Fungal Biology 130 (2026) 101717

Contents lists available at ScienceDirect

Fungal Biology

journal homepage: www.elsevier.com/locate/funbio

Reassessment of the *Erysiphe aquilegiae* complex (*Erysiphaceae*)—resolution of a widespread and economically significant group of plant pathogens

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ARTICLE INFO

Keywords:
Powdery mildews
Erysiphe hortensiae
New species
Phylogeny
Taxonomy
Revision

ABSTRACT

Species of powdery mildew in the *Erysiphe aquilegiae* complex infect a broad array of economically valuable plants. The increasing number of reports of infections from diverse hosts prompted the present comprehensive phylogenetic and taxonomic reassessment of the complex. Accurate species delimitation within the complex has been hindered by morphological similarity among members of the complex, their broad host associations, and insufficient resolution in rDNA (ITS+28S) analyses. As such, the species concepts within this complex have been controversial, ranging from recognition of a single widely circumscribed species, *E. aquilegiae* s. lat., to narrower concepts recognizing multiple species, usually based on associated host genera or host species. To better understand this complex, we have undertaken phylogenetic analyses based on eight loci: rDNA regions (ITS, 28S, IGS) and protein-coding genes (*CAM*, *GAPDH*, *GS*, *RPB2*, *TUB*). In total, we sequenced 163 collections from more than 20 countries, resulting in the deposition of over 600 sequences in GenBank. Based on these results, we have recognized two species with broad host ranges, *E. aquilegiae* s. str. (emend.) and *E. hortensiae* comb. nov., There are several host-specific species, including: *E. aquilegiae-coeruleae* sp. nov. *E. clematidicola* sp. nov. *E. clematidis-montanae* sp. nov., and *E. thalictri* sp. nov. The old name *E. nitida* is reintroduced for powdery mildew on *Aconitum* spp. and *Delphinium* spp. (*Ranunculaceae* tribe *Delphinieae*), which forms a well-supported clade outside the *E. aquilegiae* s. str. and *E. hortensiae* clade. Furthermore, *E. parnassiae* could be confirmed as a separate species belonging to the *E. aquilegiae* complex. The application of the rank forma for genetically established biological races forming subclades within the plurivorous species is discussed and conditions for the introduction of acceptable formae are outlined.

1. Introduction

The *Erysiphe aquilegiae* complex has encompassed many species of powdery mildew that infect a wide range of economically important plants, including members of the *Solanaceae* (including tomatoes), *Hydrangeaceae*, and *Ranunculaceae*. All species now recognized within the *E. aquilegiae* complex were formerly classified under *E. polygoni* sensu Salmon (1900), reflecting the broad circumscription of *E. polygoni* in his monograph. Jaczewski (1927) used a similarly wide species concept for the genus *Erysiphe*, but applied the name *E. communis* rather than *E. polygoni* for this group. He introduced many formae, assigning a separate forma to specimens collected from each different host genus. The first steps towards a narrower species concept of the former *E. polygoni* complex were made by Blumer (1933). He recognized

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https://doi.org/10.1016/j.funbio.2026.101717
Received 11 September 2025; Received in revised form 15 December 2025; Accepted 5 January 2026
Available online 9 January 2026
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diverse, previously described species, such as *E. aquilegiae*, *E. pisi*, *E. polygoni*, *E. ulmariae*, *E. urticae*, and *E. vernalis*, and described the new species *E. cruchetiana* and *E. mayorii*. *Erysiphe* specimens on various ranunculaceous hosts, including species of the genera *Aconitum*, *Ranunculus*, and *Thalictrum*, were assigned to *E. nitida*. Specimens from hosts belonging to other plant families—such as *Brassicaceae*, *Amaranthaceae* (including *Chenopodiaceae*), *Lythraceae*, *Onagraceae*, *Papaveraceae*, and others—were retained within *E. communis*, which served as a 'taxonomic dustbin' i.e. a broadly defined category for collections that did not fit more narrowly circumscribed taxa. Junell (1967) revised the taxonomy of *E. communis* sensu Blumer (1933), applying a narrower species concept that led to further subdivision of the complex. Braun (1987) and Braun and Cook (2012) followed Junell's (1967) narrower species concept.

Substantial progress to the taxonomy of *Erysiphe* s. str (Braun and Takamatsu, 2000). has been achieved by the introduction of molecular genetic methods to powdery mildew taxonomy. Takamatsu et al. (2015) identified the '*E. aquilegiae* clade' through ITS+28S analyses of *Erysiphe* species, highlighting this taxonomically intricate group of powdery mildews that lacked sufficient species-level resolution in rDNA alone. It should be noted that the existence of this complex had already been indicated in some earlier publications (Cunnington et al., 2004; Liberato and Cunnington, 2006; Jankovics et al., 2008). The recognition of this complex led to a tendency to assign powdery mildew collections on a variety of hosts from different plant families to *E. aquilegiae*. Takamatsu et al. (2015) coined the term "*E. aquilegiae* clade" for this group. Bradshaw et al. (2020) proposed the alternative term "*E. aquilegiae* complex" to emphasize that the group comprises multiple morphologically described species that remain unresolved at the genomic level. The term "complex" is commonly used to refer to groups of closely related but unresolved species, particularly when genetic, morphological, or pathogenic distinctions remain unclear.

As part of a reassessment of *Pseudoidium pedaliacearum* on *Sesamum indicum* from Japan, Korea, and Nepal, Shin et al. (2019) provided a detailed account of the history and taxonomy of the *E. aquilegiae* complex, highlighting the inconsistent results of inoculation studies—particularly those involving *E. neolycopersici*, a species within this complex that infects economically important crops such as tomato (*Solanum lycopersicum*). Bradshaw et al. (2020) further contributed to the discussion of this complex through ITS+28S sequence analyses. Their work maintained the view that the "*E. aquilegiae* complex" comprises multiple species that require multilocus phylogenetic analysis for proper resolution. They recommended applying existing species names from the complex—following Braun and Cook (2012)—when isolates exhibit clearly defined host ranges and distinct morphological features. Conversely, they advised against describing new species, particularly from cultivated hosts or hosts outside their native range, without robust supporting evidence. In such cases, specimens should be designated as *Erysiphe* sp. until their taxonomic placement can be confidently determined.

Most recently, Bradshaw et al. (2024a) revisited the "*E. aquilegiae* complex," including the first attempt to sequence non-rDNA loci. In their analysis the existence of several well-supported species at the base of this complex became evident, including the North American *E. parnassiae*. To resolve the taxonomic complexity within the "*E. aquilegiae* complex", a series of multilocus phylogenetic analyses were conducted, progressively adding genetic markers with the goal of identifying those most critical for resolving species boundaries. The final analyses incorporated eight loci—rDNA regions (ITS, 28S, IGS) and protein-coding genes (*CAM*, *GAPDH*, *GS*, *RPB2*, *TUB*)—and demonstrated that different genes contribute to phylogenetic resolution across distinct lineages within the complex.

2. Materials and methods

The nomenclature and taxonomy of host plant names follow 'Plants of the World Online' (https://powo.science.kew.org/). Names of powdery mildews are based on Braun and Cook (2012), MycoBank (https://www.mycobank.org/), supplemented by Bradshaw et al. (2020, 2024a,b).

2.1. Sample collection

Specimens were collected between 2018 and 2024 from throughout the United States. Newly collected specimens were deposited in the Farlow Herbarium (FH), Harvard University and the Larry F. Grand Mycological Herbarium (NCSLG), North Carolina State University. Additional specimens were evaluated from FH, NCSLG and other American and European herbaria (Supplementary Table 1).

2.2. Morphological examinations

Morphological examinations were accomplished following Bradshaw et al. (2022b). Morphological examinations of the asexual morph of recently collected samples were accomplished by placing clear adhesive tape on powdery mildew colonies and setting the tape onto a slide containing a drop of water or 5 % potassium hydroxide (KOH). Examinations of the sexual morph were accomplished by using a clean needle to mount chasmothecia onto a microscope slide containing water or KOH. Microphotographs were taken of the mounted material using a Zeiss AX10 (Oberkochen, Germany) or an Olympus BX40 (Tokyo, Japan) compound microscope with an Olympus SC50 camera (Tokyo, Japan) and/or an ACCU-SCOPE Excelis MPX-20RC camera (Commack, New York) with CaptaVision + interface software. Microphotographs of leaves were taken with an Olympus SZX9 dissecting microscope (Tokyo, Japan). Macrophotographs of specimens were taken with a Canon EOS 5D Mark II camera (Tokyo, Japan) and Capture One Pro photo editing software (Copenhagen, Denmark), or a Nikon Eclipse Ti2 compound microscope with a Nikon DS-Ri2 camera unit (Raleigh, North Carolina).

2.3. Sequencing

DNA extractions were performed using the Chelex method (Walsh et al., 1991; Hirata and Takamatsu, 1996) or using the DNeasy Plant Mini Kit (Qiagen), according to the manufacturers protocol. The polymerase chain reaction (PCR) was used to amplify the ITS and LSU rDNA regions using the primer pairs PM10/PM28R (Bradshaw and Tobin, 2020) for all specimens. If PCR was unsuccessful, a nested approach was applied using primers AITS (Bradshaw and Tobin, 2020)/TW14 (Mori et al., 2000) followed by PM10/PM28R or AITS/PM11 (Bradshaw and Tobin, 2020) followed by PM10/PM2 (Cunnington et al., 2003). Alternatively, the ITS region was amplified in two fragments using the primer pairs ITS5/PM6 and PM5/ITS4 (Takamatsu and Kano, 2001). For the calmodulin (*CAM*), Glyceraldehyde 3-Phosphate Dehydrogenase (*GAPDH*), Glutamine synthetase (*GS*), and RNA Polymerase II Subunit B2 (*RPB2*) region the primer pairs PMCAM1/PMCAM4R, PMGAPDH1/PMGAPDH3R, GSPM2/GSPM3R, and PMRpb2_4/PMRpb2_6R were used (Bradshaw et al., 2022a). In reactions where *GAPDH* primers amplified DNA of *Ampelomyces* mycoparasites, EGAPDH1/EGAPDH2 primers (Bradshaw et al., 2025a) were used. If these amplifications were unsuccessful for the *GS* and *RPB2* regions, the following primers from Bradshaw et al. (2023) were used: EGS1/EGS2R and ERPB2_3/ERPB2_7R. For the β-tubulin (*TUB*) region the primers BTF5b/BTR7a (Ellingham et al., 2019) were used followed by ETUB2 and ETUB2R (Bradshaw et al., 2023). Alternatively, newly designed primer pairs TUB1F (CAYCTYCARACTGGCCAATG) and TUB1R (GGAGCRAAWCCAACCATAAAA) or PM_t1F (AGGGCAAACHATHTCTGG) and PM_t3R (TCCATYTCRTCCATTCC) were used. To amplify the rDNA intergenic spacer (IGS) region, the primer pair IGS-12a/NS1R was used (Carbone and Kohn, 1999).

2.4. Phylogenetic analyses

Phylogenetic trees were generated from analysis of concatenated

ITS+28S + *CAM* + *GAPDH* + *GS* + IGS + *RPB2*+*TUB* sequences. The concatenated tree included taxa that had at least all of the following regions sequenced to ensure data completeness: ITS, IGS, *CAM*, *GAPDH*, and *GS*. Sequences were aligned and edited using Geneious Prime 2025.0.3. A GTR + G + I evolutionary model was used for phylogenetic analyses as it is the most inclusive model of evolution and includes all other evolutionary models (Abadi et al., 2019). The phylogeny was inferred using Bayesian analysis of the combined loci using a Yule tree prior (Gernhard, 2008) and a strict molecular clock, in the program BEAST version 1.10.4 (Suchard et al., 2018). A single MCMC chain of 10^7 steps was run, with a burn-in of 25 %. Posterior probabilities were calculated from the remaining 7500 sampled trees. A maximum clade credibility tree was produced using TreeAnnotator version 1.10.4 (part of the BEAST package). Stationarity was confirmed by running the analysis multiple times, which revealed convergence between runs. The resulting tree was visualized using FigTree ver. 1.3.1 (Rambaut, 2009). A maximum likelihood analysis was accomplished using raxmlGUI (Silvestro and Michalak, 2012) under the default settings with a GTR + G + I evolutionary model. Bootstrap analyses were conducted using 1000 replications (Felsenstein, 1985).

3. Results

3.1. Phylogenetic analyses

Single loci trees as well as a concatenated tree were generated for the *E. aquilegiae* complex (Fig. 1; Supplementary Fig. 1–7). A separate tree showing the phylogenetic placement of *E. tortilis* was also generated (Fig. 2). The taxa for the *E. tortilis* tree were chosen based on Bradshaw et al. (2024a). In the *E. aquilegiae* complex there is high support for the species *E. aquilegiae-coeruleae*, *E. clematidicola*, *E. clematidis-montanae, E. parnassiae* and *E. thalictri* in every tree with sequence data for the given taxa. *E. aquilegiae* s. str. has no support in any of the single loci trees except for the *CAM* tree (Supplementary Fig. 1) where only minimal support is exhibited (posterior probility = 0.7). *Erysiphe hortensiae* is supported (posterior probabilities >0.9) in the *RPB2* (0.99: Supplementary Fig. 6) and IGS (1.0: Supplementary Fig. 4) trees. All species are supported in the Bayesian and likelihood analyses in the concatenated tree (Fig. 1). A subclade reflecting *E. hortensiae* on host species of the type host genus (*Hydrangea*) is supported in the *GS* (0.97: Supplementary Fig. 3) and IGS (1.0: Supplementary Fig. 3) trees. An additional subclade comprised of sequences retrieved from *E. aquilegiae* specimens on host species of *Aquilegia*, the type host genus, is also supported in the *GS* (1.0: Supplementary Fig. 3) tree.

3.2. Taxonomy

3.2.1. Species concept within the "E. aquilegiae complex" based on results of phylogenetic multilocus analyses

The new ITS+28S and multilocus analyses of the "*E. aquilegiae* complex", in contrast to previous assumptions and treatments (Takamatsu et al., 2015; Shin et al., 2019; Bradshaw et al., 2020, 2024a), do not support the existence of many host-specific species. In contrast, in powdery mildews of the genus *Erysiphe*, ITS+28S analyses are generally sufficient to identify and define species (Bradshaw et al., 2024a, 2024b, 2025a), but there are exceptions, such as the "*E. alphitoides* complex" (Bradshaw et al., 2025b), the "*E. aquilegiae* complex" (Bradshaw et al., 2024a), the "*E. vaccinii* complex" (Bradshaw et al., 2025a, 2025c), and the "*E. trifoliorum* complex" (Bradshaw et al., 2025a).

To improve species-level resolution within the "*E. aquilegiae* complex" and identify potential cryptic species, both single-locus and multilocus phylogenetic analyses were conducted (Fig. 1; Supplementary Fig. 1–7). While earlier analyses based on ITS+28S failed to support species-level distinctions, multilocus approaches revealed two well-supported clades corresponding to *E. aquilegiae* s. str. and *E. hortensiae*. Support for these species was also evident in single-locus trees. *E. hortensiae* was supported in the *RPB2* (posterior probability = 0.99; Supplementary Fig. 6), and IGS (1.0; Supplementary Fig. 4). In contrast, *E. aquilegiae* s. str. received minimal support across single-locus trees, except for weak support in the *CAM* tree (0.7; Supplementary Fig. 1). There was high support for both species in the concatenated tree in both likelihood (≥70) and posterior probabilities (>0.9).

In addition to these species, several host-specialized lineages belonging to *Erysiphe* on *Ranunculaceae* formed distinct, well-supported

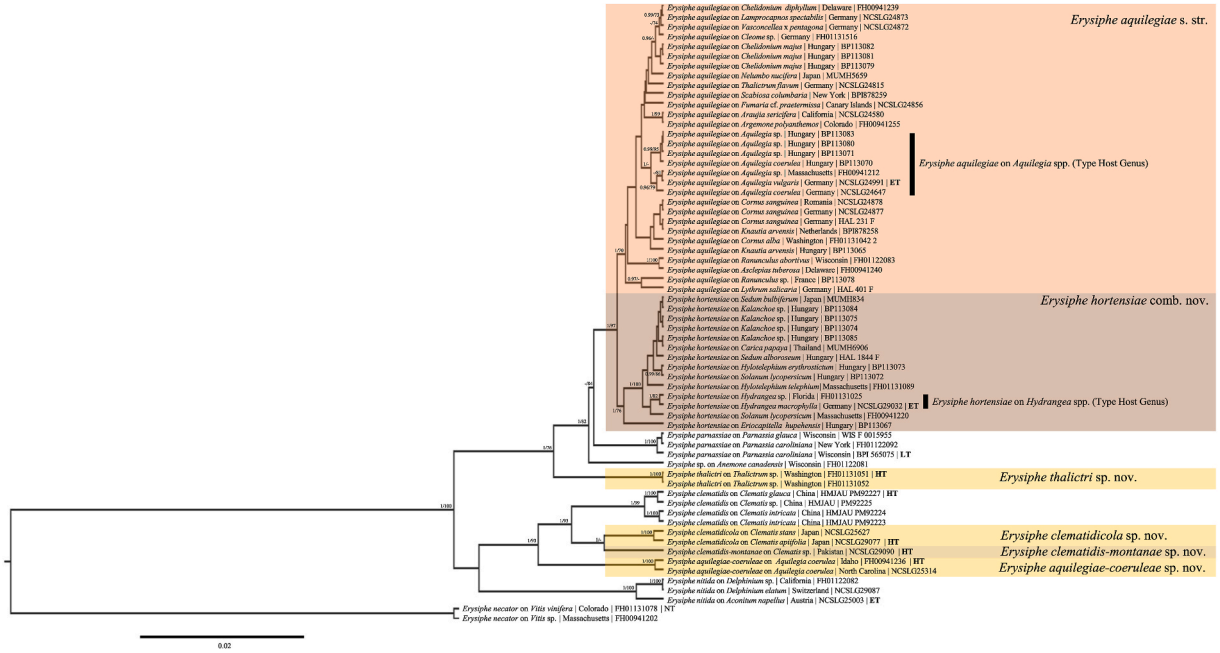


Fig. 1. Bayesian maximum clade credibility tree of concatenated ITS+28S + *CAM* + *GAPDH* + *GS* + IGS + *RPB2*+*TUB* regions of taxa in the *Erysiphe aquilegiae* complex. The phylogenetic tree revealed four undescribed species. Fungal species are denoted and followed by the host, collection locality, and voucher number. Type status (HT: Holotype, ET: Epitype) of the specimens concerned is denoted as well as reference sequences for phylogenetic purposes (RS). Posterior probabilities ≥90 are displayed followed by bootstrap values greater than 70 % for the maximum likelihood (ML) analyses.

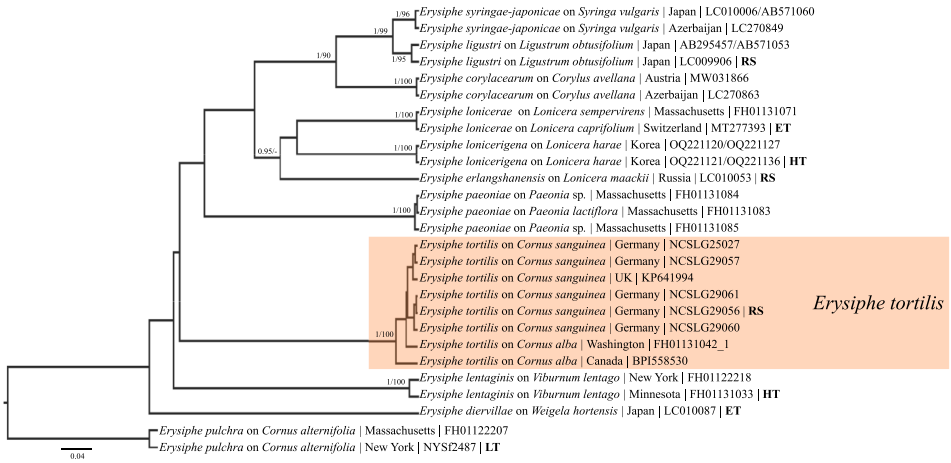


Fig. 2. Bayesian maximum clade credibility tree of concatenated ITS+28S + *CAM* + *GAPDH* + *GS* + IGS + *RPB2*+*TUB* regions of select taxa in the *Erysiphe* (*Microsphaera*) lineage. The phylogenetic tree revealed that *E. tortilis* forms a highly supported clade separate from the *E. aquilegiae* complex. Fungal species are denoted and followed by the host, collection locality, and voucher number. Type status (HT: Holotype, LT: Lectotype, ET: Epitype) of the specimens concerned is denoted as well as reference sequences for phylogenetic purposes (RS). Posterior probabilities ≥90 are displayed followed by bootstrap values greater than 70 % for the maximum likelihood (ML) analyses.

clades in both ITS+28S and multilocus trees in a basal position to *E. aquilegiae* s. str and *E. hortensiae*. These include the recognition of the previously named *E. nitida* on *Aconitum* spp. and *Delphinium* spp. (tribe *Delphinieae*), *E. clematidicola* sp. nov., *E. clematidis-montanae* sp. nov., *E. aquilegiae-coeruleae* sp. nov., *E. parnassiae*, and *E. thalictri* sp. nov. Each of these taxa was supported in all trees for which sequence data were available.

3.2.2. *Application of subspecific taxonomic ranks within the "E. aquilegiae complex"*

Based on results of the multilocus analyses from specimens from throughout the world, Bradshaw et al. (2025a,c) identified many strongly supported subclades within the *E. vaccinii* complex, which reflect morphologically indistinguishable biological races, for which the taxonomic rank 'forma' was introduced. Feng et al. (2025) continued the application of this convention when deviding *Sawadaea bicornis* into two morphologically indistinguishable formae represented by well-supported subclades within the larger species clade. The conditions for the application of the rank forma in powdery mildews has been discussed, and the advantages and justifications for using a formal taxonomic rank, ruled by the Code (ICNafp, Turland et al., 2018) have been outlined (Bradshaw et al., 2025a). In contrast to the previously used informal designation "forma specialis" for cases of biological races detected in inoculation experiments, the category "forma" is subjected to clear rules (ICNafp), including the need for a formal description and the designation of a holotype. Furthermore, genetically characterized and established biological races described as "formae" allow objective identifications based on sequence analyses, which is not given in cross inoculation tests where reproducibility cannot be assured.

The conditions for the use of such "formae" must be critically outlined, above all in cases of genetic multilocus analyses, where local populations can be reflected in highly supported clades in phylogenetic trees due to the large amounts of genomic data. Moreover, applications of formae used in the case of *E. vaccinii* (Bradshaw et al., 2025a) cannot be fully applied to the intricate *E. aquilegiae* complex, in which genetically well-supported subclades that correspond to host data have not yet been sufficiently demonstrated. The two broadly distributed species, *E. aquilegiae* s. str. and *E. hortensiae*, are taxonomically complex, comprising isolates from multiple host species and exhibiting minimal evidence of host-associated divergence. We hypothesize that these lineages are in the early stages of speciation, and it seems host specificity has not developed as strictly in this system as in other powdery mildew systems. Considering that the splitting of these taxa into cryptic species remains unsupported, even in phylogenetic multilocus analyses with many genes employed, it is best to treat these complexes as species with wider circumscriptions. In multilocus analyses, and in some cases even in single loci analyses, the presence of well-supported subclades suggests the occurrence of some host-specific specialized races within these broadly distributed species, however clear morphological differences are usually not observable. These races may be recognized as formae—genetically fixed races showing biological or ecological specializations and/or host preferences—but caution is warranted when introducing new formae. Naming local races or individual populations should be avoided, as excessive subdivision would lead to an impractical and uninformative proliferation of formae. Determining whether observed genetic groupings represent local populations or races, rather than distinct formae, can be challenging; therefore, the following criteria should be taken into consideration: (1) A higher number of sequenced specimens, above that is common for species descriptions, should be involved. (2) The specimens should be from a wide geographical range and, when applicable, a wide sampling of hosts, particularly when the hosts are known to be infected in different regions of the world. Exceptions can be made in cases of endemic host plants with restricted distribution areas or agriculturally significant crops. (3) Multilocus/full genome analyses should always take precedence over ITS analyses as basis for decisions.

We prefer to accept only multilocus/full genome analyses as the basis for the introduction of formae, and our currently available ITS and multilocus analyses suggest possible occurrences of such formae, reflected in subclades, but the available data are not yet sufficient for final conclusions. To stabilize the taxonomy and allow future formae to be described as additional data, we have pointed out where potential (hypothetical) autonyms, *E. aquilegiae* "f. *aquilegiae*" and *E. hortensiae* "f. *hortensiae*" will fall once future formae are introduced (Fig. 1). These subclades within the *E. aquilegiae* and *E. hortensiae* clades are supported by multiple specimens in the concatenated and *GS* tree (Fig. 1 and Supplementary Fig. 3). *E. hortensiae* on its type host is also supported in the IGS tree (1.0).

3.2.3. *List of accepted species within the "E. aquilegiae complex"*

E. aquilegiae DC., Fl. franç., Edn 3 (Paris) 5/6: 105, 1815, emend. (s. str.)

Type: On *Aquilegia vulgaris*, *J.F. de Chaillet* 232, herb. de Candolle (lectotype [designated by Braun, 1987]: G00122102); **Germany**: Sachsen-Anhalt, Landkreis Harz, Ilsenburg, on *Aquilegia vulgaris*, 4 Sep. 2023, *J. Kruse* (epitype [designated here, MycoBank: MBT10028451]):

NCSLG24991). Ex-epitype sequences: PX147854 (*CAM*), PX134872 (*GAPDH*), PX134418 (*GS*), PX134536 (IGS), PX091726 (ITS+28S), PX134637 (*RPB2*).

≡ *Ischnochaeta aquilegiae* (DC.) Sawada, Special Publ. Coll. Agric. Natl. Taiwan Univ. 8: 17, 1959, nom. inval. (Art. 35.1).

≡ *Alphitomorpha communis* ζ *ranunculacearum* Wallr., Verh. Ges. Naturf. Freunde Berlin 1(1): 31, 1819.

≡ *Erysiphe communis* var. *ranunculacearum* (Wallr.) Link (as '*Erysibe*'), in Willdenow, Sp. pl. 6(1): 107, 1824.

≡ *E. communis* a *ranunculacearum* (Wallr.) Fr., Syst. mycol. 3(1): 240, 1829, nom. sanct. (Fr., l.c.).

= *Erysiphe ranunculi* Grev., Fl. edin.: 461, 1824.

Type: On *Ranunculus* cf. *muricatus*, herb. Greville (neotype [designated by Junell, 1965]: E00456089).

≡ *E. aquilegiae* var. *ranunculi* (Grev.) R.Y. Zheng & G.Q. Chen, Sydowia 34: 302, 1981.

= *Erysiphe knautiae* Duby, Bot. gall. 2: 870, 1830.

Type: **France**: On *Knautia arvensis* [Desm., Pl. Crypt. N. France, Ed. 1 2198, 1851, as *E. communis* A *knautiae-arvensis*] (neotype [designated by Braun and Cook, 2012]: G00111030; isoneotypes: Desm., Pl. Crypt. N. France, Ed. 1, 2198, e.g., BPI 956326, FH01085366, K, NY, PC). Reference sequences: PX147834 (*CAM*), PX134887 (*GAPDH*), PX134473 (*GS*), PX134556 (IGS), PX091778 (ITS+28S), PX134667 (*RPB2*), PX134914 (*TUB*) [**The Netherlands**: On *K. arvensis* (BPI878258)].

= *E. communis* A *knautiae-arvensis* Desm. (as '*Erysibe*'), Pl. Crypt. N. France, Ed. 1 2198, 1851.

= *E. communis* f. *thalictri* Rabenh., Fungi Eur. Exs. 1062, 1866.

= *E. communis* f. *thalictri-minoris* Sacc., Mycoth. Ven. 602, 1876.

= *Erysiphe euphorbiae* Peck, Ann. Rep. State Bot. 1874: 80, 1876.

Type: **USA**: New York, Rensselaer County, North Greenbush, on "*Euphorbia hypericifolia*" (= *Euphorbia nutans*), *C.H. Peck* (holotype: NYSf1109). Reference sequence: PX147808 (*CAM*), PX134444 (*GS*), PX134541 (IGS), PX091671 (ITS+28S), PX134602 (*RPB2*), PX134937 (*TUB*) [**Greece**: on *Euphorbia chamaesyce* (HAL 3571 F, NCSLG24646, sequenced).]

= *Ovularia clematidis* Chittend., in Cooke, Gard. Chron., Ser. 3, 34 (879): 299, 1903.

Type: **UK**: Chelmsford, on *Clematis* sp. cult. (probably *C.* × *jackmanii*), Sep. 1903, *F.J. Chittenden* (lectotype [designated here, MycoBank MBT10028414]: Cooke (1903, Fig. 125, original drawing); **UK**: London, 51°28′51.2″ N 0°00′39.6″ E, on *Clematis* 'Perle d'Azur' [= *Clematis* × *jackmanii*], 17 Aug. 2014, *J. Millev* (epitype [designated here, MycoBank MBT10028450]: RNG OE2014PM43CS). Ex-epitype sequences: KY786586 (*actin*), KY653203 (ITS + LSU), KY786716 (*TUB*).

≡ *Oidium clematidis* (Chittend.) Sacc. & Traverso, Syll. fung. 20: 212, 1911.

= *Oidium passiflorae* Politis, Phragmat. Akad. Athen 13: 608, 1938.

Type: **Switzerland**: Vaud, Morges, rue des Tanneurs 1, on *Passiflora caerulea*, 22 Nov. 2017, A. Bolay (neotype [designated by Bradshaw et al., 2024a]: G00261083). Ex-neotype sequence: MW600369 (ITS+28S).

≡ *Pseudoidium passiflorae* (Politis) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 613, 2012.

≡ *Erysiphe passiflorae* (Politis) M. Bradshaw, U. Braun & Pfister, Mycologia 116(1): 135, 2023 [2024].

= *Erysiphe lythri* L. Junell, Svensk Bot. Tidskr. 61(1): 223, 1967.

Type: **Finland**: Åland, Lemland, Kobbaklintar, Vitfågelskär, on *Lythrum salicaria*, 3 Sep. 1949, *I. Kukkonen & L.E. Kari* [Kari, Fungi Exs. Fenn. 13, as *E. communis*] (holotype: UPS F-938535; isotypes: Kari, Fungi Exs. Fenn. 13, e.g., BPI 873813, M−0014889, MC0231338, NCU-F-23126). Reference sequences: OR427451 (*CAM*), OR427539 (*GAPDH*), OR427627 (*GS*), PX134544 (IGS), OR424939 (ITS), OR427700 (*RPB2*), OR427785 (*TUB*). [**Germany**: Bavaria, Oberbayern, Kreis Traunstein, Siegsdorf, on *L. salicaria*, 11 Aug. 1996, *U. Braun* (HAL 401 F, FH01131513, sequenced).]

= *Erysiphe takamatsui* Y. Nomura, Taxonomical study of *Erysiphaceae* of Japan: 208, 1997.

Type: **Japan**: Niigata Prefecture, Niigata, Hakusan Shrine, on *Nelumbo nucifera*, Oct. 1974, *S. Takamatsu*, "YNMH 9886" (holotype: TNS-F-116660). Reference sequences: PX147837 (*CAM*), PX134890 (*GAPDH*), PX134442 (*GS*), PX134508 (IGS), PX091745 and AB916689 (ITS+28S), PX134666 (*RPB2*), PX134924 (*TUB*). [**Japan**: Niigata Prefecture, Niigata, Hakusan Shrine, on *N. nucifera*, 20 Oct. 2012, *S. Takamatsu* (TNS-F-88199 [previously TSU-MUMH5659])].

= *Oidium lauracearum* Graniti & U. Braun, Phytopathol. Medit. 37(3): 146, 1998.

Type: **Italy**: Tuscany, Florence, garden, 43°46′ N 11°15′ E, alt. c. 60 m, on *Laurus nobilis*, 31 May 1998, *A. Graniti* (holotype: HAL 1495 F; isotypes: FH01096134, Triebel, Microf. Exs. 384, e.g. BPI 748726, GZU000312230, M−0019237, UPS F-013605, MA-Fungi 46835). Ex-isotype (FH01096134) sequences: OR045080 (*CAM*), OR045146 (*GAPDH*), OR045206 (*GS*), OR036345 (ITS+28S), OR045260 (*RPB2*), OR045312 (*TUB*).

≡ *Pseudoidium lauracearum* (Graniti & U. Braun) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 609, 2012.

≡ *Erysiphe lauracearum* (Graniti & U. Braun) M. Bradshaw, U. Braun & Pfister, Mycologia 116(1): 135, 2023 [2024].

= *Erysiphe caricae* U. Braun & Bolay, Cryptog. Helv. 20: 46, 2005.

Type: **Switzerland**: Valais, Conthey, Les Fougères, on *Vasconcellea* × *pentagona* [≡ *Carica* × *pentagona*], 28 Nov. 1989, *A. Bolay* (holotype: HAL 3200 F; isotypes: G00298363, FH01131511, NCSLG25226). Ex-isotype (FH01131511) sequences: OR427420 (*CAM*), OR427514 (*GAPDH*), PX134463 (*GS*), PX134535 (IGS), OR424905 (ITS), OR427679 (*RPB2*), OR427783 (*TUB*).

= *Oidium meliacearum* U. Braun, Schlechtendalia 14: 88, 2006.

Type: **The Netherlands**: Baarn, garden, on *Melia azedarach*, 5 Apr. 2005, *W. Gams* (holotype: HAL 1872 F; isotype: FH01096135). Ex-isotype sequences: OR036346 (ITS+28S); OR045081 (*CAM*); OR045147 (*GAPDH*); OR045207 (*GS*); OR045261 (*RPB2*); OR045313 (*TUB*).

≡ *Pseudoidium meliacearum* (U. Braun) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 611, 2012.

= *Erysiphe asclepiadis* U. Braun & V. Kumm., Mycotaxon 107: 286, 2009.

Type: **Germany**: Brandenburg, Potsdam, Botanical Garden, on *Asclepias tuberosa*, 7 Sep. 2004, *V. Kummer* 1457 (holotype: HAL 2273 F). Ex-holotype sequence: MT524080 (ITS+28S).

Description: Mycelium amphigenous, also on stems and sometimes petioles, effuse or in patches, evanescent to ± persistent; hyphae 3–8 µm wide; hyphal appressoria lobed, solitary or in opposite pairs, 3–7 µm diam.; conidiophores erect from top of mother cells, 40–150 µm long, foot cells cylindrical, straight or occasionally flexuous, slightly curved-sinuous at the base, (15–)20–80(–120) × 6–11(–12) µm, followed by (0–)1–2(–3) shorter cells or cells of about the same length, second cell occasionally longer, forming conidia singly; conidia ellipsoid-ovoid, doliiform, subcylindrical, 25–50(–60) × 10–25(–29) µm, length/width ratio 1.6–2.5, conidial germination (on the type host, *Aquilegia vulgaris*) characterized by forming usually ± terminal (perihilar), short to moderately long germ tubes, length 0.25–2.5 times the conidial width, median 0.5–0.75, excluding up to 11 % showing longitubus pattern, sometimes septate, conidial appressoria rather variable according to host, unlobed, slightly, moderately to multilobed, most lobing one-sided. Chasmothecia scattered to gregarious, globose, subglobose to slightly flattened at the base, (65–)75–125(–150) µm; peridium cells irregularly polygonal, 8–25 µm diam.; appendages arising from the lower half, rarely few appendages in the upper half, few to rather numerous, 4–30(–50), mycelioid, rather coarse and straight to flexuous, sinuous-geniculate, long, length variable, 0.3–12 times the chasmothecial diam., (3–)4–8(–10) µm wide, unbranched or occasionally apically irregularly to subdichotomously branched, septate, colorless to brown

throughout when mature or paler towards the apex, wall thin to slightly thickened (up to 1 μm), smooth, sometimes faintly verruculose; asci (2–)3–8(–12), ellipsoid-obovoid, clavate-saccate, 40–70(–80) × 25–45(–55) μm, sessile or short-stalked, (2–)3–6(–8)-spored; ascospores ellipsoid-ovoid, (10–)15–35(–38) × 8–18 μm, hyaline or faintly yellowish.

Host range and distribution (based on specimens examined by multilocus sequence analyses): *Apocynaceae* [*Araujia sericifera*, *Asclepias tuberosa*], *Berberidaceae* [*Epimedium* sp.], *Caprifoliaceae* [*Knautia* (*arvensis*, *longifolia*), *Scabiosa columbaria*, *Succisa pratensis*], *Caricaceae* [*Vasconcellea* × *pentagona*], *Cleomaceae* [*Cleome* sp.], *Cornaceae* [*Cornus* (*alba*, *sanguinea*)], *Lauraceae* [*Laurus nobilis*], *Lythraceae* [*Lythrum salicaria* (=*L. anceps*)], *Meliaceae* [*Melia azedarach*], *Nelumbonaceae* [*Nelumbo nucifera*], *Papaveraceae* [*Argemone polyanthemos*, *Chelidonium* (*majus*, *diphyllum*), *Fumaria* (*muralis*, *praetermissa*), *Lamprocapnos spectablilis*], *Passifloraceae* [*Passiflora caerulea*], *Ranunculaceae* [*Aquilegia* (*canadensis*, *coerulea*, *scopulorum*, *vulgaris*, sp.), *Clematis flammula*, *Ranunculus* (*abortivus*, *acris*, *flammula*, *lanuginosus*, *repens*), *Thalictrum* (*aquilegiifolium*, *flavum*)]; Africa (Spain: Canary Islands), Asia (Japan), Europe (France, Germany, Hungary, the Netherlands, Romania, Switzerland), North America (USA: California, Colorado, Delaware, Massachusetts, North Carolina, Washington, Wisconsin).

Owing to the wide distribution of the species reduced to synonymy with *E. aquilegiae*, it can be assumed that this plurivorous powdery mildew species has a worldwide distribution. Furthermore, the host range of *E. aquilegiae* s. str. is undoubtedly much wider then currently assumed. Based on the available single-locus trees, including the ITS+28S tree, compared with the concatenated multilocus tree, *E. aquilegiae* s. lat. on the following hosts likely pertains to *E. aquilegiae* s. str., pending confirmation based on multilocus examinations in the future (this list includes hosts from described *Erysiphe* species which are potential synonyms of *E. aquilegiae* s. str.): *Apocynaceae* [*Catharanthus roseus* (*Pseudoidium vincae*); *Pachypodium lamerei* (*E. pachypodii*)], *Aristolochiaceae* [*Aristolochia debilis* (*E. ruyongzhengiana*)], *Berberidaceae* [*Epimedium* (*brevicornu*, *pinnatum*) (*E. epimedii*)], *Bignoniaceae* [*Catalpa bignonioides* (*E. catalpae*); *Incarvillea sinensis* (*E. scholzii*)], *Chloranthaceae* [*Chloranthus serratus* (*E. chloranthi*)], *Coriariaceae* [*Coriaria* (*japonica*, *napalensis*) (*E. coriariae*)], *Euphorbiaceae* [*Euphorbia* (*nutans*, *prostrata*) (*E. euphorbiae*)], *Fabaceae* [*Lupinus* sp.], *Geraniaceae* [*Geranium* (*palustre*, sp.) (*E. geraniacearum*)], *Lythraceae* [*Punica granatum* (*E. punicae*)], *Onagraceae* [*Circaea lutetiana* (*E. circaeae*)], *Papaveraceae* [*Macleaya* (*cordata, microcarpa*) (*E. macleayae*)], *Plantaginaceae* [*Veronica urticifolia*], *Ranunculaceae* [*Clematis* (*integrifolia*, *recta*, *terniflora*), *Ranunculus* (*montanus*, *platanifolius*), *Thalictrum tuberiferum*], *Rosaceae* [*Potentilla* (*indica*, *supina*)], *Rutaceae* [*Boronia megastigma* (*Pseudoidium boroniae*)].

Notes: *E. aquilegiae* s. str. is highly supported in the concatenated analysis. *E. aquilegiae* on its type host can be genetically identified from the *GS* region which will likely be important for distinguishing formae in future analyses (Supplementary Fig. 3).

Type material of *O. clematidis*—described by Chittenden in Cooke (1903) on *Clematis* sp. (probably *C.* × *jackmanii*) from the UK—is not preserved. Therefore, the original drawing is designated as lectotype in accordance with Art. 9.4 and 9.12 (Turland et al., 2018). The designated epitype, a sequenced specimen collected on *Clematis* × *jackmanii* in London, UK, is a perfect choice to clarify the phylogenetic-taxonomic status of *O. clematidis*. The ex-epitype sequence clusters within the *E. aquilegiae* complex. The identity of *O. clematidis* as a powdery mildew anamorph had already been ascertained by Salmon (1905), who assigned it to *E. polygoni* sensu Salmon (1900).

Southwell et al. (2018) identified an *Erysiphe* species of the *E. aquilegiae* complex on *Araujia sericifera* in Australia based in ITS sequences. In the present multilocus analysis, this *Erysiphe* species on *A. sericifera* from California, USA, was identified as *E. aquilegiae* s. str.

E. aquilegiae-coeruleae M. Bradshaw & Andr. Paul **sp. nov.** Fig. 3.
MycoBank: MB860633.

Etymol.: Epithet derived from the name of the type host, *Aquilegia coerulea*.

Diagnosis: Morphologically, *E. aquilegiae-coeruleae* is distinguished from *E. aquilegiae* by its cylindrical-doliiform conidia with a length/width ratio of 2.6–3.1, on average 2.9 [vs. much broader (16–24 μm) ellipsoid-ovoid, doliiform conidia with a length/width ratio of 1.5–3.3, on average 2.1, in *E. aquilegiae* on *Aquilegia* spp., Schmidt and Braun 2020]. Furthermore, *E. aquilegiae-coeruleae* is genetically clearly distinct from all allied species and forms highly supported species clades in all single locus trees, as well as the concatenated tree.

Type: **USA:** North Carolina, Wake County, 4415 Baryl Road, JC Raulston Arboretum, on *Aquilegia coerulea* planted in the Arboretum, 23 Oct. 2024, *U. Crouch* (holotype: NCSLG25314) Ex-type sequences: PX147879 (*CAM*), PX134897 (*GAPDH*), PX134584 (*RPB2*), PX091676 (ITS+28S), PX134909 (*TUB*).

Additional specimen examined (paratype): **USA:** Idaho, Boise, Idaho Botanical Garden, on *Aquilegia coerulea* 'Red Hobbit', 20 Sep. 2021, *D. Murphy* (FH00941236).

Description: Mycelium on leaves, amphigenous, also on stems and petioles, white, effuse, more or less persistent. Hyphae 3–6 μm wide. Hyphal appressoria nipple-shaped to sublobate, solitary or in opposite pairs, (3–)4.5–6(–8) μm diam. Conidiophores erect from top of mother cell, straight to slightly curved, foot cells (35–)44–50(–62) μm long and 6–7 μm wide, followed by 1(–2) shorter cells, forming conidia singly. Conidia cylindrical-doliiform, (28–)33–38(–49) × (9–)11–13(–15) μm, length/width ratio 2.6–3.1. Germ tubes ± terminal, short to moderately long, 0.2–2.1 times conidial length, median 0.8, sometimes septate; conidial appressoria frequently unlobed, club-shaped, occasionally 1–2 lobes with resemblance to extensitubus pattern. Chasmothecia not observed.

Host range and distribution: on *Aquilegia coerulea*; North America (USA: Idaho, North Carolina). Probably on *Aquilegia* sp. (as "*A. vulgaris*") in Europe (UK).

Notes: Sequences retrieved from *Erysiphe* specimens on *Aquilegia coerulea* in North America form a well-supported clade in a basal position to the *E. aquilegiae* complex, i.e., outside of the *E. aquilegiae* s. str. and *E. hortensiae* clades, in all phylogenetic analyses with data available. A sequence retrieved from a specimen cited as *Aquilegia* '*vulgaris*' from the UK clusters in the *E. aquilegiae-coeruleae* clade in the ITS analyses (Supplementary Fig. 5). The host identity of this collection from a garden is not clear; it might be *A. vulgaris*, but it might also pertain to *A. coerulea* or a hybrid with this species (referred to as *Aquilegia* × *cultorum*), which are also often cultivated in gardens. The taxa are not easily distinguishable. A sequence obtained from a German specimen on *A. coerulea*, collected in a botanical garden as well as another specimen from Hungary on this host, cluster in the *E. aquilegiae* s. str. clade suggesting that *A. coerulea* is a host of two species of the *E. aquilegia* complex.

Schmidt and Braun (2020) described the anamorph of *E. aquilegiae* on *Aquilegia* spp., including a German specimen on *A. coerulea*, in detail: Foot cells of the conidiophores cylindrical, straight to somewhat curved or sinuous, 20–60 × 8–10.5 μm, followed by 1–2 cells shorter than the foot cell or about as long; conidia formed singly, 30–56 × 16–24 μm, length/width ratio 1.5–3.3, on average 2.1; germ tubes short, with a slightly to multilobed terminal appressorium, or long (longitubus pattern), 15–215 μm long, straight to sinuous, apex usually swollen, sometimes undifferentiated, germ tubes mostly with a single septum at the base or distant from the point of attachment, up to about the middle of the germ tube, longer germ tubes often with two septa distant from each other.

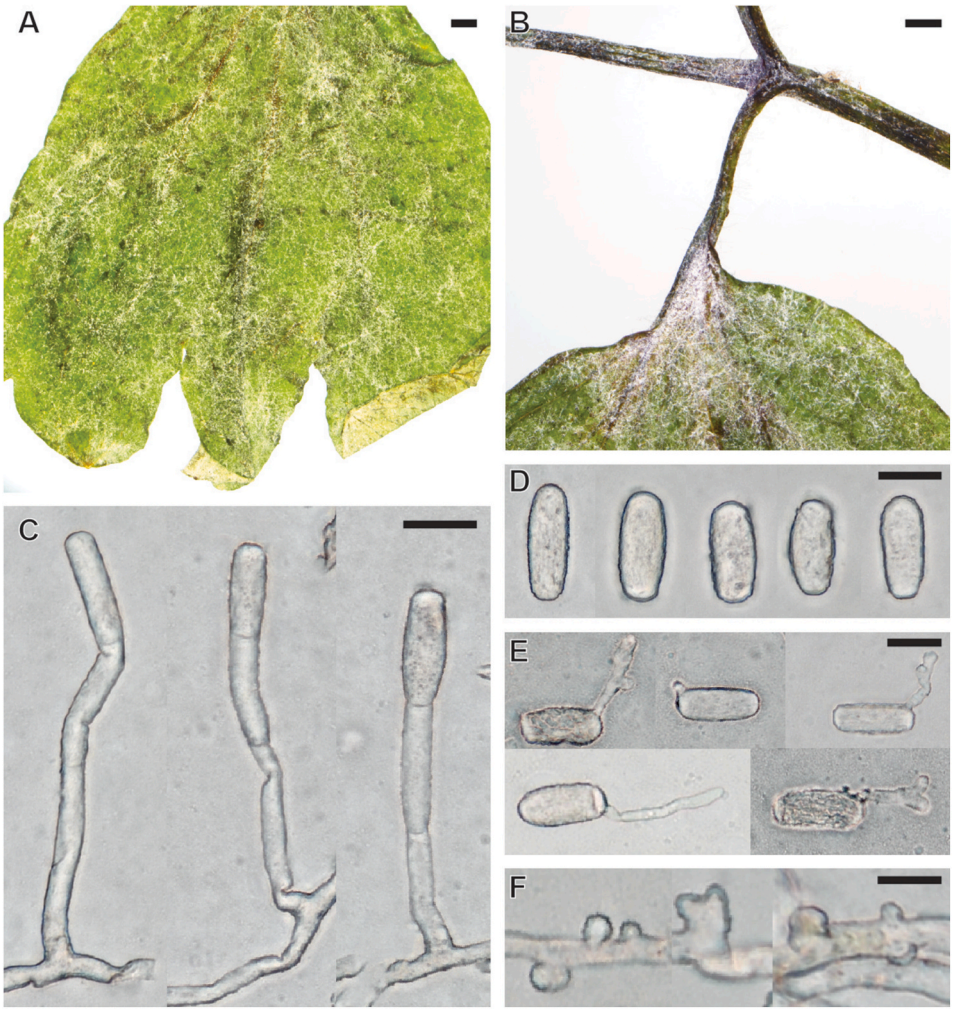


Fig. 3. *Erysiphe aquilegiae-coeruleae*. Images from NCSLG25314 (holotype). A. Macroscopic view of infected leaflet. B. Macroscopic view of infected petiole. C. Conidiophores with visible foot cells. D. Conidia. E. Several conidial germ tubes showing appressorial variation. F. Hyphal appressoria. Scale bars: A, B = 1000 μm; C, D = 20 μm; E, F = 10 μm.

A. coerulea, used as an ornamental plant in Europe, is infected in Europe also by *E. aquilegiae* (see present tree). A comparison between *E. aquilegiae* on *Aquilegia* spp. in Europe and the American type material of *E. aquilegiae-coeruleae* suggests significant differences in the conidial shape and size, above all much narrower [(9–)11–13(–15) μm] cylindrical-doliiform conidia with a length/width ratio of 2.6–3.1, on average 2.9 in the latter species, vs. much broader [16–24 μm], broad ellipsoid-ovoid, doliiform conidia with a length/width ratio of 1.5–3.3, on average 2.1, in *E. aquilegiae* on *Aquilegia* spp. in Europe. Schmidt and Braun (2024) described conidia of *E. aquilegiae* on *Thalictrum aquilegii-folium* to be 16–20.5 μm wide.

Erysiphe clematidicola M. Bradshaw, S. Takam. & Andr. Paul **sp. nov.** Fig. 4.

MycoBank: 860634.

Etymol.: Epithet derived from the name of the host genus, *Clematis* + -icola (dweller).

Diagnosis: Distinguished from *E. clematidis* by forming a separate highly supported species clade in different analyses, including *CAM*, *GAPDH*, IGS, and ITS+28S. Morphologically differentiated by having chasmothecia containing 3–5 asci (vs. 4–10 in *E. clematidis*), with 4–5 ascospores (vs. (1–)2–4 ascospores in *E. clematidis*). Confined to hosts of *Clematis* sect. *Clematis* (*Clematis* clade C in Lehtola et al., 2016). Morphologically and phylogenetically closely allied to *E. clematidis-montanae*. Differs from this *Erysiphe* species in forming a separate highly supported species clade in all analyses.

Type: **Japan**: Kagoshima Prefecture, Shibushi-cho, on *Clematis apiifolia*, 17 Nov. 1984, *T. Sakata* 3065 (holotype: NCSLG29077; isotypes: HAL 979 F, TUAMH 3065). Ex-holotype sequences: PX147877 (*CAM*), PX134899 (*GAPDH*), PX134563 (IGS), PX091674 (ITS+28S).

Additional specimens examined (paratypes): NCSLG25619, NCSLG25627.

Description: Mycelium on leaves, amphigenous, also on stems, forming irregular white patches or effuse, often covering the entire leaf blade, persistent; hyphae branched, septate, hyaline, thin-walled, smooth, 3–7 μm wide; conidiophores arising from the upper surface of supporting hyphae, 60–90 μm long, basal septum slightly elevated above the supporting hypha; foot cells 20–40 × 8–10 μm wide, cylindrical or somewhat curved-sinuous, followed by 1–2 shorter cells, 12.5–25 μm; conidia ellipsoid-doliiform, 25–35 × 12–16 μm. Chasmothecia amphigenous, scattered to subgregarious, subglobose, 80–110 μm diam.; peridium cells irregularly polygonal, 5–20 μm diam.; number of appendages variable, mostly numerous, arising from the lower half of the chasmothecium, mycelioid, unbranched, occasionally irregularly to subdichotomously branched, length variable, 0.5–4.5 times as long as the chasmothecial diam., 3–8 μm wide, hyaline throughout, later sometimes slightly yellowish or brownish near the base, sparingly septate, distance between individual septa large, walls thin, smooth or almost so; asci 3–5, broad ovoid-saccate, subsessile to short-stalked, 35–60 × 30–45 μm, wall 1–2 μm wide, terminal oculus with thinner

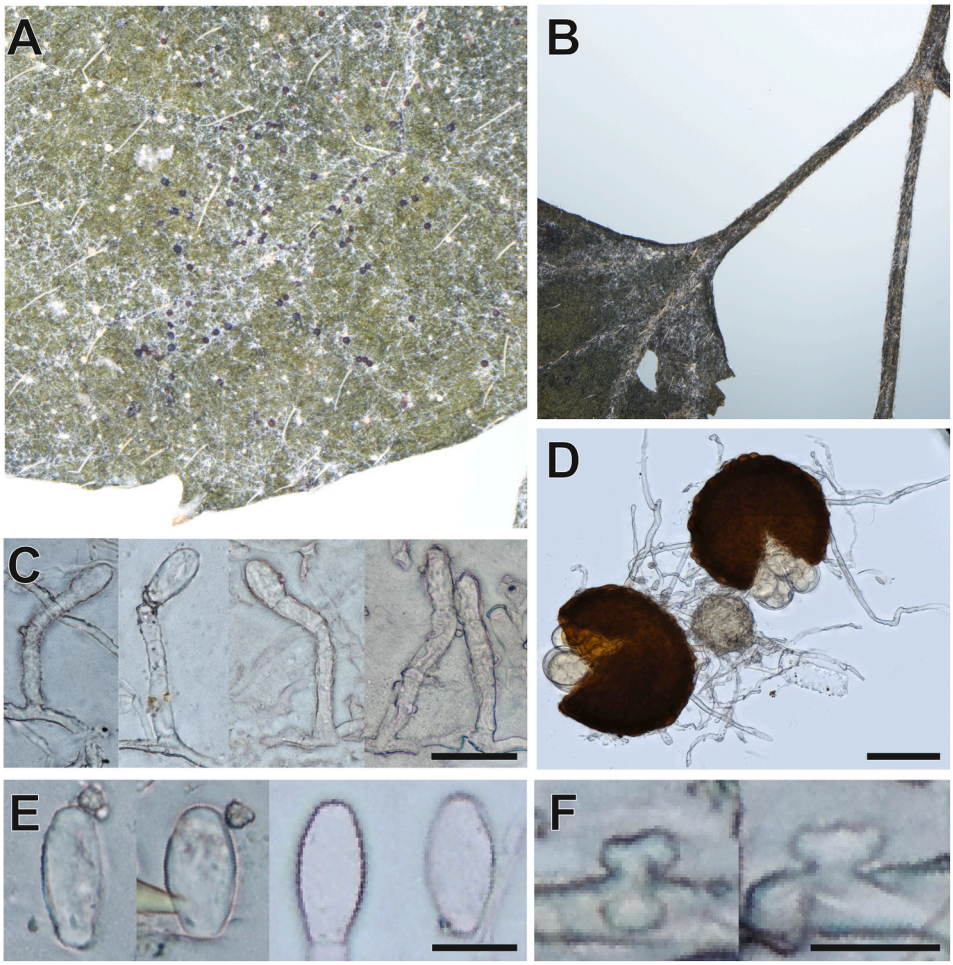


Fig. 4. *Erysiphe clematidicola.* Images from NCSLG29077 (holotype). A. Macroscopic view of leaf surface with chasmothecia. B. Macroscopic view of stem with mycelial growth. C. Conidiophores. D. Chasmothecia. E. Conidia. F. Hyphal appressoria. Scale bars: C = 20 μm; D = 50 μm; E = 20 μm; F = 10 μm.

wall not very conspicuous, c. 8–10 μm diam, asci 4–5-spored; ascospores broad ellipsoid-ovoid, 15–25 × 10–14 μm, colourless.

Host range and distribution: on *Clematis* (*apiifolia*, *stans*); Asia (Japan).

Erysiphe clematidis Zhao Y. Zhang & S.Y. Liu, MycoKeys 118: 126, 2025.

Type: **China:** Qinghai Province, Xining City, 36°38′02″ N 101°45′36″ E, c. 2260 m alt., on *Clematis macropetala*, 15 Oct. 2023, *Z.-Y. Zhang & L. Liu* (holotype: HMJAU-PM92226; isotype: HMAS 353407). Ex-holotype sequences: PP971974 (IGS), PP968504 (ITS+28S).

Host range and distribution: on *Clematis* (*glauca*, *intricata*, *macropetala*); Asia (China).

Notes: *E. clematidis* was recently introduced for *Erysiphe* specimens on diverse *Clematis* spp. in China (type host *C. macropetala*) forming a clade outside of the *E. aquilegiae* complex (Zhang et al., 2025). Sequences retrieved from specimens on *Clematis glauca* and *Clematis intricata* form subclades within the *E. clematidis* clade, suggesting that this complex of *Erysiphe* on *Clematis* spp. in China requires further research. *C. intricata* and *C. glauca* are phylogenetically allied species of *Clematis* sect. *Meclatis* (yellow-flowered *Clematis* spp., Wang, 2006), whereas *C. macropetala*, the type host, is not closely allied to the other hosts. Together with *C. sibirica*, *C. macropetala* belongs to clade H in Lehtola et al. (2016) and clade 3 in the phylogenetic analyses published by Xiao et al. (2022), largely corresponding to the previous sect. *Atragenes* (Johnson, 2001).

Erysiphe on *Clematis* spp. in Asia seems to represent a complex of multiple species, as demonstrated in the present study by the introduction of two additional new species, viz., *E. clematidicola* on *C. apiifolia* and *C. stans* (*Clematis* sect. *Clematis*; *Clematis* clade C in Lehtola et al., 2016) in Japan, as well as *E. clematidis-montanae* (*Clematis* clade E in Lehtola et al., 2016) on *Clematis montana* in Pakistan. The whole complex is morphologically characterized by chasmothecia forming colourless or pale chasmothecial appendages with few distant septa and irregular to almost dichotomous branchings.

Erysiphe clematidis-montanae M. Bradshaw, Afshan & M. Riaz, **sp. nov.** Fig. 5.

MycoBank: 860635.

Etymol.: Epithet derived from the name of the host species of the type, *Clematis montana*.

Diagnosis: Morphologically and phylogenetically closely allied to *E. clematidicola* and *E. clematidis*. Distinguished from *E. clematidis* by forming a separate highly supported species clade in the ITS+28S tree, supported by the IGS and the concatenated analyses. Morphologically differentiated by having chasmothecia with large peridium cells, 8–23 μm diam. (vs. 5–13 μm diam. *E. clematidis*), 2–6 asci (vs. 4–10 in *E. clematidis*), with (3–)4–6 ascospores (vs. (1–)2–4 ascospores in *E. clematidis*). *E. clematidis-montanae* is confined to *C. montana*, distributed in temperate East Asia and the Himalaya region, pertaining to *Clematis* clade E (Lehtola et al., 2016), in contrast to the hosts of *E. clematidis* that belong to unrelated *Clematis* spp. (see notes under *E. clematidis*). The related and morphologically similar *E. clematidicola* on *C. apiifolia* and *C. stans* (*Clematis* sect. *Clematis*, *Clematis* clade C in Lehtola et al., 2016) in Japan forms a clearly separate highly supported species clade.

Type: **Pakistan**: Khyber Pakhtunkhwa, Hazara Division, Mansehra District, Lassan Nawab, on *Clematis* cf. *montana*, Dec. 2015, *M. Fiaz & K. Habib* (holotype: NCSLG29090; isotypes: HAL 3139 F). Ex-holotype

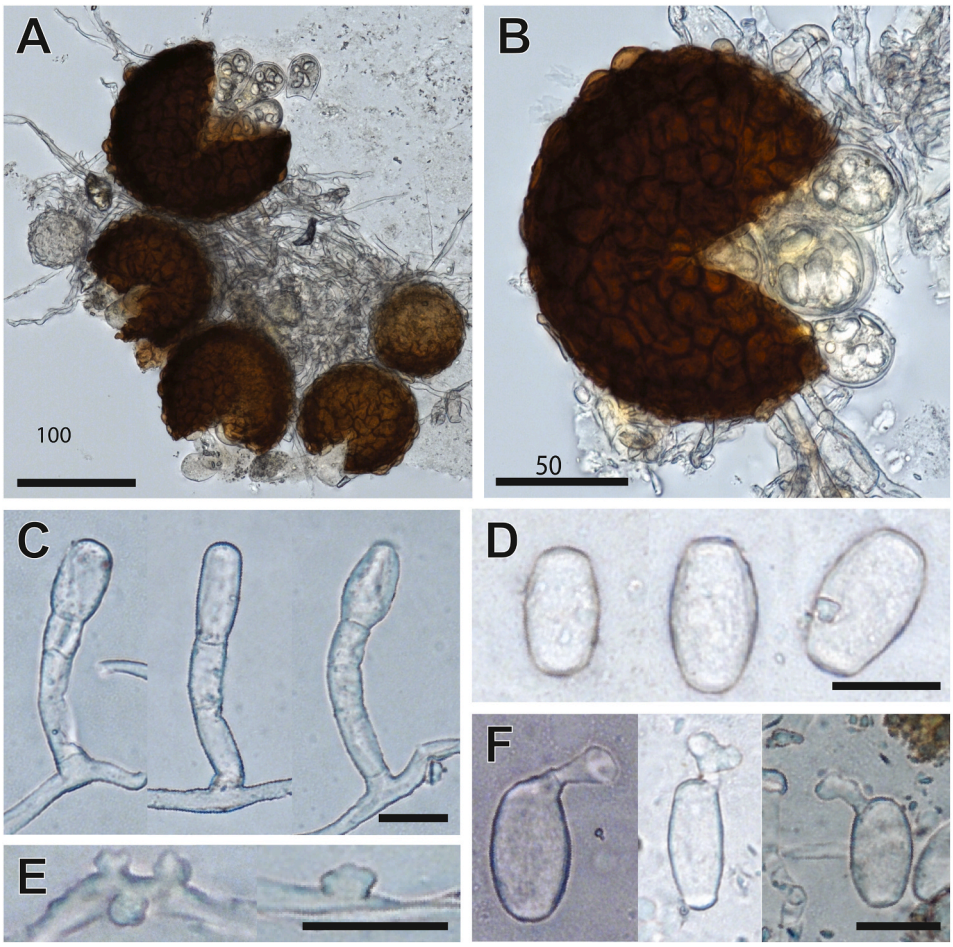


Fig. 5. *Erysiphe clematidis-montanae.* Images from NCSLG29090 (holotype). A. Chasmothecia with asci. B. Opening chasmothecium with asci. C. Conidiophores. D. Conidia. E. Hyphal appressoria. F. Conidial appressoria. Scale bars: A = 100 µm; B = 50 µm; C-F = 20 µm.

sequences: PX147878 (*CAM*), PX134401 (*GS*), PX134560 (IGS), PX091675 (ITS+28S), PX134594 (*RPB2*), PX134910 (*TUB*).

Additional specimens examined (paratypes): **Pakistan**: Khyber Pakhtunkhwa, Hazara Division, Abbottabad District, Ayubia, 2.438 m a. s. l., on *C. montana*, 30 Oct. 2017, *N.S. Afshan & M. Riaz* MA# 51 (LAH 35657); Khyber Pakhtunkhwa, Hazara Division, Abbottabad District, Ayubia, 2.438 m a. s. l., on *C. montana*, 26 Oct. 2018, *N.S. Afshan & M. Riaz* MA# 52 (LAH 36966).

Illustration: Afshan and Riaz (2022: 72, Fig. 1, as *E. aquilegiae* on *C. montana*).

Description: Mycelium amphigenous, also at stems, persistent, effuse or forming irregular white patches; hyphae branched, septate, thin-walled, smooth, 3–8 µm wide; hyphal appressoria solitary, nipple-shaped to moderately lobate, 3–7 µm diam.; conidiophores arising from the upper surface of supporting hyphae, in the middle of the hyphal cell or somewhat towards one septum, 60–90 µm long, basal septum at the junction with the supporting hypha or slightly elevated, up to 8 µm, foot cells 20–40 × 8–10 µm, cylindrical or somewhat curved-sinuous, followed by 1–2 cells, mostly shorter than the foot cell, 12.5–25 µm, occasionally followed by a single cell, about as long as the foot cell or even somewhat longer, conidia formed singly, broad ellipsoid-ovoid, doliiform, 30–43 × 14–20 µm, length/width ratio 1.7–2.4. Chasmothecia 70–110 µm diam., subglobose; peridium cells irregularly polygonal, 8–23 µm diam.; appendages numerous, arising from the lower half, length variable, 0.3–11 times as long as the chasmothecial diam., 2–9 µm wide, mycelium-like, simple, occasionally irregularly to almost dichotomously branched or even forked near the base, thin-walled (to 1 µm wide), smooth or almost so, hyaline (even in mature chasmothecia), at most slightly yellowish to very pale brownish near the base, sparingly septate, septa distant from each other, 30–80 µm, reaching the upper half; asci 2–6 per chasmothecium, 40–65 × 30–50 µm, broad ellipsoid-ovoid, saccate, short-stalked or sessile, ascus wall 1–2 µm wide, terminal oculus with thinner wall not very conspicuous, c. 8–10 µm diam., (3–)4–6-spores; ascospores broad ellipsoid-ovoid, 15–26 × 10–17 µm, colourless or finally somewhat yellowish.

Host range and distribution: on *Clematis montana*; Asia (Pakistan).

Erysiphe hortensiae (Jørst. ex S. Blumer) M. Bradshaw & U. Braun, **comb. nov.**

MycoBank: 860637.

Basionym: *Oidium hortensiae* Jørst. ex S. Blumer, Z. Pflanzenkrankh. Pflanzenschutz 38(3/4): 78, 1928. [*Oidium hortensiae* Jørst., Skr. Norske Vidensk.-Akad. Oslo, Mat.-Naturvidensk. Kl. 10: 106, 1925, nom. inval. (Art. 36.1[a], 38.1[a]).]

≡ *Pseudoidium hortensiae* (Jørst. ex S. Blumer) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 606, 2012, nom. inval. (Art. 41.5).

Type: **Norway**: Oslo, Skøyen, on *Hydrangea macrophylla*, 22 May 1924, *Johansen* (lectotype [designated by Shin et al., 2019]: O-F-72683). **Germany**: Sachsen-Anhalt, Halle (Saale), Geist Street, potted plant, 6 Oct. 2024, *U. Braun* (epitype [designated here, MycoBank, MBT10028417]: NCSLG29032; isoepitype: HAL 3785 F. Ex-epitype sequences: PX147811 (*CAM*), PX134857 (*GAPDH*), PX134410 (*GS*), PX091691 (ITS+28S), PX134615 (*RPB2*), PX134961 (*TUB*).

= *E. communis* f. *sedi* Jacz., Karm. Opred. Grib. Vip. 2 Muchn.-rosj. Griby: 238, 1927.

= *Erysiphe sedi* U. Braun, Feddes Repert. 92(7–8): 502, [Sep.] 1981.

Type: **Japan**: Hokkaido Prefecture, Sapporo, on *Hylotelephium erythrostictum* (≡ *Sedum erythrostictum*), Sep. 1920, *Tochinai* (holotype: TNS-F-217879). Reference sequence: JX173289 (ITS) [**South Korea**: on *H. erythrostictum* (KUS-F25536)].

= *E. sedi* R.Y. Zheng & G.Q. Chen, Sydowia 34: 253. [31 Dec.] 1981, nom. illeg. (Art. 53.1).

Type: **China**: Hebei Province, Xiaowutaishan, on *Phedimus aizoon* [≡ *Sedum aizoon*], 9 Aug. 1957, *L.W. Xu* et al. 226 (holotype: HMAS 39988). Reference sequence: LC010045 (ITS+28S) [**Russia**: Far East, on *P. aizoon* [≡ *S. aizoon*], 2 Oct. 1989, *V.P. Heluta* (TNS-F-87870, previously MUMH2575)], Takamatsu et al. (2015).

= *Erysiphe malloti* Zhi X. Chen & R.X. Gao, Acta Mycol. Sin. 3(2): 75, 1984.

Type: **China**: Fujian Province, Wuyishan, on *Mallotus lianus*, 10 Nov. 1981, *Z.X. Chen* et al. Wuyi-81515 (holotype: FJFC; isotype: HMAS 44238). Ex-isotype sequences: PP971945 (IGS), PP968474 (ITS+28S).

= *E. malloti* Y. Nomura & Tanda, Trans. Mycol. Soc. Japan 26(2): 115, 1985, nom. illegit. (Art. 53.1).

Type: **Japan**: Kanagawa Prefecture, Kawasaki-shi, Ikuta, on *Mallotus japonicus*, 3 Nov. 1977, *S. Tanda* (holotype: TUAMH 0354). Reference sequence: AB808657 (ITS) [**Japan**: Nara Prefecture, Nara, Kinki University, Department of Agriculture, Nara campus, on *M. japonicus*, 2012, KMP-01], Nonomura et al. (2013).

= *Oidium kalanchoes* Lüstner ex U. Braun (as "*calanchoeae*"), Beih. Nova Hedwigia 89: 602, 1987. [*Oidium kalanchoes* Lüstner (as "*calanchoeae*"), Nachrichtenbl. Deutsch. Pflanzenschutzdienst 15(4): 41, 1935, nom. inval. (Art. 39.1)].

Type: **Germany**: Niedersachsen, Braunschweig, Julius Kühn Institute, greenhouse, on *Kalanchoe blossfeldiana*, Jan. 2018, *M. Götz* (neotype [designated by Götz et al., 2019]: HAL 3298 F). Ex-neotype sequence: MK411006 (ITS+28S).

≡ *Pseudoidium kalanchoes* (Lüstner ex U. Braun) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 608. 2012.

= *Oidium neolycopersici* L. Kiss, Mycol. Res. 105(6): 695, 2001.

Type: **France**: Département Gard, Aigues-Mortes, on *Solanum lycopersicum* [≡ *Lycopersicon esculentum*], Dec. 1999, *M. Bardin & P.C. Nicot* Et1 (holotype: BPI 747013; isotype: HAL 452 F). Ex-holotype sequence: AF229019 (ITS+28S).

≡ *Pseudoidium neolycopersici* (L. Kiss) L. Kiss, in Braun and Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 612, 2012.

≡ *Erysiphe neolycopersici* (L. Kiss) H.Y. Hsiao & Y.M. Shen, Diversity 14(3, no. 204): 12, 2022.

= *Oidium pedaliacearum* H.D. Shin, Schlechtendalia 17: 45, 2008. [= *Oidium sesami* H.D. Shin, Korean J. Plant Pathol. 6(1): 9, 1990, nom. inval. (Art. 40.7), non *O. sesami* (Y.S. Paul & J.N. Kapoor) Hosag., Vijay., Udaiyan & Manian, 1992.]

Type: **South Korea**: Gangneung, on *Sesamum indicum*, 16 Sep. 1991, *H.D. Shin* (holotype: KUS-F-11074); **South Korea**: Miryang, Naeil-dong, on *Sesamum indicum*, 10 Oct. 2017, *H.D. Shin* (epitype [designated by Shin et al., 2019]: KUS-F-30128). Ex-epitype sequence: LC342963 (ITS+28S).

≡ *Pseudoidium pedaliacearum* (H.D. Shin) H.D. Shin, in Braun and Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 615, 2012.

≡ *Erysiphe pedaliacearum* (H.D. Shin) H.D. Shin, Mycol. Progr. 18: 239, 2019.

= *E. caricae-papayae* Meeboon & S. Takam., Mycosphere 8(9): 1407, 2017.

Type: **Thailand**: Chiang Rai, on *Carica papaya*, 22 Nov. 2013, *J. Meeboon* (holotype: TNS-F-88225 [previously TSU-MUMH5749]). Ex-holotype sequence: LC228610 (ITS).

Description: Mycelium on leaves, amphigenous, also on stems, effuse or forming patches, white, persistent; hyphae branched, septate, hyaline, thin-walled, straight, sinuous to tortuous, branched, septate, hyphal cells about 40–50 × 2–7 µm; hyphal appressoria solitary or in opposite pairs, almost nipple-shaped, slightly lobed to multilobed, 5–25 µm diam.; haustoria globose, 17.5–18.5 µm diam.; conidiophores arising from the upper surface of the mother cell, in the middle or somewhat towards one septum, erect, straight, 30–150 µm long, foot cells straight, cylindrical to slightly curved-sinuous, (10–)15–50(–75) × 4–10(–13) µm, followed by 1–3(–4) shorter cells, sometimes following cell about as long as the foot cell or even longer; conidia formed singly, ellipsoid-ovoid, doliiform-cylindrical, (20–)25–45(–55) × (9–)12–20(–24) µm, length/width ratio (1.25–)1.4–2.8(–3.1), germ tubes perihilar, short to long (longitubus pattern), apex undifferentiated, somewhat enlarged or with lobate appressorium. Chasmothecia scattered to gregarious, subglobose, 80–185 µm diam.; peridial cells irregularly polygonal, (5–)8–25 (–30) µm diam.; chasmothecial appendages usually numerous, 5–20, in the lower half, mycelium-like, usually simple, occasionally irregularly branched, 0.5–3(–4) times as long as the chasmothecial diam., 3–8 µm wide, septate, thin-walled or somewhat thickened below, 1–2.5(–3.5) µm, smooth to verruculose, hyaline, pale to medium dark brown below, paler or hyaline towards the apex, short appendages sometimes pigmented throughout; asci 4–9(–12), ellipsoid-obovoid, saccate, (35–) 40–85 × 25–55(–60) µm, sessile or short-stalked, wall 2–4 µm wide, (2–) 3–5(–6)-spored; ascospores ellipsoid-ovoid, colourless or somewhat yellowish, 10–25(–30) × 8–17(–20) µm.

Host range and distribution (based on specimens examined by multilocus sequence analyses, including *GAPDH,* IGS, *RPB2*, and the concatenated analysis): *Caricaceae* [*Carica papaya*], *Crassulaceae* [*Crassula capitella*, *Hylotelephium erythrostictum* [= *Sedum alboroseum*], *Kalanchoe* sp., *Sedum bulbiferum*)], *Hydrangeaceae* [*Hydrangea* (*macrophylla*, sp.)], *Pedaliaceae* [*Sesamum indicum*], *Solanaceae* [*Nicandra physalodes*, *Solanum lycopersicum*]; Asia (India, Japan, Thailand), Europe (Germany, Hungary, Romania), North America (USA: Florida, Massachusetts, Washington). Based on the taxa that are now part of *E. hortensiae,* it is likely this species has an almost worldwide distribution, and a much wider host range.

Notes: The nomenclature and typification of *Oidium hortensiae* have been clarified in Shin et al. (2019). The *E. hortensiae* clade is strongly supported in the concatenated analysis of the *E. aquilegiae* complex and clearly separated from the highly supported *E. aquilegiae* s. str. clade (Fig. 1). The *E. hortensiae* clade is also well-supported in the IGS and *RPB2* analyses and moderately supported in the *GAPDH* analysis. Diverse hosts of the *Crassulaceae* and *Solanaceae* are principal hosts of *E. hortensiae*, besides *Hydrangea macrophylla* and *Sesamum indicum.* However, only a single *S. indicum* specimen had multilocus data, and this was from Hungary in a greenhouse, geographically distant from the type locality of *E. pedaliacearum*. Future research will need to evaluate multilocus data from specimens on *Sesamum* from Asia to better understand the powdery mildew on this host. Only a single specimen on *Carica papaya* was evaluated as well with multilocus data, which was collected from the backyard of a house in Thailand. It should be noted that a single Chinese sequence retrieved from powdery mildew on *Punica granatum* (*Lythraceae*) group in the *E. hortensiae* clade in the *RPB2* analysis. These results are somewhat unusual as we hypothesize that *E. punicae* is a synonym of *E. aquilegiae* s. str. Future research with more loci and specimens is needed to ensure the correct placement of *E. punicae.* Sequences retrieved from *E. hortensiae* on its type host, *Hydrangea macrophylla*, form a well-supported subclade within the *E. hortensiae* species clade that can be genetically identified by the IGS and *GS* region, which is important for distinguishing a potential "forma *hortensiae*" when in future additional formae should be introduced (Supplementary Figs. 3 and 4). It should also be noted that specimens on *Solanum*, *Crotalaria*, and *Sesamum* form a supported group in the ITS analysis which could favor the future description of a forma. However it should be noted that only a single nucleotide is causing this support and this was not seen in any other single locus tree.

The phylogenetic-taxonomic status of *Erysiphe* species on *Eriocapitella hupehensis* (≡ *Anemone hupehensis*), *Ranunculaceae*, remains unclear with a sequence clustering in basal position to the *E. hortensiae* clade in

the concatenated analysis (Fig. 1) as well as in the IGS analysis (Suppl. Fig. 4). This powdery mildew probably does not pertain to *E. hortensiae* and might represent a further undescribed species or forma, but additional collections and sequences are required.

Erysiphe nitida (Wallr.) Rabenh. (as '*Erysibe*'), Deutschl. Krypt.-Fl. 1: 231, 1844.

Basionym: *Alphitomorpha nitida* Wallr., Fl. crypt. Germ. 2: 757, 1833.

Type: **Germany**: "Harz Mts, Elend, garden of Meyer." [Sachsen-Anhalt, Landkreis Harz, Elend], on leaves of *Aconitum* sp., undated, without collector (lectotype [designated by Braun and Cook, 2012: 362]: STR); **Germany**: Sachsen-Anhalt, Landkreis Harz, Bodetal, ca. 2 km von Treseburg in Richtung Thale, Erlenwald an der Bode, on *Aconitum vulparia*, 3 Aug. 1977, *U. Braun* (epitype [designated here, MycoBank: MBT10028416]: NCSLG29094; isoepitype: HAL 1007 F). Ex-epitype sequences: PX134494 (IGS), PX091677 (ITS+28S), PX134896 (*GAPDH*).

= *E. communis* f. *aconiti* Rabenh. (as '*Erysibe*'), Fungi Eur. Exs. 1060, 1866.

Published descriptions and illustrations: Blumer (1933: 234, Fig. 79 A, chasmothecium), Grigaliūnaitė (1997: 70, Fig. 34, chasmothecium on *Delphinium californicum*), Rachimova et al. (2014: 30, Fig. 60, on *Aconitum rotundifolium*, symptoms; Fig. 61, on *Delphinium* sp., symptoms; Fig. 63, on *Aconitum* sp., chasmothecium), Schmidt and Braun (2020: 35–36, Figs. 7–8, anamorph and conidial germination on *Delphinium* spp.).

Description: Mycelium on leaves, amphigenous, also on stems, effuse or forming patches, white, persistent; hyphae branched, 3–7 µm wide, septate, hyaline, thin-walled, smooth; hyphal appressoria mostly solitary, slightly lobate to multilobate, 4–8 µm diam.; conidiophores arising from the upper surface of the mother cells, in the middle or mostly towards one septum, erect, straight, foot cells cylindrical, straight, occasionally somewhat curved-sinuous, 20–50 × 7–11 µm, followed by 1–2 cells, shorter than the foot-cell, about as long or occasionally even longer; conidia formed singly, ellipsoid-ovoid, subcylindrical, 25–45 × 12–22 µm (herbarium samples and fresh conidia), length/width ratio 1.4–2.3 (average 1.8), usually with a single perihilar germ tube, occasionally with a second basal germ tube, short, terminating in a lobate to multilobate appressorium or long (longitubus pattern), without appressorium or apex swollen, club-shaped, germ tubes with a single septum at or near the base, sometimes with a second septum distant from the base. Chasmothecia scattered to gregarious, 75–120 µm diam., subglobose; peridial cells irregularly polygonal, 8–25 µm diam.; chasmothecial appendages usually 5–30, attached to the basal half of the chasmothecium, usually relatively short, 0.2–2.5 times as long as the chasmothecial diam., 3–10 µm wide, mycelioid, simple, rarely irregularly branched, aseptate to sparingly septate, wall thin or somewhat thickened, above all below, 1–2 µm, smooth or almost so to verruculose, colourless or pigmented (pale to medium dark brown) below and paler or hyaline towards the tip, or shorter appendages pigmented throughout; asci (1–)2–6(–8) per chasmothecium, broad ellipsoid-ovoid, saccate, 40–70 × 25–45 µm, sessile to short-stalked, wall 1–2 µm thick, terminal oculus not very conspicuous, 8–15 µm diam., (2–)3–6-spored; ascospores broad ellipsoid-ovoid, 12–25 × 7–15 µm, hyaline to faintly greenish or yellowish.

Host range and distribution (based on sequenced specimens): *Ranunculaceae* subfam. *Ranunculoideae* tribe *Delphinieae* [*Aconitum* (*grossedentatum*, *lycoctonum*, *napellus*, *vulparia*), *Delphinium* (*elatum*, sp.)]; Asia (India, Japan), Australia [on *Delphinium* sp., Cunnington et al., 2004], Europe (Austria, Germany, Finland, UK).

Notes: Powdery mildew infecting *Aconitum* and *Delphinium* species forms strongly supported clades in all trees with available sequence data. The name *E. nitida* is available for these powdery mildews and is reintroduced. Based on the host genera involved, this clade is unsurprising because *Aconitum* and *Delphinium* are closely related in the tribe *Delphinieae*. The structure of the ITS+28S as well as the multilocus tree suggest a further internal structure that might reflect either formae or cryptic species. However, to answer this question, a larger number of sequences are needed from additional collections from throughout the world. *E. nitida* is likely widespread and cosmopolitan on *Aconitum* spp. and *Delphinium* spp. [Amano (1986) listed numerous host species of the two genera from Africa (Kenya, Malawi, Morocco, South Africa, and Tanzania), Asia, Australia and New Zealand, Europe, North America (Canada and USA), and South America (Argentina, Chile).] Braun (1995) listed *E. nitida* as *E. aquilegiae* on diverse *Aconitum* and *Delphinium* species from all parts of Europe.

Lectotype material from Wallroth's collection of *A. nitida* is about 200 years old. It is likely too old for sequencing, and permission to carry out destructive examination has not been received. Because *E. nitida* belongs to the intricate *E. aquilegiae* complex, which requires molecular examinations for reliable identifications, epitypification with ex-epitype sequences is essential. The designated epitype is fitting material from the Harz Mt. region in Germany where the lectotype had been collected.

Erysiphe parnassiae (Halst.) Jacz., Karm. Opred. Grib. Vip. 2 Muchn.-rosj. griby: 165, 1927.

Basionym: *Erysiphopsis parnassiae* Halst., Bull. Torrey Bot. Club 26 (11): 594, 1899.

Type: **USA**: Wisconsin, Madison, on "*Parnassia caroliniana*" [= *Parnassia glauca*], Aug. 1893, *B.D. Halsted & S.M. Tracy* (lectotype [designated by Braun and Cook, 2012]: BPI 565075; isolectotype: WIS-F-0015953; possible isolectotype: ILL00088612). Ex-lectotype sequences: OR045045 (*CAM*), OR045110 (*GAPDH*), OR045175 (*GS*), OR036301 (ITS), OR045235 (*RPB2*), OR045290 (*TUB*).

Host range and distribution: on *Parnassia* (*glauca*, sp.); North America (Canada: Ontario; USA: New York, Wisconsin).

Notes: The status of *E. parnassiae* as a species is confirmed in phylogenetic analyses. In all analyses including sequence data for this species (see also Bradshaw et al., 2024a), *E. parnassiae* forms a clade outside of and in basal position to *E. aquilegiae* s. str and *E. hortensiae*. In the *GAPDH* single-locus analysis, sequences form a clade in basal position, but with minimal support.

Prior reports of *P. caroliniana* as a host in northern North America are most likely a misapplication and refer instead to *P. glauca* (Ball, 1993+).

Erysiphe santali M. Bradshaw, U. Braun & Pfister, Mycologia 116(1): 136, 2023 [2024].

Replaced synonym: *Oidium santalacearum* U. Braun & Hosag., Int. J. Mycol. Lichenol. 4(1–2): 187.

Type: **India**: Tamil Nadu, Coimbatore, Botanical Garden, on *Santalum album*, 13 Oct. 1988, *V.B. Hosagoudar* (holotype: HAL 3536 F; isotype: FH01085256). Ex-isotype sequences: OR045059 (*CAM*), OR045122 (*GAPDH*), OR045184 (*GS*), OR424976 (ITS), OR045293 (*TUB*).

≡ *Pseudoidium santalacearum* (U. Braun & Hosag.) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 617, 2012.

Host range and distribution: on *Santalum album*; Asia (India).

Notes: The status of *E. santali* as an independent species was established by Bradshaw et al. (2024a), but the phylogenetic-taxonomic status of this species is still unclear. Additional sequence analyses are needed to exclude or confirm the possible involvement of multiple powdery mildew species in the sequenced specimen and/or contamination. As such, this species was not included in the present analysis and this issue will be discussed in an upcoming publication.

Erysiphe thalictri M. Bradshaw & J.K. Mitch. **sp. nov.**, Fig. 6.

MycoBank: MB860636.

Etymol.: Epithet derived from the name of the host genus, *Thalictrum*.

Diagnosis: Sequences retrieved from *E. thalictri* form strongly supported species clades, clearly separate from all clades of allied species, in the *CAM*, *GAPDH*, ITS+28S, and *RPB2* analyses and in the concatenated

tree. *E. thalictri* is morphologically distinguished from *E. aquilegiae* s. str. on ranunculaceous hosts, including *Thalictrum* spp., by having much narrower ellipsoid-ovoid to cylindrical conidia, 8–17 µm wide [vs. much broader (16–24 µm) ellipsoid-ovoid, doliiform conidia in *E. aquilegiae* on *Aquilegia* spp. and other hosts] and chasmothecial appendages with thickened walls, up to 2 µm (vs. thin-walled in *E. aquilegiae*, not thicker than 1 µm).

Type: **USA**: Washington, Seattle, University of Washington, Center for Urban Horticulture Nursery, 47°39′22.6″ N 122°17′20.99″ W, on "*Thalictrum revolutum*" [= *Thalictrum amphibolum*], 23 Aug. 2018, *M. Bradshaw* MJB UW213 (holotype: FH01131051). Ex-holotype sequences: OR045018 (*CAM*), OR045086 (*GAPDH*), OR045152 (*GS*), OR036271 (ITS+28S), OR045211 (*RPB2*), OR045268 (*TUB*).

Additional specimen examined (paratype): **USA**: Washington, Seattle, University of Washington, Center for Urban Horticulture Nursery, 47°39′26.71″ N 122°17′21.02″ W, on *Thalictrum delavayi*, 23 Aug. 2018, *M. Bradshaw* MJB UW212 (FH01131052).

Description: Mycelium foliicolous, amphigenous, also caulicolous and petiolicolous, white, effuse with thicker, floccose patches; hyphae thin-walled, delicate, sinuous-geniculate, about 3.5–6 µm wide; hyphal appressoria frequent, lobed, solitary or in opposite pairs, pairs sometimes clustered in groups, 3.5–9.5(–14) µm diam.; conidiophores delicate, frequently collapsed, variable, about 30–70(–100) × 5.5–12 µm, foot-cells cylindrical, straight or curved-sinuous at the base, about 15–50 × 5.5–9.5 µm, followed by 1–2 shorter cells or cells of about the same length, second cell occasionally longer, forming conidia singly; conidia ellipsoid-ovoid to cylindrical, 22–41(–47) × 8–17 µm, length/width ratio 1.4–3.3(–4.8), germ tubes ± terminal. Chasmothecia scattered to subgregarious, foliicolous, amphigenous, also caulicolous and petiolicolous, 110–140 µm diam., peridium very dark; peridium cells irregularly polygonal, 10–25 × 8–16 µm diam.; appendages about 18–37, arising between base and equator, horizontally spread, simple, occasionally with a very short side branch, mostly straight but slightly geniculate, flexuous, long, 1.5–5 times the chasmothecial diam., 5–8.5 µm wide, septate, brown throughout when mature or paler towards the apex, wall slightly to moderately thickened, 0.8–2.0 µm, smooth, sometimes with faintly rough patches; asci 5–8(–9), ellipsoid-obovoid or -ovoid, clavate-saccate, 50–65 × 30–45 µm, sessile or short-stalked, (3–)

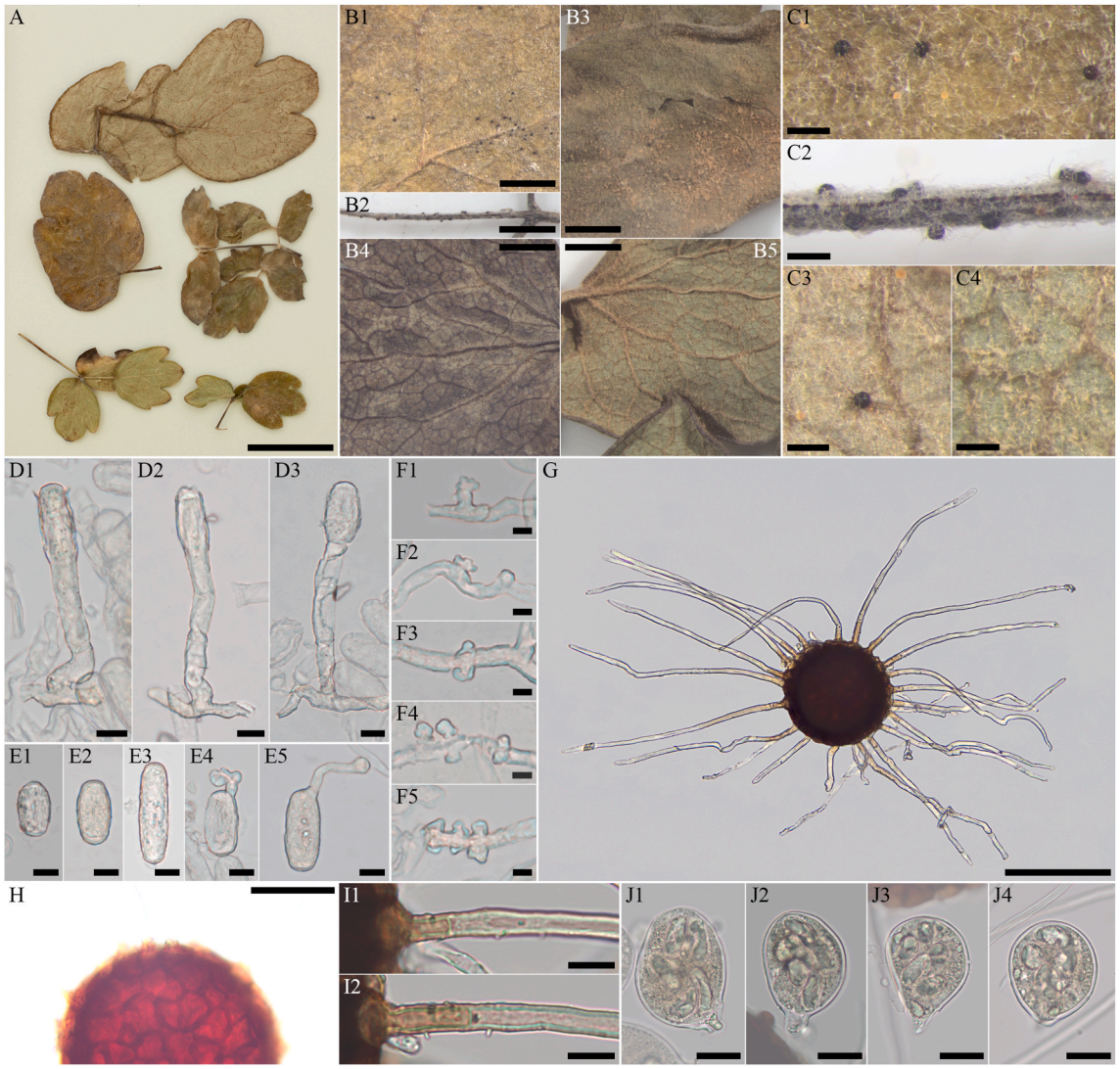


Fig. 6. Morphological details of the holomorph (conidiophores and chasmothecia) of *Erysiphe thalictri* sp. nov. A–C. Infected plant material bearing conidiophores on leaves, including upper (A, B3) and lower (A, B4, B5, C4) leaf surfaces, and chasmothecia on petioles (B2, C2) and leaves, including upper (A, B1, C1) and lower (A, C3) leaf surfaces. D. Conidiophores. E. Conidia, including germinating conidia (E4, E5). F. Hyphal appressoria. G. Chasmothecium with appendages. H. Peridial cell arrangement. I. Details of chasmothecial appendage bases showing septa. J. Asci released from broken chasmothecia with ascospores. Tape mount in KOH: D–F; water with KOH pretreatment: G–J. FH01131051 (holotype) = A, B1, B3, B5, C1, C3, C4, D1, D2, E1–5, F1–5, G, H, I1–2, J2–4; FH01131052 = B2, B4, C2, D3, J1. Scale bars: A = 2 cm; B = 2 mm; C = 0.25 mm; G = 100 µm; H = 40 µm; J = 20 µm; D, E, I = 10 µm; F = 5 µm.

4–6(–7)-spored; ascospores ellipsoid-ovoid, 14–24 × 7.5–12 μm, hyaline or faintly yellowish.

Host range and distribution (based on sequenced specimens): on *Thalictrum* (*amphibolum*, *delavayi*, *thalictroides* [≡ *Anemonella thalictroides*]); North America (USA: Washington, Wisconsin).

Notes: The genus *Thalictrum* belongs to subfam. *Thalictroideae* tribe *Thalictreae* of the family *Ranunculaceae* in which it takes an isolated position in the monotypic subtribe *Thalictrinae* (Wang et al., 2009). The sequences retrieved from North American specimens on *Thalictrum* spp. form a strongly supported species clade in ITS+28S as well as the multilocus trees. In the ITS+28S tree, a sequence obtained from a North American specimen on *Thalictrum thalictroides* (≡ *A. thalictroides*) belongs to the *E. thalictri* clade. This host was previously considered a species of the monotypic genus *Anemonella*, but Cossard et al. (2016) reduced the latter genus to synonymy with *Thalictrum*, based on a phylogenetic multilocus revision; this result was also confirmed by Xiang et al. (2022). These results suggest that *E. thalictri* is a North American species. ITS(+28S) sequences retrieved from *Erysiphe* specimens on *T. aquilegiifolium* (Germany, USA), *Th. minus* (Iran), *Th. shensiense* (China), and *Th. tuberiferum* (Japan) cluster within the *E. aquilegiae* clade (s. lat.), confirming that multiple *Erysiphe* spp. are to be expected on *Thalictrum* spp.

3.2.4. Hosts and synonyms assignable to *E. aquilegiae* s. lat. (complex) based on ITS(+28S) sequences

ITS(+28S) sequences are sufficient to assign powdery mildew specimens to the *E. aquilegiae* complex (Takamatsu et al., 2015; Shin et al., 2019; Bradshaw et al., 2020, 2024a). However, proper identifications based on the separation of *E. aquilegiae* s. lat. into *E. aquilegiae* s. str., and *E. hortensiae*, as defined in the present work, require multilocus analyses. Numerous ITS (+28S) sequences exist for historical *Erysiphe* names associated with this complex and for powdery mildew specimens from various hosts falling within the *E. aquilegiae* complex. Although many of these likely represent synonyms of *E. aquilegiae* s. str., based on current phylogenetic analyses (see notes under *E. aquilegiae*), they cannot yet be confidently assigned to either of the two species in the complex without multiple loci sequenced. ITS data alone are insufficient for definitive identifications; all such cases require future multilocus analyses.

3.2.4.1. Species names assignable to E. aquilegiae s. lat. (complex). The listed names are comprised of species confirmed to pertain to the *E. aquilegiae* complex by results of ITS(+28S) analyses and in a few cases by inoculation experiments (Whipps et al., 1998).

Erysiphe abelmoschicola Tanda, J. Agric. Sci. (Tokyo) 48(2): 51, 2003.

Type: **Japan**: Kanagawa Prefecture, Atsugi-shi, Funako, Tokyo University of Agriculture, on *Abelmoschus manihot*, 11 Dec. 2001, *S. Tanda* (holotype: TUAMH 6110).

Note: This species pertains possibly to *E. hortensiae* (based on results of inoculation experiments carried out by Whipps et al., 1998), but final conclusions require multilocus sequence analyses.

Erysiphe actinostemmatis U. Braun (as "*actinostemmae*"), Mycotaxon 18(1): 123, 1983.

Type: **Japan:** Kochi Prefecture, Tosa District, Takasu-mura, Kadzurashima, on *Actinostemma lobatum*, 23 Oct. 1910, *T. Yoshinaga* (holotype: TNS-F-229705). Reference sequences: PP971942 (IGS), PP968470 (ITS+28S) [**China**: on *Actinostemma tenerum*, 14 Sep. 2017 (HMJAU-PM92195)], unpublished.

Note: This species pertains possibly to *E. hortensiae* (based on results of inoculation experiments carried out by Whipps et al., 1998), but final conclusions require multilocus sequence analyses.

Erysiphe begoniae R.Y. Zheng & G.Q. Chen, Acta Microbiol. Sin. 20(4): 361, 1980.

Type: **China**: Yunnan Province, Lijiang, on *Begonia modestiflora* (= *Begonia yunnanensis*), 13 Nov. 1958, *S.J. Han & L.Y. Chen* 5136 (holotype: HMAS 38951). Reference sequences: PP971947 (IGS), MZ958710 (ITS+28S) [**China**: on *Begonia* × *hiemalis*, 31 Mar. 2021 (HMJAU-PM91929)], unpublished.

Erysiphe catalpae Simonyan, Mikol. Fitopatol. 18(6): 463, 1984, nom. cons.

Type: **Armenia**: Yerevan, Botanical Garden, on *Catalpa bignonioides*, 9 Oct. 1957, *S.A. Simonyan* 1710 (holotype: EREM; isotype: HAL 1429 F). Reference sequences: KY786660 (*actin*), KY653194 (ITS+28S) [**UK**: Reading, University of Reading, Campus Central, Whiteknights, 51°26′25.1″ N 0°56′39.8″ W, on *Catalpa bignonioides*, 5 Jul. 2015, *O. Ellingham* (RNG OE2016PMCS16)], Ellingham (2017), see Takamatsu et al. (2015) and Bradshaw et al. (2020).

Erysiphe caucasica Simonyan, Biol. Zhurn. Armenii 38(9): 820, 1985.

Type: **Armenia**: Yerevan, Botanical Garden, Armenian flora section, on "*Centaurea pulcherrima* Willd." [= *Dipsacaceae* sp., see Braun and Cook, 2012], 13 Aug. 1970, *S. Simonyan* (holotype: EREM 9046).

Erysiphe chloranthi (Golovin & Bunkina) U. Braun, Mycotaxon 18(1): 120, 1983.

≡ *E. communis* f. *chloranthi* Golovin & Bunkina, Novosti Sist. Nizsh. Rast. 5: 140, 1968.

Type: **Russia**: Primorsky Krai, Ussuriysk City Under Krai Jurisdiction, Suputinsky Zapovednik [Ussurisky Nature Reserve], on *Chloranthus serratus* (= *C. japonicus*), 5 Sep. 1958, *I.A. Bunkina* (holotype: LE 34538). Reference sequences: LC009931 (ITS+28S) [Japan, on *C. serratus*, TNS-F-8722282 (=MUMH0202, NCSLG25609), Takamatsu et al., 2015].

Erysiphe circaeae L. Junell, Svensk Bot. Tidskr. 61(1): 224, 1967.

Type: **Germany**: Berlin, Tiergarten, on *Circaea lutetiana*, Sep. 1886, *P. Sydow* [P. Syd., Mycoth. March. 1143] (holotype: UPS; isotypes: P. Syd., Mycoth. March. 1143, e.g., FH01085367, BPI 1054948). Reference sequence: LC010044 (ITS+28S) [**Ukraine**: Crimea, on *Circaea lutetiana*, 24 Jul. 1996, *V.P. Heluta* (TNS-F87869, previously TSU-MUMH2574)].

Erysiphe coriariae (Y. Nomura) U. Braun & S. Takam., Schlechtendalia 4: 7, 2000.

≡ Basionym: *Microsphaera coriariae* Y. Nomura, Taxonomical study of *Erysiphaceae* of Japan: 118, 1997.

Type: **Japan**: Miyagi Prefecture, Mt. Sengatake, on *Coriaria japonica*, 28 Aug. 1973, *Y. Nomura* YNMH 2947 (holotype: TNS). Reference sequence: LC009927 (ITS) [**Japan**: Niigata Prefecture, Oyashirazu, on *C. japonica*, 20 Oct. 1996, *S. Takamatsu* (TNS-F-87274, previously TSU-MUMH0172)].

Erysiphe epimedii (F.L. Tai) R.Y. Zheng & G.Q. Chen, Acta Microbiol. Sin. 20(4): 356, 1980.

≡ *Erysiphe polygoni* var. *epimedii* F.L. Tai, Bull. Torrey Bot. Club 73 (2): 113, 1946.

Type: **China**: Henan, Sunghsien, on *Epimedium brevicornu*, 1942, *J.X. Wang* 2520 (holotype: HMAS 11570).

Note: ITS sequences obtained from *Erysiphe* on *Epimedium* spp. in New Zealand and the United States cluster within the *E. aquilegiae* s. lat. clade.

Erysiphe geraniacearum U. Braun & Simonyan, Mycotaxon 19: 378, 1984.

Type: **Belarus**: Brest Region, Mar'yanovo, in a wet meadow, on *Geranium pratense*, *S.J. Schembel* (holotype: LE).

Note: ITS sequenes obtained from *Erysiphe* on *Geranium* spp. in Germany and the United States cluster within the *E. aquilegiae* s. lat. clade.

Erysiphe hommae U. Braun, Feddes Repert. 92(7–8): 501, 1981.

Type: **Japan**: Hokkaido Prefecture, Togachi Subprefecture, Shintoku, on *Elsholtzia ciliata*, 29 Sep. 1929, *Tokunaga* (holotype: TNS-F-217950). Reference sequence: LC009926 (ITS+28S) [**Japan**: Niigata Prefecture, Oyashirazu, on *E. ciliata*, 20 Oct. 1996, *S. Takamatsu* (TNS-F-87272, previously TSU-MUMH0167)], Takamatsu et al. (2015).

Erysiphe lini Tanda, J. Agric. Sci. (Tokyo) 48(2): 54, 2003.

Type: **Japan**: Kanagawa Prefecture, Atsugi-shi, Funako, Tokyo University of Agriculture, on *Linum usitatissimum*, 11 Nov. 1999, *S. Tanda* (holotype: TUAMH 5808).

Note: This species pertains possibly to *E. hortensiae*, but final conclusions require multilocus sequence analyses. This assumption is based on inoculation experiments published by Whipps et al. (1998).

Erysiphe macleayae R.Y. Zheng & G.Q. Chen, Sydowia 34: 290, 1981.

Type: **China**: Zhejiang Province, Moganshan, on *Macleaya cordata*, 17 Oct. 1979, *H. Huang* (holotype: HMAS 40100). Reference sequence: KJ160268 (ITS) [**China**: On *M. cordata* (HMJAU00624)].

Erysiphe pachypodii Lebeda, Mieslerová & Doležalová, Mycotaxon 92: 285, 2005. [*E. pachypodii* Lebeda, J. Phytopathol. 150(3): 152, 2002, nom. inval. (Art. 39.1).]

Type: **Czech Republic**: Smržice, on *Pachypodium lamerei*, 20 Aug. 1999, *A. Lebeda* ELP 1 (holotype: OL). Reference sequence: OK631965 (ITS+28S) [**Germany**: Niedersachsen, Oldenburg, Botanical Garden, on *P. lamerei*, 26 Feb. 2021, *T. Brand* (HAL 3377 F)], Bradshaw et al. (2024b).

Erysiphe pileae (Jacz.) Bunkina ex U. Braun, Feddes Repert. 92(7–8): 503, 1981.

Basionym: *E. communis* f. *pileae* Jacz., Karm. Opred. Grib. Vip. 2 Muchn.-rosj. griby: 289, 1927.

Type: **Japan**: Hokkaido Prefecture, Kushiro Subprefecture, Akan, on *Pilea mongolica*, 17 Sep. 1933, *Ishizuka* (neotype [designated by Braun, 1981]: TNS-F-217952). Reference sequences: LC010059 (ITS); LC010058 (28S) [**Japan**: Iwate Prefecture, Iwate-shi, Iwate University, Botanical Garden, on *Pilea pumila*, 21 Oct. 2003, *S. Takamatsu* (TNS-F-87908, previously TSU-MUMH2987)], Takamatsu et al. (2015).

≡ *E. pileae* (Jacz.) Bunkina, Komarovskie Chteniya (Vladivostok) 21: 72, 1974, nom. inval. (Art. 41.5).

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

Type: **Azerbaijan**: Absheron Peninsula, Botanical Garden, on *Punica granatum*, 15 Oct. 1964, *T.M. Achundov* (holotype: BAK; isotype: LE 34530). Reference sequence: MW581143 (ITS+28S) [**Montenegro**: on *P. granatum*, 1 Oct. 2010, *A. Bolay* (HAL 2441 F)], Bolay et al. (2021).

Notes: In the *RPB2* tree one specimen of *E. punicae* groups within the *E. hortensiae* clade (Suppl. Fig. 6). However, in the IGS tree, two specimens group separate to *E. hortensiae* (Suppl. Fig. 4). More collections or, preferably, ex-type sequences are needed to confirm its placement and ensure no contamination has occurred.

Erysiphe ruyongzhengiana S.R. Yu & S.Yan Liu, Mycoscience 63(4): 170, 2022.

Type: **China**: Jiangsu Province, Lianyungang City, Development District, Chaoyang Street, 34°36′16.7″ N 119°10′15.5″ E, on *Aristolochia debilis*, 4 Nov. 2020, *S.-R. Yu* (holotype: HMAS 0249832). Ex-holotype sequence: OM103692 (ITS+28S).

Erysiphe scholzii U. Braun & Bolay, in Bolay, Cryptog. Helv. 20: 71, 2005.

Type: **China**: Inner Mongolia, ca. 60 km ENE of Baotou and 50 km NE of Donghe, Jihuluntu Mountain of the Yin Shan mountain range, ca. 3 km NE of Wudang Lamasery, 40°47′ N, 110°35′ E, on *Incarvillea sinensis*, 31 Jul. 2004, *P. Scholz* (holotype: HAL 1825 F; isotypes: NCSLG28255, TNS-F-95697, U. Braun, Fungi Sel. Exs. 38, e.g., BPI 872125, GZU 000312228, HMAS, IMI, KR-M-0024042, KUS, LE, M−0019413, PDD 89295, VPRI). Ex-isotype sequence (BPI 872125): OR036317 (ITS+28S), Bradshaw et al. (2024a).

Erysiphe thuemenii U. Braun, in Braun and Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 412, 2012. [*E. thuemenii* U. Braun, Mycotaxon 18(1): 121, 1983, nom. inval. (Art. 41.5).]

Replaced synonym: *Erysiphe lamprocarpa* f. *potentillae-bifurcae* Thüm., Mycoth. Univ. 2056, 1881.

Type: **Russia**: Krasnoyarsk Krai, Minusinsk, on *Sibbaldianthe bifurca* (≡ *Potentilla bifurca*), Oct. 1880, *N. Martianoff* [= *N.M. Martyanov*], [Thüm., Mycoth. Univ. 2056 p.p.] Reference sequences: PP975471 (IGS), PP968447 (ITS+28S) [**China**: Inner Mongolia, Hohot City, Arboretum, on *Potentilla supina*, 2003, *T.Z. Liu* (CFSZ 03092)], unpublished.

≡ *E. communis* f. *potentillae* Jacz., Karm. Opred. Grib. Vip. 2 Muchn.-rosj. griby: 285, 1927, nom. illegit. (Art. 52.1).

Notes: The nomenclature of this name is complicated by the earliest name, *E. lamprocarpa* f. *potentillae-bifurcae* Thüm., long having been considered a *nomen nudum*. Further complicating matters, Mycotheca Universalis 2056 must have been a mixed collection; Jaczewski (1927) clearly described an *Erysiphe* from his piece, but most apparently bear only type material of *Sphaerotheca aphanis* var. *hyalina* U. Braun (Braun, 1983; Braun and Cook, 2012). As a name is already available for the latter taxon, we propose to fix the application of *E. thuemenii* to the *E. aquilegiae* complex fungus by lectotypification of *E. lamprocarpa* f. *potentillae-bifurcae* with a specimen of Mycoth. Univ. 2056 containing the *Erysiphe*. It can be assumed that such duplicates, available to Jaczewski, are preserved at LE and/or LEP, but a formal lectotypification must be postponed until corresponging material has been traced and re-examined.

Oidium bignoniae Jacz., Ezheg. Svěd. Bolězny. Povrezhden. Kul't. Dikorast. Polezn. Rast. 5: 247, 1910 [1909].

Type: **Ukraine**: Crimea, Yalta, Nikitsky Botanical Gardens, on *Bignonia catalpa* [= *Catalpa bignonioides*], 1909, *Novikov* (holotype: LEP). Reference sequences: KY786660 (*actin*), KY653194 (ITS+28S) [**UK**: Reading, University of Reading, Campus Central, Whiteknights, 51°26′25.1″ N 0°56′39.8″ W, on *Catalpa bignonioides*, 5 Jul. 2015, *O. Ellingham* (RNG OE2016PMCS16)], Ellingham (2017).

Oidium boroniae Crooks, Proc. Roy. Soc. Victoria N.S. 47(2): 366, 1935.

Type: **Australia**: Victoria, Healesville, on *Boronia megastigma*, Sep. to Oct. 1933, *K.M. Crooks* (lectotype [designated here, MycoBank: MBT10028415]: Crooks (1935) unnumbered fig. on page 366, original drawing). Reference sequence: LC010093 (ITS+28S) [**Australia**: Tasmania, on *B. megastigma* (VPRI18337)], Takamatsu et al. (2015).

≡ *P. boroniae* (Crooks) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 599, 2012.

Oidium goosii Bappamm., Hosag. & Udaiyan, New Botanist, Int. Quart. J. Pl. Sci. Res. 22(1–4): 125, 1995.

Type: **India**: Tamil Nadu, Nilgiris, Doddabetta, on *Passiflora calcarata* [= *Passiflora subpeltata*], 20 Jan. 1993, *A. Subbarayan* (holotype: HCIO 41324).

Notes: Braun and Cook (2012) reduced the name *O. goosii* to synonymy with *P. passiflorae* suggesting that this species pertains to the *E. aquilegiae* complex. However, this synonymy requires confirmation by multilocus sequencing.

Oidium vincae Bolay, Cryptog. Helv. 20: 109, 2005.

Type: **Switzerland**: Geneva, Botanical Garden, on *Vinca minor*, 16 Oct. 1995, *A. Bolay* (holotype: G00266076). Reference sequence: LC009903 (ITS+28S) [**Ukraine**: on *V. minor* (KW58396)], Takamatsu

et al. (2015).

≡ *Pseudocercospora vincae* (Bolay) Bolay, in Braun and Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 621, 2012.

3.2.4.2. Additional hosts assigned to E. aquilegiae s. lat. (complex) based on ITS(+28S) sequences. Apocynaceae: *Catharanthus roseus* [≡ *Vinca rosea*] (Liberato and Cunnington, 2006).

Casuarinaceae: *Casuarina cunninghamiana* (Wolcan et al., 2012; Bradshaw et al., 2020).

Convolvulaceae: *Calystegia* sp. (Bradshaw et al., 2020).

Crassulaceae: *Cotyledon orbiculata*, *Dudleya palmeri*, *Echeveria gibbiflora* (Bradshaw et al., 2020), *Crassula ovata* (Götz et al., 2019), *Kalanchoe* [*blossfeldiana*, *daigremontiana*, *delagoensis*, *laetivirens*, *pinnata*, *thyrsiflora*] (Götz et al., 2019; Yeh et al., 2025, as *E. sedi*; note: *Kalanchoe* sp. has been confirmed as host of *E. hortensiae*, so that probably all records on diverse *Kalanchoe* spp. pertain to the latter species), *Orostachys japonica* (Cho et al., 2016a).

Euphorbiaceae: *Excoecaria cochinchinensis* (Xu et al., 2020).

Fabaceae: *Arachis pintoi* (Kelly et al., 2025), *Cassia fistula* (Kiss et al., 2020), *Senna bicapsularis* (Mukhtar et al., 2019).

Hydrangeaceae: *Hydrangea serrata* (Cho et al., 2018).

Lamiaceae: *Ocimum basilicum* (Bradshaw et al., 2020), *Scutellaria barbata* (Yeh et al., 2025, as *E. hommae*).

Moringaceae: *Moringa oleifera* (Liu et al., 2019).

Myrtaceae: *Eucalyptus* [*grandis*, *urophylla*, and their hybrids] (Zhu et al., 2023).

Papaveraceae: *Macleaya microcarpa* (Bradshaw et al., 2020; Kruse et al., 2025).

Plantaginaceae: *Veronica urticifolia* (present work, HAL 559 F).

Ranunculaceae: *Actaea simplex*, *Aquilegia buergeriana* (Cho et al., 2016b), *Caltha palustris*, *Nigella damascena*, *Ranunculus* [*asiaticus*, *japonicus*, *peduncularis*] (Cunnington et al., 2004; Takamatsu et al., 2015)).

Rosaceae: *Potentilla supina* (Bolay et al., 2021).

Sapindaceae: *Cardiospermum halicacabum* (Hsiao et al., 2022).

Saxifragaceae: *Astilbe* × *rosea* [= *Astilbe* × *arendsii*] (Bradshaw et al., 2020), *Saxifraga stolonifera* (Takamatsu et al., 2015).

Solanaceae: *Datura* sp., *Nicotiana* [*plumbaginifolia, tabacum*] (Yeh et al., 2025), *Nierembergia* sp. (Takamatsu et al., 2015), *Solanum betaceum* (Hidayat et al., 2014).

Urticaceae: *Pellionia scabra*, *Pilea microphylla* (Yeh et al., 2025), as *E. pileae*.

Notes: The sequence KY653196 (deposited as '*Erysiphe simulans*' on *Rosa* sp., UK) clusters within the *E. aquilegiae* complex. The identification of this powdery mildew is likely incorrect. The true *E. simulans* pertains to the '*Uncinula* lineage' (Bradshaw et al., 2023). The sequence KY653196 is either the result of contamination, a host misidentification, or *E. aquilegiae* s. lat. is able to infect *Rosa* spp. A similar situation obtains for sequence OQ947649 (China, '*E. coriariigena*' on *Coriaria napalensis*, unpublished). *E. coriariigena* U. Braun & S. Takam. (≡ *Uncinula coriariae* R.Y. Zheng & G.Q. Chen) is also a species of the '*Uncinula lineage*.' It can be assumed that this sequence pertains to *E. coriariae*, a species of *E. aquilegiae* s. lat. It is possible this sequence came from a specimen co-infected by *E. coriariae* and *E. coriariicola*.

3.2.5. Affinity of Erysiphe tortilis (previously confused with E. aquilegiae)

Diverse host species of the genus *Cornus* are commonly infected by *E. aquilegiae* s. str. Co-infections by *E. aquilegiae* s. str. and *E. tortilis* occur frequently, which previously led to misinterpretations of sequence analyses (Bradshaw et al., 2020). *E. aquilegiae* s. str. produces only anamorphs on *Cornus* spp., whereas *E. tortilis* usually forms chasmothecia. Since all sequences previously retrieved from specimens identified as *E. tortilis* clustered within the *E. aquilegiae* clade, the wrong conclusion was drawn that *E. tortilis* must be part of the *E. aquilegiae* complex. This 'result' was considered rather unusual and odd, due to the *Microsphaera*-like morphology of the chasmothecial appendages of *E. tortilis* (Bradshaw et al., 2020). In the latter publication, an epitype with 'ex-epitype' sequence was designated. The epitype is a specimen with typical *E. tortilis* chasmothecia, so that this epitypification holds true despite the wrong 'ex-epitype' sequence being published. Meanwhile, further attempts to retrieved sequences of the true *E. tortilis* have successfully been made, which helped to clarify the true phylogenetic affinity of this species. In our concatenated tree, based on multilocus analyses, the genuine *E. tortilis* forms a strongly supported clade distant from the *E. aquilegiae* complex (Fig. 2).

E. tortilis (Wallr.) Link (as '*Erysibe*'), in Willdenow, Sp. pl. 6(1): 111, 1824.

Basionym: *Alphitomorpha tortilis* Wallr., Verh. Ges. Naturf. Freunde Berlin 1: 35, 1819.

Type: **Germany**: On *Cornus sanguinea*, herb. Wallroth, without any further data (lectotype [designated by Braun and Cook, 2012]: STR); **Germany**: Saxony, Annaberg-Buchholz, on *C. sanguinea*, 20 Oct. 1986, *W. Dietrich* (epitype [designated by Bradshaw et al., 2020]: HAL 231 F; isoepitype: NCSLG25190). Ex-epitype sequences: OR045071 (*CAM*), OR045137 (*GAPDH*), OR045197 (*GS*), OR036333 and MT524082 (ITS+28S).

4. Discussion

The *E. aquilegiae* complex is highly relevant to applied plant pathology and plant protection, particularly because it includes economically significant hosts. The broad scope of the *E. aquilegiae* complex was presented in the comprehensive phylogenetic study of *Erysiphe* species by Takamatsu et al. (2015), which demonstrated that ITS (+28S) sequences alone are insufficient for reliable species-level resolution within this group. The concepts of *E. aquilegiae* and its circumscriptions differed widely, from broader approaches considering *E. aquilegiae* as a circumglobal species with a wide host range (Liberato and Cunnington, 2006) to the long-prevailing opinion that this complex might be comprised of multiple cryptic species that simply require multilocus analyses to be detected and confirmed (Shin et al., 2019; Bradshaw et al., 2020, 2024a). Our current multilocus analyses of taxa assigned to this complex was undertaken to fill this gap of knowledge. The analyses revealed that certain genes are optimal and required for resolution of the different taxa involved. Furthermore, previous assumptions that multilocus analyses with a sufficiently large number of genes would improve resolution and support the division of the *E. aquilegiae* complex into many species were not confirmed. However, our multilocus analyses showed that this complex could be split into two large clades that represent two circumglobal species with wide host ranges: *E. aquilegiae* s. str. (emend.) and *E. hortensiae*. The two species are hypothesized to be phylogenetically young, meaning they are still undergoing speciation and exhibit continually expanding host ranges. The composition of these taxa as complex assemblages of both broad-host-range and specialized races was anticipated and is supported by the present analyses. Based on current results, the previously assumed division of *E. aquilegiae* s. lat. into multiple narrowly host-specific species cannot be maintained.

As indicated by the available sequence data, *E. aquilegiae* s. str. (emend.) and *E. hortensiae* are cosmopolitan or nearly cosmopolitan species, with *E. aquilegiae* clearly exhibiting the broader host range. The host ranges of the two species are characterized by interesting differences, at least as to the currently phylogenetically confirmed hosts. Plant species belonging to the *Ranunculaceae* are common hosts of *E. aquilegiae* s. str., but are lacking as hosts of *E. hortensiae*. In contrast, many species of diverse crassulaceous and solanaceous genera are common hosts for *E. hortensiae*, previously assigned to *E. sedi* and *E. neolycopersici*, respectively, which also applies to sequences retrieved from powdery mildew on *Hydrangea macrophylla*, the type host of *E. hortensiae*. Sequences obtained from all these hosts exclusively cluster within the *E. hortensiae* clade. These results suggest clear host preferences of the two species, although both taxa are capable of infecting a wide diversity

of hosts.

Whipps et al. (1998) carried out the most comprehensive inoculation experiments based on the tomato powdery mildew until recently referred to as *E. neolycopersici*. They confirmed a wide range of hosts susceptible to the tomato powdery mildew, including diverse solanaceous hosts, such as *Nicotiana* spp., *Solanum lycopersicum*, and *S. melongena* amongst the most sensitive hosts (group 3), as well as *Datura*, *Petunia*, and *Physalis* spp., and *S. tuberosum* as less sensitive hosts (group 1 and 2). Publications dealing with the wide host range of the tomato powdery mildew amongst other solanaceous hosts are numerous (Fletcher et al., 1988; LaMondia et al., 1999; Lebeda and Mieslerová, 1999; Huang et al., 2000; Mieslerová et al., 2000; Kashimoto et al., 2003; Hidayat et al., 2014; Fu et al., 2015; Liu et al., 2019; Xu et al., 2020). *Phedimus spurius* (≡ *Sedum spurium*), previously assigned as a host of *E. sedi*, and *Sesamum indicum* (*E. pedaliacearum*) were also found to be highly susceptible to the tomato powdery mildew in these inoculation experiments. These results are in line with our phylogenetic multilocus examinations in which such hosts pertained to the host range of *E. hortensiae*. Other hosts susceptible to the tomato powdery mildew, such as *Abelmoschus*, *Manihot*, and *Linum perenne*, suggest the possible synonymy of previously introduced powdery mildew species, such as *E. abelmoschicola* and *E. lini* (respectively Tanda and Hirose, 2003), with *E. hortensiae*. Similarly, the susceptibility of *Mallotus japonicus* (Nonomura et al., 2013) to tomato powdery mildew suggests the synonymy of *E. malloti* Y. Nomura & Tanda (Nomura and Tanda, 1985) with *E. hortensiae*. Highly sensitive cucurbitaceous host species, e.g., *Cucurbita melo*, *C. pepo*, *C. sativa*, *Cyclanthera pedata*, and *Lagenaria siceraria* within susceptibility group 2 and 3 let us assume that *E. actinostemmatis*, described from Japan on *Actinostemma lobatum*, might be a synonym of *E. hortensiae* as well. The transferability of the results of inoculations tests performed by Whipps et al. (1998) in greenhouse experiments to natural field conditions has been called into question (Jankovics et al., 2008; Bradshaw et al., 2020), but in the light of the results of the present multilocus analyses, a high degree of plurivory within the *E. aquilegae* complex appears to be the case and is supported by observations of an increasing number of spontaneous infections of unusual new hosts ('singleton infections'), such as *Astilbe* × *rosea* (= *Astilbe* × *arendsii*) found in a garden centre in Germany (Bradshaw et al., 2020) or *Erysiphe* sp. (*E. aquilegiae* complex) on the apocynaceous host *Araujia sericifera*, which was first collected and sequenced (ITS) in Australia by Southwell et al. (2018), and confirmed as *E. aquilegiae* s. str. based on multilocus analyses of a specimen collected in California in the course of the present examinations. To the best of our knowledge, cross-inoculation experiments between hydrangea and tomato powdery mildew have not yet been conducted. Future research will need to incorporate multilocus sequencing and controlled inoculation assays to determine whether these pathogens represent the same or distinct taxa and, consequently, whether a new forma should be proposed for the tomato powdery mildew. It is important to note, however, that strains of tomato powdery mildew may vary in their host range, which could lead to differing outcomes in cross-inoculation studies. For example, we observed minor genetic differences among the tomato powdery mildew strains examined in the *GS*, *CAM*, and *TUB* loci, indicating potential strain-level diversity that may relate to host specificity.

An additional outcome of the recently performed phylogenetic examinations of the *E. aquilegiae* complex lies in the detection of multiple highly supported species belonging to the *E. aquilegiae* complex (s. lat.), which group outside of the *E. aquilegiae* s. str. and *E. hortensiae* clades and constitute separate species in basal position. This group of outliers comprises the North American *E. aquilegiae-coeruleae* on *Aquilegia coerulea*, the widespread *E. nitida* on *Aconitum* and *Delphinium* species, the North American *E. parnassiae* on *Parnassia* spp., *E. thalictri* on *Thalictrum* spp. in North America, the Asian *E. santali* on *Santalum album*, and three Asian species on diverse *Clematis* species (*E. clematidicola* sp. nov. in Japan, *E. clematidis* in China, and *E. clematidis-montanae* sp. nov. in Pakistan).

The new North American species *E. aquilegiae-coeruleae* and *E. thalictri* occur on hosts of two genera, *Aquilegia* and *Thalictrum*, respectively, of the derived subfamily *Thalictroideae* within the *Ranunculaceae* (Wang et al., 2009). The previously described *E. nitida* was reintroduced for species on *Aconitum* and *Delphinium* (*Ranunculaceae* subgen. *Ranunculoides* tribe *Delphinieae*), which was confirmed as species outside of the *E. aquilegiae* complex in our molecular ITS+28S as well as multilocus analyses. The first indication that *Erysiphe* on *Delphinium* spp. might be a separate species goes back to Cunnington et al. (2004) who revealed that it represents a host-specialized taxon in RFLP and sequence analyses. Furthermore, the ITS+28S as well as multilocus analyses revealed an Asian complex of *Erysiphe* species on Asian *Clematis* spp., comprised of *E. clematidicola*, *E. clematidis* (Zhang et al., 2025), and *E. clematidis-montanae*. Together with *Anemone*, the genus *Clematis* belongs to tribe *Anemoneae* within the family *Ranunculaceae* (Wang et al., 2009). The three Asian *Erysiphe* species on *Clematis* are not only phylogenetically closely allied, but also morphologically rather similar by forming chasmothecia with colourless or almost colourless appendages, sparingly septate, (i.e., with only few widely spaced septa), occasionally apically irregularly to almost dichotomously branched, which is in clear contrast to pigmented, usually unbranched, pluriseptate chasmothecial appendages in specimens of *E. aquilegiae* s. str. on *Clematis* spp. The relatively large number of species on ranunculaceous hosts, close to but outside of the *E. aquilegiae* complex and highly supported in ITS+28S as well as multilocus analyses, suggests that the latter complex evolved from phylogenetically ancestral, specialized *Erysiphe* species, confined to hosts of the ranunculaceous subfamilies *Ranunculoideae* and *Thalictroideae*, by widening the host ranges. Within subfamily *Ranunculoideae*, the ancestral, separate species are confined to tribe *Anemoneae* and tribe *Delphinieae*. These circumstances suggest clear tendencies of co-evolution between *Erysiphe* spp. of the *E. aquilegiae* complex and hosts of the *Ranunculaceae*, although, despite the enormous progress in the phylogeny of the latter plant family, the phylogenetic relationships among the tribes of subfamy *Ranunculoideae* are still insufficiently resolved (Zhai et al., 2019).

During this study, the question arose as to whether cryptic species or specialized races exist within *E. aquilegiae* s. str. and *E. hortensiae*, and whether these can be formally described. The further splitting of *E. hortensiae* at the species level can be ruled out based on previous biological inoculation experiments (Whipps et al., 1998) and the current phylogenetic multilocus examinations. The case with *E. aquilegiae* s. str., with its enormous host range, is less clear. The present multilocus analyses support treating *E. aquilegiae* s. str. as a single species encompassing both broad-host-range lineages and more specialized forms. Evidence for such specialized forms appears in both individual loci and multilocus datasets. The criteria for recognizing these forms have been previously outlined (Bradshaw et al., 2025a; Feng et al., 2025), and are consistent with the treatment of genetically validated biological forms presented in Bradshaw et al. (2025a) as formae of *E. vaccinii*. This taxonomic rank is recommended for comparable biological forms within the *E. aquilegiae* complex—though the two cases are not entirely analogous. The criteria for introducing new formae, as outlined in Bradshaw et al. (2025a), currently preclude the formal naming of genetically defined biological forms within this complex. One major concern is that genetic groupings observed in multilocus analyses may reflect population structure rather than true taxonomic boundaries. To avoid such misinterpretations, broad and representative sampling across diverse geographic regions is essential—particularly for widespread taxa, including those with intercontinental distributions or broad host ranges. Robust conclusions require extensive sampling and large sequence datasets. Additionally, the designation of formae should be grounded in multilocus analyses, as effectively demonstrated for *E. vaccinii* by Bradshaw et al. (2025a). We have established epitypes for *E. hortensiae* (including a potential "f. *hortensiae*" as prospective autonym) and

E. aquilegiae (including a potential "f. *aquilegiae*" as prospective autonym) to provide a baseline for future research introducing additional formae for these species.

CRediT authorship contribution statement

Michael Bradshaw: Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Uwe Braun:** Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Márk Z. Németh:** Writing – review & editing, Funding acquisition, Formal analysis, Data curation. **Andrew Paul:** Methodology, Formal analysis. **James K. Mitchell:** Writing – review & editing, Methodology, Formal analysis. **Uma Crouch:** Writing – review & editing, Methodology. **Jackie Thomas:** Data curation. **Bailey Pelt:** Data curation. **Susumu Takamatsu:** Writing – review & editing, Methodology, Data curation. **Julia Kruse:** Writing – review & editing, Methodology, Data curation. **Volker Kummer:** Writing – review & editing, Data curation. **Diána Seress:** Funding acquisition, Data curation. **Donald H. Pfister:** Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the curatorial team at FH (Michaela Schmull, Hannah Merchant, Genevieve E. Tocci, and Allen W. Milby) for helping with the herbarium specimens. We would like to thank the curation teams at BP, BPI, HAL, MUMH, NEBC, TNS, and WIS for filling our large and complex specimen requests. We would also like to thank the Daniel E. Stuntz Memorial Foundation, the Puget Sound Mycological Society, and the Sonoma County Mycological Association for funding this research. Additionally, we would like to thank the National Science Foundation, Award Number 2402193 for funding this research. This work was also supported by the Research Capacity Fund (HATCH), project award no. 7006142, from the U.S. Department of Agriculture's National Institute of Food and Agriculture. Project no. NKFIH FK142735 has been implemented with the support provided by the Ministry of Culture and Innovation of Hungary from the National Research, Development and Innovation Fund. The work of MZN was supported by the EKOP-24 University Excellence Scholarship Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funbio.2026.101717.

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