

# Taxonomy, Phylogeny, and Host Expansion of Powdery Mildew Fungi Parasitic to *Veronica* Species

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## ABSTRACT

Powdery mildew is a prevalent fungal disease that affects various *Veronica* spp. (Plantaginaceae), caused by species in the genera *Podosphaera* and *Golovinomyces* (Erysiphales). There have been recent taxonomic changes in these groups and ongoing disease occurrence on a range of *Veronica* species previously unrecognized as hosts; however, the pathogen found in Korea remains unidentified. This study aimed to identify the causative agent of powdery mildew on *Veronica* spp. in Korea through molecular phylogenetic analysis of internal transcribed spacer (ITS) and large subunit (LSU) sequences of rDNA and morphological examination. Our study identified *Golovinomyces bolayi* as the sole pathogen affecting all nine *Veronica* species in Korea and confirmed that *G. cichoracearum* s. str., which was previously identified as the pathogen, was not the causal agent. These results expand the known host range of *G. bolayi*, including the addition of five *Veronica* species in Korea: *V. hederifolia*, *V. kiusiana* var. *glabrifolia*, *V. longifolia*, *V. polita*, and *V. serpyllifolia*. Notably, *V. kiusiana* has been added as a new global host of powdery mildew. These findings substantially enhance our understanding of the taxonomy of powdery mildew pathogens on *Veronica* species and provide valuable insights into their evolutionary host expansion.

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## 1. Introduction

*Veronica*, commonly known as speedwell, is the largest genus within the family Plantaginaceae, containing approximately 450 species [1]. They originated in the temperate and Arctic regions of the Northern Hemisphere and are particularly diverse in Asia, Europe, and New Zealand, with many native species [2]. These plants are widely grown for ornamental and medicinal purposes in these regions, reflecting their climatic and environmental adaptability [3]. Despite their global prevalence and ecological significance, *Veronica* species are increasingly susceptible to various fungal and oomycete diseases [4], among which powdery mildews pose a significant threat to many species.

Powdery mildew occurrence on *Veronica* species is widespread, with reports from various regions of Europe, Asia, North America, and Oceania [4,5]. Historically, this has been attributed to six powdery mildew fungi (Erysiphales) (Table 1): *Podosphaera fuliginea* (Schltld.) U. Braun & S. Takam. (syn. *Sphaerotheca fuliginea* (Schltld.) Pollacci), *Oidium* sp., *Golovinomyces asperifoliorum* (Grev.) U. Braun &

H.D. Shin (syn. *Erysiphe asperifoliorum* Grev.), *G. cichoracearum* (DC.) Heluta (syn. *E. cichoracearum* DC.), *G. orontii* (Castagne) Heluta (syn. *E. orontii* Castagne and *E. polyphaga* Hammarl.), and *G. bolayi* S. Takam., Lebeda & M. Götz. [4]. Among these, *P. fuliginea* is frequently reported across North America, Asia, and Europe [5]. However, recent studies have reported *G. cichoracearum* as a powdery mildew pathogen of *Veronica* [9, 24, 26], in many countries, including Korea [32]. The taxonomy of both aforementioned pathogens in relation to *Veronica* species assumes that powdery mildews have a broad host spectrum across plant families; however, this leads to an incomplete understanding of their diversity and host specificity.

In Korea, 43 species of *Veronica* have been recorded, on which three fungal and oomycete diseases (powdery mildew, downy mildew, and leaf blight) have often been reported [33]. Four *Veronica* species (*V. arvensis*, *V. linariifolia*, *V. persica*, and *V. rotunda* var. *subintegra*) are documented as hosts of powdery mildew caused by *G. cichoracearum* s. lat. [10, 32]. However, the identification

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**Table 1.** Powdery mildew fungi previously recorded on *Veronica* species.

Host plant	Powdery mildew species	Geographic origin [reference]	
<i>Veronica arvensis</i>	<i>Erysiphe asperifoliorum</i> (= <i>Golovinomyces asperifoliorum</i> )	Scotland [6]	
	<i>E. cichoracearum</i> (= <i>G. bolayi</i> ?)	France [6], Japan [7], New Zealand [7], Scotland [8]	
	<i>G. bolayi</i>	Japan [9]	
	<i>G. cichoracearum</i>	Korea [10]	
	<i>G. orontii</i> (= <i>G. bolayi</i> ?)	Japan [11,12], Switzerland [13]	
	<i>Oidium</i> sp.	New Zealand [9]	
	<i>Podosphaera fuliginea</i>	Asia [5], Europe [5], North America [5]	
	<i>Sphaerotheca fuliginea</i> (= <i>Podosphaera fuliginea</i> )	Germany [7], Italy [7], Japan [7]	
	<i>Sphaerotheca fuliginea</i> var. <i>fuliginea</i> (= <i>P. fuliginea</i> )	Germany [14], Italy [14]	
	<i>V. hederifolia</i>	<i>E. cichoracearum</i> (= <i>G. bolayi</i> ?)	Russia [7]
		<i>P. fuliginea</i>	Asia [5], Europe [5], North America [5]
		<i>S. fuliginea</i> (= <i>P. fuliginea</i> )	Finland [7], Hungary [7], Italy [7]
	<i>V. kiusiana</i> var. <i>glabrifolia</i>	Unknown as a host plant of powdery mildew	
<i>S. fuliginea</i> (= <i>P. fuliginea</i> )		Finland [14], Hungary [14], Italy [14]	
<i>V. linariifolia</i>	<i>S. fuliginea</i> var. <i>fuliginea</i> (= <i>P. fuliginea</i> )	No country data [7]	
	<i>G. cichoracearum</i>	Estonia [14]	
<i>V. longifolia</i>	<i>E. cichoracearum</i> (= <i>G. bolayi</i> ?)	Korea [10]	
	<i>Erysiphe communis</i>	Poland [2, 7], Russia [7]	
	<i>E. orontii</i> (= <i>G. bolayi</i> ?)	Russia [7]	
	<i>E. polyphaga</i> (= <i>G. bolayi</i> ?)	Poland [14,15], Russia [14]	
	<i>P. fuliginea</i>	Switzerland [7]	
	<i>S. fuliginea</i> (= <i>P. fuliginea</i> )	Russia [16], Switzerland [13], Ukraine [17]	
		Canada [18], Estonia [19], Finland [20], Germany [6], Poland [15, 21]	
	<i>S. fuliginea</i> f. <i>veronicae</i>	Russia [22]	
	<i>S. fuliginea</i> var. <i>fuliginea</i> (= <i>P. fuliginea</i> )	Austria [14], Belgium [14], Czech Republic [14], Denmark [14], Finland [14], France [14], Germany [14], Netherlands [14], Norway [14], Poland [14], Romania [14], Sweden [14], Switzerland [14], United Kingdom [14], Russia [14]	
	<i>V. persica</i>	<i>E. cichoracearum</i> (= <i>G. bolayi</i> ?)	New Zealand [8, 23]
		<i>G. bolayi</i>	China [24], Iran [25]
<i>G. cichoracearum</i> (= <i>G. bolayi</i> ?)		China [26], Korea [10]	
<i>G. orontii</i> (= <i>G. bolayi</i> ?)		Switzerland [13]	
<i>Oidium</i> sp.		Australia [7], Germany [7], Switzerland [7]	
<i>P. fuliginea</i>		Argentina [27]	
<i>S. fuliginea</i> (= <i>P. fuliginea</i> )		Germany [28], Sweden [7]	
<i>V. polita</i>	<i>S. fuliginea</i> var. <i>fuliginea</i> (= <i>P. fuliginea</i> )	Germany [14], Sweden [14]	
	<i>S. macularis</i> (= <i>P. macularis</i> )	Japan [7]	
	<i>Oidium erysiphoides</i> (= <i>G. biocellulatus</i> )	Spain [29]	
	<i>Oidium</i> sp.	Spain [7]	
	<i>P. fuliginea</i>	Asia [5], Europe [5], North America [5]	
	<i>S. fuliginea</i> (= <i>P. fuliginea</i> )	Finland [7], Poland [7, 15]	
<i>V. rotunda</i> var. <i>subintegra</i>	<i>S. fuliginea</i> var. <i>fuliginea</i> (= <i>P. fuliginea</i> )	Finland [14], Poland [14]	
	<i>G. cichoracearum</i>	Korea [10]	
<i>V. serpyllifolia</i>	<i>E. polyphaga</i> (= <i>G. bolayi</i> ?)	Switzerland [7]	
	<i>P. fuliginea</i>	Asia [5], Europe [5], North America [5]	
	<i>S. fuliginea</i> (= <i>P. fuliginea</i> )	Poland [30]	
	<i>S. fuliginea</i> var. <i>fuliginea</i> (= <i>P. fuliginea</i> )	Estonia [14], Finland [14], France [14], Romania [14], Switzerland [14]	
	<i>S. humuli</i> (= <i>P. macularis</i> )	United States [31]	
	<i>S. macularis</i> (= <i>P. macularis</i> )	France [7]	
	<i>Sphaerotheca</i> sp. ( <i>Podosphaera</i> sp.)	Poland [15], Switzerland [7]	

relied solely on morphology, highlighting the need for reclassification based on molecular phylogenetic studies. In addition, powdery mildew symptoms have been observed on five *Veronica* species: *V. hederifolia*, *V. kiusiana* var. *glabrifolia*, *V. longifolia*, *V. polita*, and *V. serpyllifolia*, which have not been previously recorded as hosts of this disease in Korea.

Our study integrates extensive field surveys, morphological characterization, and molecular phylogenetic analysis to accurately identify powdery mildew samples on nine *Veronica* species in Korea, including five previously unrecorded species and four known host species and to infer

their evolutionary strategy for colonizing *Veronica* plants.

## 2. Materials and methods

### 2.1. Field survey

During the last 30 years, a comprehensive effort was made to collect a range of *Veronica* plants infected with powdery mildew in Korea. The collected specimens were deposited at the Korea University Herbarium (KUS-F) for preservation and examination. Each specimen was documented with detailed information regarding its collection site, date, host plant, and GenBank accession numbers, as outlined in Table 2.

**Table 2.** Powdery mildew specimens of *Veronica* species collected in Korea.

Host plant	Herbarium no.	Date	Geographic location	GenBank acc. no.	
				ITS	LSU
<i>V. arvensis</i>	KUS-F30934	May 9 2019	Naju	–	PP410278
	KUS-F30483	May 19 2018	Asan	PP410253	PP410279
	KUS-F29772	May 25 2017	Seogwipo	PP410252	PP410280
<i>V. hederifolia</i>	KUS-F29156	May 14 2016	Seoul	–	PP410268
	KUS-F33634	May 3 2023	Gwangju	PP410255	PP410276
	KUS-F33631	May 3 2023	Gwangju	PP410254	PP410277
<i>V. kiusiana</i> var. <i>glabrifolia</i>	KUS-F27762	October 19 2013	Gapyeong	PP410264	PP410272
	KUS-F27753	October 19 2013	Gapyeong	PP410260	PP410273
	KUS-F27040	October 3 2012	Gapyeong	–	–
	KUS-F26758	July 26 2012	Gapyeong	–	–
	KUS-F26391	November 3 2011	Osan	–	–
	KUS-F26310	October 13 2011	Gapyeong	–	–
<i>V. linariifolia</i>	KUS-F25908	July 6 2011	Gapyeong	–	–
	KUS-F19691	September 20 2003	Pyeongchang	–	–
<i>V. longifolia</i>	KUS-F14945	August 28 1998	Seoul	–	–
	KUS-F29267	June 28 2016	Daegu	PP410265	PP410266
<i>V. persica</i>	KUS-F25543	October 20 2010	Incheon	PP410262	PP410275
	KUS-F29718	November 29 2016	Jeju	PP410263	PP410281
	KUS-F29060	November 12 2015	Mokpo	PP410257	PP410269
	KUS-F28531	November 18 2014	Iksan	PP410256	PP410270
	KUS-F28507	November 10 2014	Daegu	PP410261	PP410271
	KUS-F33535	November 10 2022	Gochang	–	–
	KUS-F33371	October 16 2022	Jangsu	–	–
	KUS-F28588	December 9 2014	Jeju	–	–
	KUS-F28344	October 9 2014	Miryang	–	–
	KUS-F27258	November 25 2012	Jeju	–	–
	KUS-F25799	June 17 2011	Gyeongju	–	–
	KUS-F21613	October 29 2005	Jeju	–	–
	KUS-F19534	May 29 2003	Jinju	–	–
	KUS-F18099	November 12 2000	Wando	–	–
	KUS-F17988	October 29 2000	Jinju	–	–
	KUS-F15554	October 24 1998	Daegu	–	–
	<i>V. polita</i>	KUS-F15149	September 18 1998	Jinju	–
KUS-F14398		October 11 1997	Seoul	–	–
KUS-F12384		May 9 1993	Gangneung	–	–
KUS-F11597		May 17 1992	Gangneung	–	–
KUS-F26661		May 8 2012	Jeju	–	PP410274
KUS-F25629		November 8 2010	Busan	–	–
KUS-F21044		December 3 2004	Jeju	–	–
<i>V. rotunda</i> var. <i>subintegra</i>	KUS-F19522	May 28 2003	Jinju	–	–
	KUS-F19343	November 1 2002	Jeju	–	–
<i>V. serpyllifolia</i>	KUS-F11870	August 19 1992	Suwon	–	–
	KUS-F29231	June 13 2016	Mokpo	PP410259	PP410267

## 2.2. Morphological analysis

Morphological examinations of the dried herbarium specimens with powdery mildew infection were conducted. A piece of the infected leaves was mounted in lactic acid, and after heating gently, the mycelial mat was carefully scraped off and examined under a differential interference contrast microscope (Zeiss Imager M2 AX10; Carl Zeiss, Jena, Germany) equipped with an AxioCam 512 microscope camera (Carl Zeiss). At least 30 measurements were performed for each morphological structure.

## 2.3. Molecular phylogenetic analysis

DNA was extracted from the powdery mildew mycelia using the MagListo 5M Plant Genomic DNA Extraction Kit (Bioneer, Daejeon, South Korea). The internal transcribed spacer (ITS) and large subunit (LSU) regions of rDNA were amplified with primer sets PM10/ITS4 and PM3/TW14, respectively [34]. The PCR products were purified using the AccuPrep<sup>®</sup> PCR/

Gel Purification Kit (Bioneer) and sequenced bidirectionally using a DNA sequencing service (Macrogen, Seoul, South Korea) with the same primers used for the amplification. The resulting sequences were aligned with reference sequences of *Golovinomyces* species available in the GenBank database. Sequence editing and assembly were performed using the DNASTAR software package (Lasergen, Madison, WI). A phylogenetic tree was reconstructed using the minimum evolution method based on the Tamura-Nei model using MEGA 11 software [35]. To assess the reliability of the phylogenetic tree, the confidence level of each branch was evaluated using 1000 bootstrap replications.

## 3. Results

### 3.1. Seasonal powdery mildew occurrence on *Veronica* species in Korea

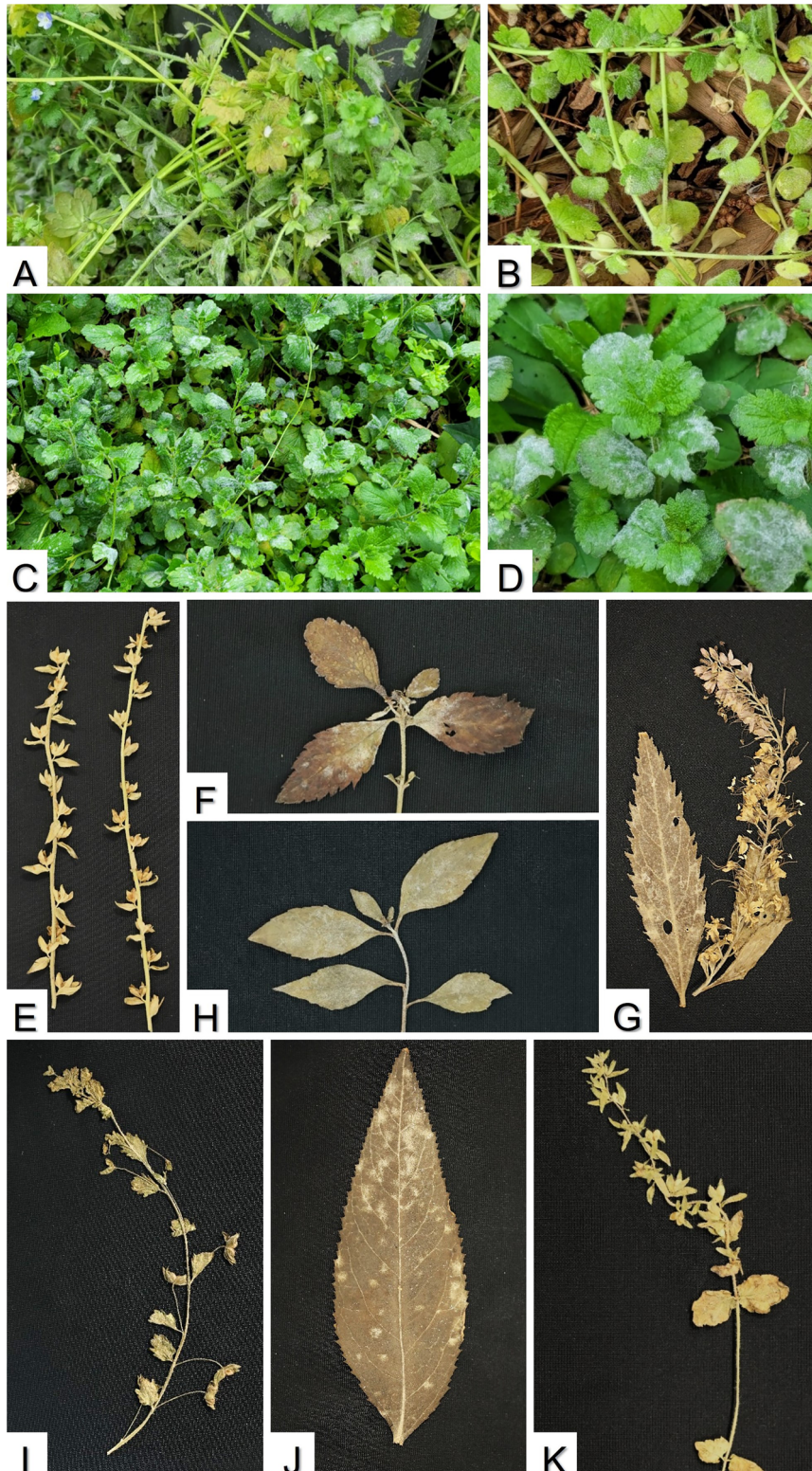
A total of 43 samples of nine *Veronica* species affected by powdery mildew have been collected from various regions of Korea since 1992. Powdery

mildew on the leaves of various *Veronica* plants begin to appear no earlier than May and persist until December (for detail information, see Table 2).

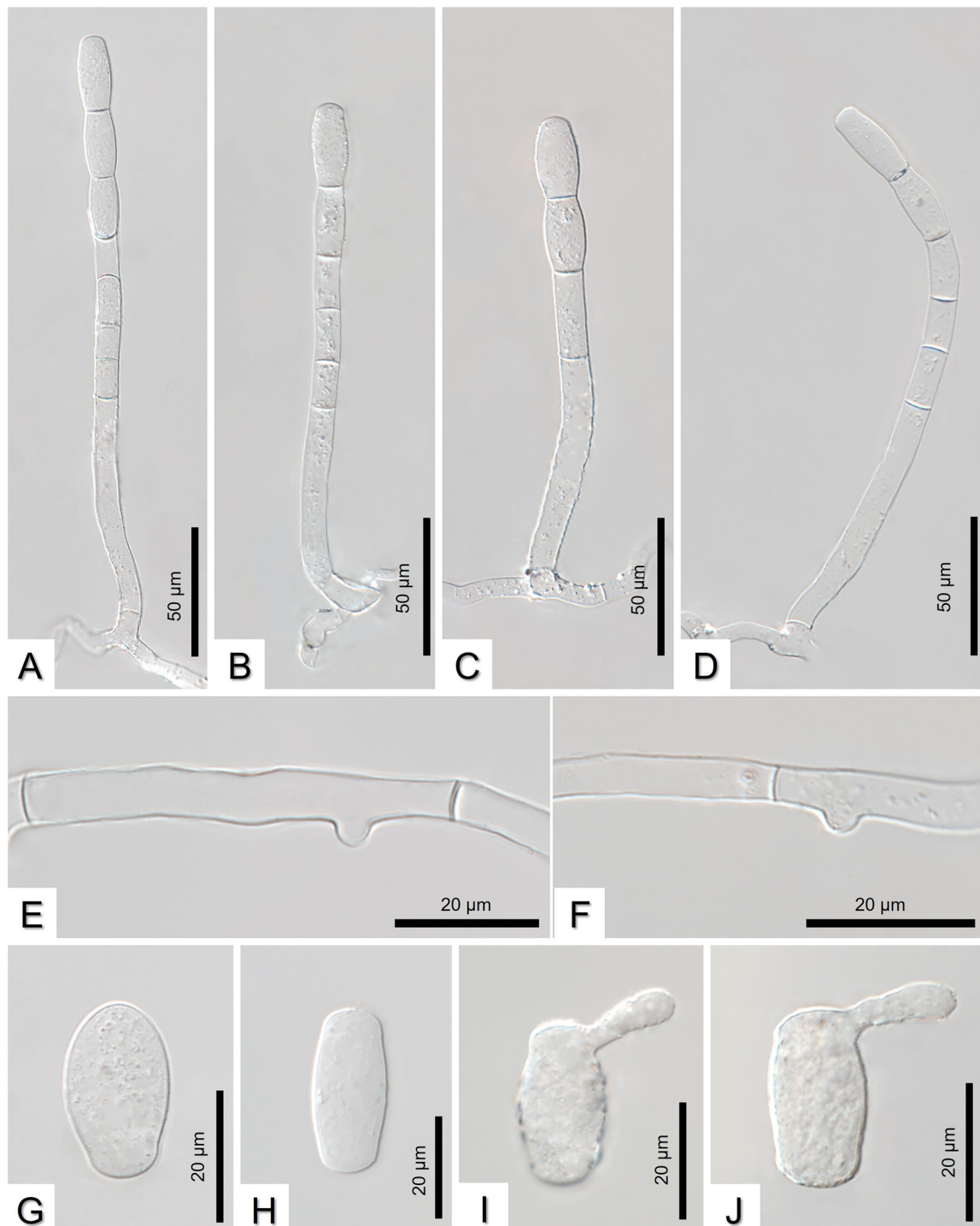
### 3.2. Morphology

Careful examination of the diseased *Veronica* spp. revealed typical symptoms of powdery mildew. The

infected leaves displayed round to irregularly shaped white patches, which infected the entire leaf and stem as the disease progressed (Figure 1). The fungal hyphae were straight to sinuous, in width of between 4.3 and 6.5  $\mu\text{m}$  (Figure 2). Hyphal appressoria were characterized as nipple-shaped and 4–6  $\mu\text{m}$  in diameter. Conidiophores were 144–292 (av. 176)  $\mu\text{m}$  and produced two to four immature conidia in



**Figure 1.** Powdery mildew symptoms on nine *Veronica* species. (A, B) *Veronica hederifolia*; (C, D) *V. persica*; (E) *V. arvensis*; (F) *V. kiusiana* var. *glabrifolia*; (G) *V. linariifolia*; (H) *V. longifolia*; (I) *V. polita*; (J) *V. rotunda* var. *subintegra*; (K) *V. serpyllifolia*.



**Figure 2.** Morphological characteristics of *Golovinomyces bolayi* on *Veronica hederifolia*. (A–D) Conidiophore; (E, F) Appressorium formed on a hypha; (G, H) Conidium; (I, J) Conidium with a germ tube.

a chain (catenescence), with a distinct sinuate outline. Foot cells of conidiophores were straight or curved at the basal cell, cylindrical, and  $48\text{--}136 \times 8\text{--}11$  (av.  $72 \times 9$ )  $\mu\text{m}$ . Conidia were ellipsoid-ovoid, doliiform to somewhat limoniform,  $25\text{--}35 \times 12\text{--}16$  (av.  $29 \times 14$ ) with a length-to-width ratio ranging from 1.6 to 2.7. These conidia lacked distinct fibrosin bodies, and their germ tubes typically arose in a subterminal position, indicative of the *Euoidium* type. No chasmothecia were observed. These

morphological characteristics are consistent with those of *Golovinomyces bolayi* [9].

### 3.3. Molecular phylogeny

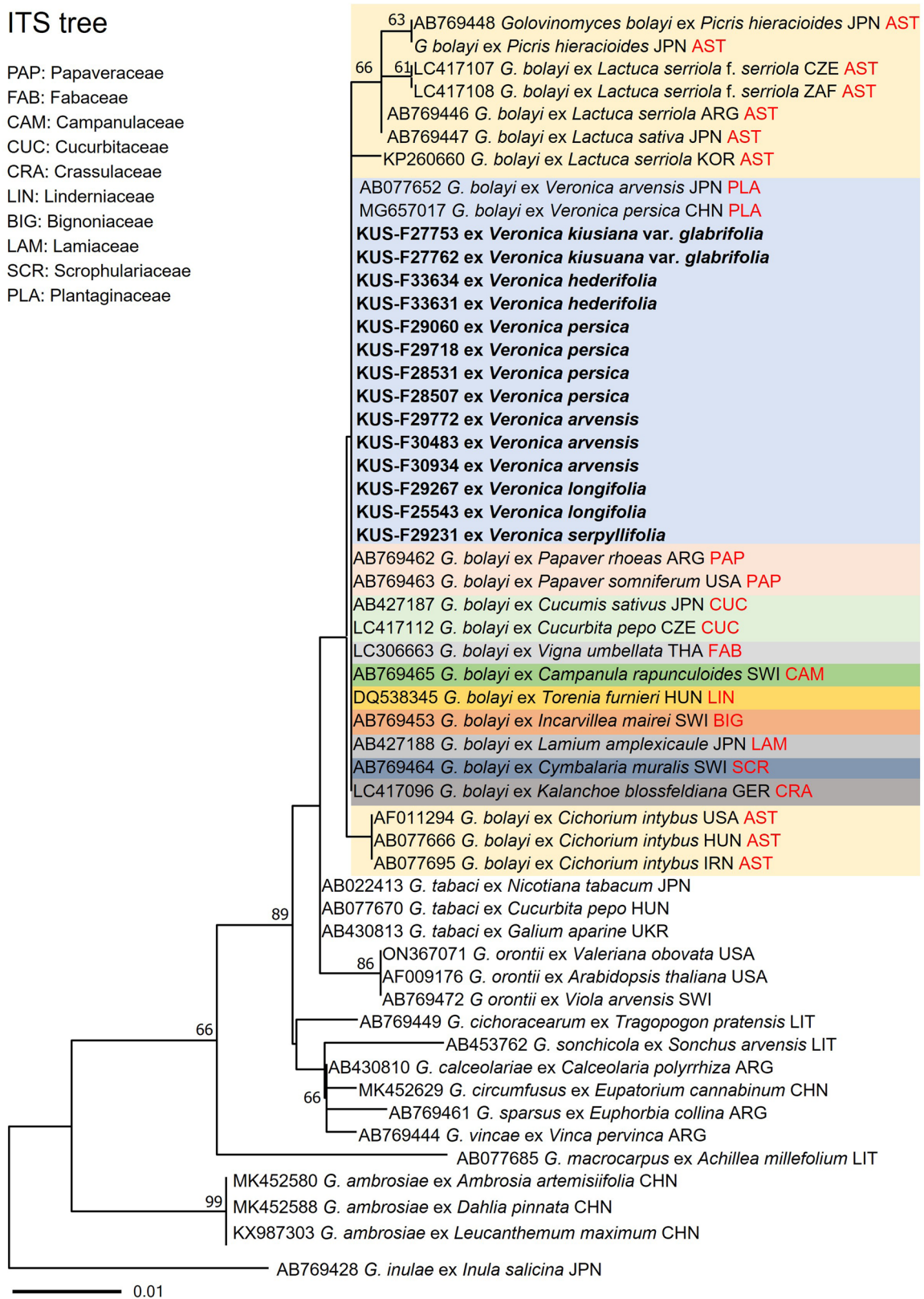
The molecular analysis yielded 14 ITS (511 bp) and 16 LSU (823 bp) sequences, with no nucleotide differences to each other. A BLASTn comparison of these sequences against the GenBank database showed that the ITS sequences shared 99.8–100%

similarity with the *G. bolayi* reference sequences (e.g., LC417096, LC417112, and LC417116), whereas the LSU sequences shared 100% similarity with *G. bolayi* sequences (e.g., AB427187, AB427188, AB769453, and AB769465). All newly obtained

sequences of ITS and LSU were deposited in GenBank (Table 2). Compared to *G. cichoracearum* s. str. (AB769449), the sequences shared similarities of 98.8% (502/508 bp) for ITS and 99.6% (819/822 bp) for LSU.

### ITS tree

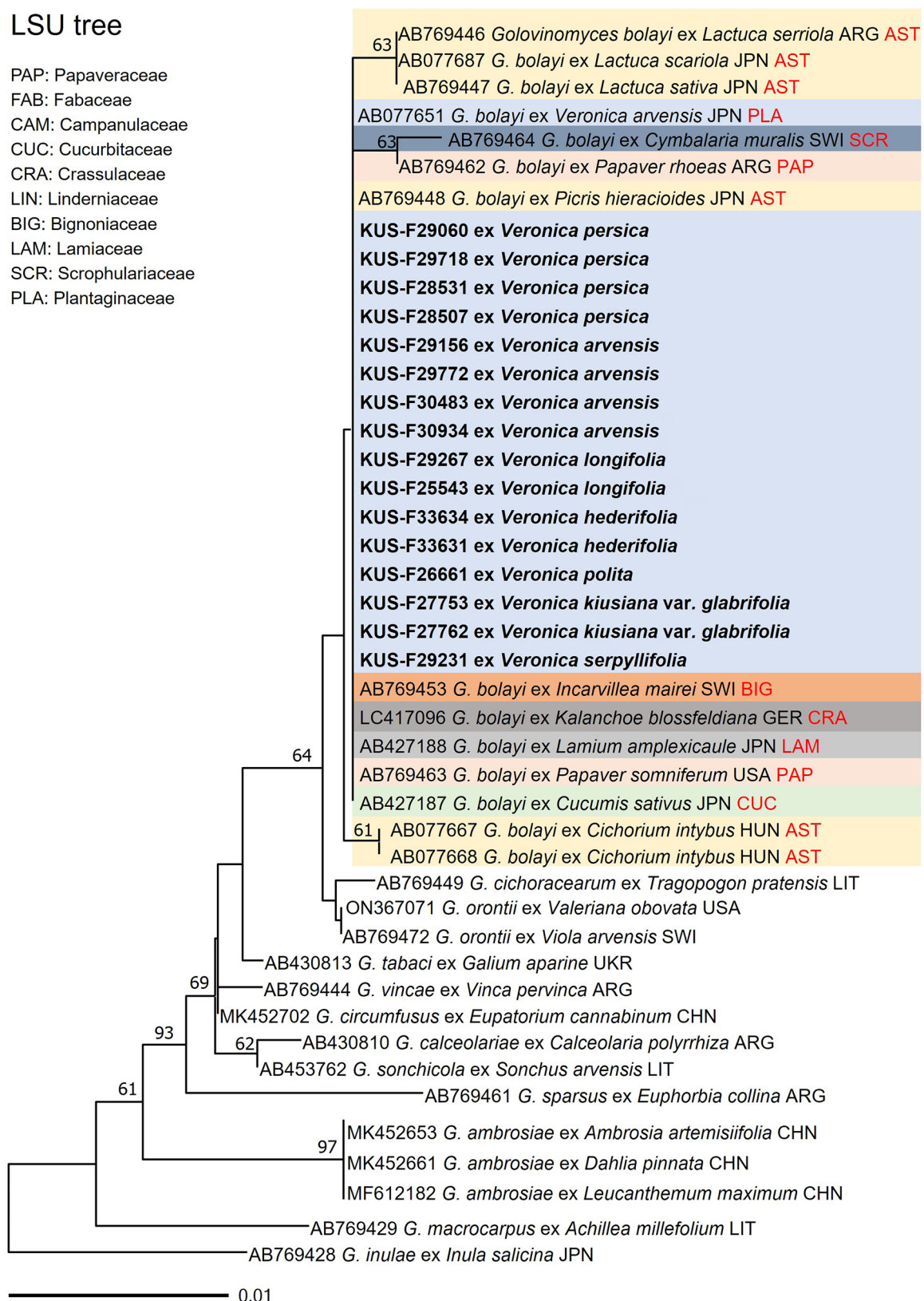
PAP: Papaveraceae  
 FAB: Fabaceae  
 CAM: Campanulaceae  
 CUC: Cucurbitaceae  
 CRA: Crassulaceae  
 LIN: Linderniaceae  
 BIG: Bignoniaceae  
 LAM: Lamiaceae  
 SCR: Scrophulariaceae  
 PLA: Plantaginaceae



**Figure 3.** Minimum evolution tree of *Golovinomyces* species based on ITS rDNA sequences. Bootstrapping support values higher than 60% are given at branches. The blue box represents *G. bolayi* samples parasitic on *Veronica* spp., including the Korean specimens in bold. Color boxes were categorized based on the host families.

## LSU tree

PAP: Papaveraceae  
 FAB: Fabaceae  
 CAM: Campanulaceae  
 CUC: Cucurbitaceae  
 CRA: Crassulaceae  
 LIN: Linderniaceae  
 BIG: Bignoniaceae  
 LAM: Lamiaceae  
 SCR: Scrophulariaceae  
 PLA: Plantaginaceae



**Figure 4.** Minimum evolution tree of *Golovinomyces* species based on LSU rDNA sequences. Bootstrapping support values higher than 60% are given at branches. The blue box represents *G. bolayi* samples parasitic on *Veronica* spp., including the Korean specimens in bold. Colored boxes were categorized based on the host families.

For phylogenetic analysis, the sequences retrieved in this study were aligned with *Golovinomyces* sequences from GenBank, with *G. inulae* serving as an outgroup. Minimum evolution trees were

reconstructed separately for ITS (Figure 3) and LSU (Figure 4) sequences. In phylogenetic trees, the Korean samples were placed within a distinct clade with sequences of *G. bolayi*. In addition,

*G. bolayi* clade included samples from 10 plant families: Papaveraceae, Fabaceae, Campanulaceae, Cucurbitaceae, Crassulaceae, Linderniaceae, Bignoniaceae, Lamiaceae, Scrophulariaceae, and Plantaginaceae. The samples were distantly related to *G. cichoracearum* s. str. ex *Tragopogon pratensis* in both trees.

#### 4. Discussion

*Podosphaera fuliginea* is a powdery mildew predominantly associated with various *Veronica* spp. across North America, Asia, and Europe [4, 5]. However, recent studies have reported *Golovinomyces* spp. as powdery mildew pathogens of *Veronica* plants [6–9, 11–15, 23–26]. In Korea, powdery mildew found on four *Veronica* species (*V. arvensis*, *V. linariifolia*, *V. persica*, and *V. rotunda* var. *subintegra*) was classified as *G. cichoracearum* s. lat. [10, 32], according to the broad species concept for *Golovinomyces* [36]. However, some studies have reported *G. orontii* as the powdery mildew agent [9, 25] and recognized that *G. cichoracearum* s. str. exclusively parasitizes plants in the tribe Cichorieae [37]. Recent morphological and phylogenetic research led to the separation of *G. orontii* s. lat. into three distinct species: *G. orontii* s. str., *G. tabaci*, and *G. bolayi* [9]. This necessitated reevaluation and reclassification of previous records attributing the disease to *G. cichoracearum* s. lat.

This study confirmed that *G. bolayi* was the sole powdery mildew pathogen affecting nine *Veronica* species in Korea. Although we failed to sequence powdery mildew samples from *V. linariifolia* and *V. rotunda* var. *subintegra* due to their weak infection, their morphological characteristics (sinuate outline of conidiophores, straight or curved foot cells, etc.) were consistent with those of *G. bolayi* [9]. The occurrences of *G. bolayi* have also been recorded on *V. arvensis* in Japan and *V. persica* in China and Iran [9, 24–26]. Our phylogenetic analysis, corroborating a study by Braun [9, 37], still suggests that *G. bolayi* is a generalist, infecting a wide range of plants across at least 10 families. This adaptability challenges the traditional view that a powdery mildews species mostly has a narrow host spectrum, infecting a specific genus or even species. Therefore, host expansion could potentially be a common evolutionary event in powdery mildew species [38]. For example, Vági et al. [12] demonstrated that *Golovinomyces* sp. infecting *Arabidopsis* can also infect *Torenia*, a previously unreported host; this pathogen was identified as *G. bolayi* [9]. Our discovery of *G. bolayi* on *V. kiusiana* var. *glabrifolia*, a previously unreported host, further demonstrates its adaptability and ability to infect new hosts.

The broad host range of *G. bolayi* and its presence in previously unrecorded host plants suggests that *G. bolayi* has undergone host expansion, now including *Veronica* spp. within its host range. *G. bolayi* primarily infected Cichorieae plants (Asteraceae) in Europe but expanded its host range to include various plants, including native European *Veronica* spp. These plants and the pathogen spread globally, resulting in the infection of *Veronica* species native to Northeast Asia (China, Japan, and Korea) by *G. bolayi*, presumably introduced alongside European *Veronica*. These findings suggest a complex and unpredictable pattern of fungal transmission and host selection of powdery mildew fungi.

Therefore, deeper knowledge of the ecological and evolutionary mechanisms underlying the host expansion of powdery mildew fungi is required. Understanding these dynamics is critical for developing effective disease management strategies and preserving commercial *Veronica* plants that may be increasingly vulnerable to newly introduced pathogens, such as *G. bolayi*.

#### Disclosure statement

No potential conflict of interest was reported by the author(s).

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