyssum alyssoides* (KU672364, from the Czech Republic). As supposed by Pastirčáková et al. (2016), we assign this clade to *E. cruciferarum s. str*. Other sequences from the other genera of *Brassicaceae* formed a sister clade without BS support. With the data available, *E. cruciferarum s. str.* has hyaline appendages with regular, symmetric, or asymmetric branching and has a narrow host range, *i.e.*, *Alyssum*, *Descurainia*, and *Berteroa*. In contrast, the second subclade has geniculate, brown appendages with irregular branching and occurs on a wider host range. Since sequences from genera other than *Alyssum*, *Descurainia*, and *Berteroa* are diverse and cannot be grouped even by host genera, we prefer to maintain them as *E. cruciferarum s. lat.*

Based on our phylogeny (Fig. 1), sequences of *E. cruchetiana* on *Ononis* spp. (Clade 4) form a distinct clade far from *E. pisi* sequences on *Pisum* and *Lathyrus* (Clade 6). *Erysiphe cruchetiana* was introduced by Blumer in 1933 but was synonymized with *E. pisi* var. *cruchetiana* by Braun (Braun 1987, Braun &Cook 2012). However, precise morphological and molecular examination of the type material (HAL 3488 F, on *Ononis repens* from Germany, GB number: OQ266914) revealed that *E. cruchetiana* should be reinstated (Darsaraei et al. 2023c). *Erysiphe caulicola* sequence, as well as the sequence of *E. lycopsidis*, were placed individually out of other subclades. *Erysiphe howeana* sequences formed a separate clade with 98% BS support. The sequence OM856018 on *Urtica* sp. (IRAN 16919F) differed in five nucleotides from another sequence from Iran (AB104524) that was previously submitted to GenBank (Khodaparast et al. 2003). These sequences were placed in two sister groups with 100% BS support, and each has at least 32 bases different from *E. pileae* on *Pilea pumila* (LC010059, from Japan), the other *Erysiphe* species reported from *Urticaceae*. Meanwhile, *E. pileae* has wider and longer chasmothecial appendages (up to 4 times as long as the chasmothecial diam.) than *E. urticae*. Since efforts for sequencing the neotype specimen of *E. urticae* (on *Urtica dioica*, Germany, Klotzsch, Herb. Viv. Mycol. 65 (HAL)) failed, it is not clear that which clade is the accurate representative of *E. urticae*. Thus, we suggest a new species candidate (*Erysiphe* sp. 1) that is morphologically identical and indistinguishable from *E. urticae*, but can be differentiated by the ITS sequence.

Unfortunately, sequencing of five powdery mildew species *i.e.*, *E. limonii*, *E. paeoniae*, *E. mayorii*, *E. punicae*, and *Erysiphe* sp. 2 failed; therefore, the identification of these species was based solely on their morphological characteristics. As a result, the ITS rDNA barcode for at least 19 species of *E.* sect. *Erysiphe* from Iran is here provided.

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

1a. Always (or mostly) only asexual state is present 2 b. The sexual state is present, chasmothecial appendages mycelioid, simple or with irregular branching

2a. Conidiophores arising from the top of the mother cell, often straight, 44–90 × 7–10 µm, foot-cells cylindrical, 25–42 × 7–10 µm, followed by 1–2 other cells; mycelia amphigenous, in white patches, hyphal appressoria multilobed, solitary or in opposite pairs; conidia cylindrical, ellipsoid, (29) 37–46 × 13–18 (21) µm; on *Bryophyllum* sp. and *Kalanchoe* sp.

(*Crassulaceae*) ***E. sedi***

b. Conidiophores arising from one end of the mother cell 3

3a. Mycelia compact and white, occasionally covers the entire surface of the leaves; conidiophores erect, 41–74 µm, foot-cells cylindrical, straight, 22–46 × 7–10 µm, followed by 1–2 cells of the same length or shorter cells; conidia ellipsoid, ovoid, almost barrel-shaped to somewhat cylindrical, 24–38 × 10–19 µm, conidial germination terminal or sum-terminal, conidial appressoria lobed; on *Oenothera biennis* (*Onagraceae*) ***E. howeana***

b. Mycelia white, dense or in scattered patches, mostly epiphyllous, caulicolous, hyphal appressoria nipple shaped and lobed; conidiophores erect, 45.6–110.4 × 4.8–7.2 µm, foot cells cylindrical, rarely swollen in the middle and constricted at the base, 26.4–57.6 × 4.8–7.2 µm, followed by 1–3 shorter cells; conidia ellipsoid-ovoid, sub-cylindrical, 21.6–40.8 × 12–16.8 µm; on *Lycopersicon esculentum* Mill. (*Solanaceae*) ***E. neolycopersici***

4a. Chasmothecial appendages numerous, mycelioid, irregular and coral-like, occasionally dichotomously branched, hyaline or faint brown, length about 0.5–2 (3) times as long as the chasmothecial diam.; on *Apiaceae* ***E. heraclei***

b. Chasmothecial appendages simple or irregularly dichotomously branched; not on *Apiaceae* 5

5a. Appendages length about the chasmothecial diam. or shorter 6

b. All or at least part of appendages longer than the chasmothecial diam. 9

6a. Chasmothecial appendages very thin and slender, chasmothecia 83–120 µm diam., hyaline or brown; on *Urtica* spp. (*Urticaceae*) ***E. urticae/Erysiphe* sp. 1 on *Urtica* spp.**

b. Chasmothecial appendages wider 7

7a. Chasmothecia (95) 100–132 (140) µm diam., appendages length about the chasmothecial diam., simple or with irregular branches; on *Beta vulgaris* and *Spinacia* sp. (*Amaranthaceae*) ***E. betae*** b. Chasmothecial diam. always less than 120 µm 8

8a. Chasmothecia 89–119 µm diam., appendages with irregular branches, brown, length mostly less than the chasmothecial diam.; ascospores (4) 5–7; on *Lactuca macrophylla* (*Asteraceae*) ***E. mayorii* var. *japonica***

b. Chasmothecia 95–119 µm (or maximum 130–140 µm), appendages brown, length mostly less than the chasmothecial diam., with irregular or coral-like branches; ascospores 3–6; on *Paeonia* sp. (*Paeoniaceae*) ***E. paeoniae***

9a. Appendages more than 4 (up to 7.5) times as long as the chasmothecial diam. 10

b. Appendages shorter, up to 4 times as long as the chasmothecial diam. 13

10a. Chasmothecia less than 115 µm diam. 11

b. Chasmothecia at least partly more than 120 µm diam. 12

11a. Chasmothecia (87) 93–112 µm diam., appendages mostly simple, length up to 5 times as long as the chasmothecial diam.; on cf. *Potentilla* sp. (*Rosaceae*) ***Erysiphe* sp. 2**

b. Chasmothecia (70) 85–113 µm diam., appendages simple, length 1.5–7.5 times as long as the chasmothecial diam.; on *Punica granatum* (*Lythraceae*) ***E. punicae***

12a. Chasmothecia 83–156 µm diam., appendages at least brown at the lower half, septate with 1–5 septa, simple, length up to 5 times as long as the chasmothecial diam.; on *Pisum sativum* (*Fabaceae*) ***E. pisi***

b. Chasmothecia 69–137 µm diam., appendages brown or paler towards the tip, with irregular branches, length more than 4 times as long as the chasmothecial diam.; on *Aquilegia* spp. and *Ranunculus* spp. (*Ranunculaceae*) ***E. aquilegiae* var. *aquilegiae***

13a. Appendages length not exceeding 4 times as long as the chasmothecial diam. 14

b. Appendages length less than 3 times as long as the chasmothecial diam. 15

14a. Appendages up to 4 times as long as the chasmothecial diam., often unbranched; on *Aquilegia*, *Ranunculus*, and *Thalictrum* (*Ranunculaceae*) ***E. aquilegiae* var. *ranunculi***

b. Appendages length up to 3.5 times as long as the chasmothecial diam., brown thoroughly or brown at the lower half, irregularly and dichotomously branched, geniculate, septate with more than 10 septa, chasmothecia 88–122 (–151) µm; asci 4–7; ascospores 2–5 (mostly 3); on *Rumex* spp. (*Polygonaceae*) ***E. rumicicola***

15a. Chasmothecia on leaves and stems, 99–130 µm diam., appendages dichotomously branched near the base or towards the tip, brown, septate; on *Ononis spinosa* (*Fabaceae*) ***E. cruchetiana***

b. Chasmothecia severely caulicolous, dark black, 127–172 µm diam., appendages with irregular branches, geniculate and denticulate, flexuous; asci 5–13; ascospores 5–7 (–9); on *Astragalus polybotrys* (*Fabaceae*) ***E. caulicola***

c. Chasmothecia often on leaves, occasionally caulicolous 16

16a. Chasmothecia less than 130 µm diam. and appendages length up to 2.5 times as long as the chasmothecial diam. 17

b. Chasmothecia larger than 130 µm diam. and/or appendage length not exceeding 1.5 times as long as the chasmothecial diam. 19

c. Chasmothecia larger than 130 µm diam. and/or appendages length up to 3 times as long as the chasmothecial diam. 21

17a. Appendages length 1–2 times as long as the chasmothecial diam., hyaline or pale brown, dichotomously branched, geniculate, chasmothecia 103–130 µm diam.; on *Alyssum* and *Descurainia* (*Brassicaceae*) ***E. cruciferarum s. str.***

b. Appendages length up to 2.5 times as long as the chasmothecial diam. 18

18a. Chasmothecia 90–120 (130) µm diam., appendages simple, brown; asci 3–5; ascospores 3–6 (mostly 4–5); on *Medicago sativa* (*Fabaceae*) ***E. medicaginis***

b. Chasmothecia (71) 85–105 (118) µm diam., appendages geniculate, outline irregular, occasionally dichotomously branched near the base or towards the tip; asci 3–5; ascospores (2) 3–4; on *Circaea lutetiana* (*Onagraceae*) ***E. circaeae***

c. Chasmothecia 81–120 µm diam., appendages length about 0.5–2 times as long as the chasmothecial diam., hyaline or brown, simple or irregularly dichotomously branched, arising from the lower half of the chasmothecia; asci 4–6; ascospores 3–6 (mostly 4–5); on *Malva* spp. (*Malvaceae*) ***E. malvae***

19a. Chasmothecial appendages hyaline, turn brown when mature, simple or irregularly branched; asci 4–9, ascospores 2–5; on *Polygonum* spp. (*Polygonaceae*) ***E. polygoni***

b. Chasmothecial appendages 0.5–1.5 times as long as the chasmothecial diam., hyaline or brown when mature 20

20a. Appendages hyaline or pale brown, interwoven with each other, chasmothecia (86) 98–149 µm; asci (3) 4–9; ascospores (2) 3–5; on *Mesostemma kotschyana*, *Acanthophyllum* cf. *mucronatum* and *Silene latifolia* (*Caryophyllaceae*) ***E. buhrii***

b. Appendages hyaline or brown, simple or irregularly branched, chasmothecia 94–132 µm diam.; on *Limonium meyeri* (*Plumbaginaceae*) ***E. limonii***

c. Appendages mostly brown, geniculate, chasmothecia 101–132 µm diam.; asci 4–6; ascospores 3–5 (6); on *Anchusa* spp. (*Boraginaceae*) ***E. lycopsidis***

21a. Chasmothecia 86–150 µm diam., appendages brown, dichotomously branched and geniculate, irregular outline; on several genera of *Brassicaceae* ***E. cruciferarum s. lat.***

b. Chasmothecia 99–150 µm diam., appendages hyaline or pale brown, simple and irregularly branched 22

22a. Ascospores 3–5; on *Convolvulus* spp. (*Convolvulaceae*) ***E. convolvuli* var. *convolvuli***

b. Ascospores 3–6 (7); on *Convolvulus* and *Calystegia* (*Convolvulaceae*) ***E. convolvuli* var. *calystegiae***

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به‌روزرسانی آرایه‌شناسی با استفاده از بررسی‌های تبارشناختی و خط شناسه گذاری DNA برای گونه‌های *Erysiphe* sect. *Erysiphe* (*Erysiphaceae*, *Helotiales*) در ایران

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چکیده: آرایه‌شناسی و تبارشناسی (*Erysiphaceae*, *Helotiales*) *Erysiphe* sect. *Erysiphe* در ایران مورد بازبینی قرار گرفت. یکصد نمونه از هرباریوم قارچ‌شناسی دانشگاه گیلان (GUM)، مجموعه مرجع قارچ‌های وزارت جهاد کشاورزی (IRAN) و نمونه‌های تازه جمع‌آوری شده در سال‌های ۱۴۰۰ –۱۳۹۷، براساس ویژگی‌های ریخت‌شناختی و توالی نوکلئوتیدی ناحیه‌های ژنی ITS و LSU از DNA ریبوزومی مورد بررسی قرار گرفتند. بر اساس نتایج به دست آمده در مطالعه‌ی حاضر، بخش *Erysiphe* دارای ۲۳ گونه‌ی تأیید شده شامل *E. aquilegiae*، *E. betae*، *E. buhrii*، *E. caulicola*، *E. circaeae*، *E. convolvuli*، *E. cruchetiana*، *E. cruciferarum*، *E. heraclei*، *E. howeana*، *E. limonii*، *E. lycopsidis*، *E. malvae*، *E. mayorii*، *E. medicaginis*، *E. neolycopersici*، *E. paeoniae*، *E. pisi*، *E. polygoni*، *E. punicae*، *E. rumicicola*، *E. sedi* و *E. urticae*، و ۲ گونه‌ی ناشناخته در ایران می‌باشد. گونه‌های *E. sedi* و *E. paeoniae* برای اولین بار از ایران گزارش می‌شوند. علاوه بر این گونه گیاهی (*Caryophyllaceae*) *Mesostemma kotschyana* به عنوان میزبان جدید برای *E. buhrii* در جهان گزارش می‌شود. گونه‌ای ناشناخته که احتمالاً روی گزنه (*Urtica* spp.) وجود دارد نیز مورد بحث قرار گرفته است.

کلمات کلیدی: تنوع زیستی، تبارشناسی، سفیدک‌های پودری، DNA ریبوزومی، آرایه‌شناسی

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