

## Article

# New Records of Powdery Mildews from Taiwan: *Erysiphe ipomoeae* comb. nov., *E. aff. betae* on Buckwheat, and *E. neolycopersici* comb. nov. on *Cardiospermum halicacabum*

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**Abstract:** *Erysiphe* is the largest genus of powdery mildews (PMs), a group of obligate plant pathogenic fungi. Exploration of biodiversity generally relies on regional surveys and our aim is to investigate the PMs in Taiwan. Collections of the fungi on five plant species around agricultural environments were subjected to morphological and molecular characterization, using both internal transcribed spacer (ITS) and  $\beta$ -tubulin gene (*TUB2*) regions for the phylogenetic analyses. *Erysiphe ipomoeae* comb. nov., a species able to infect *Ipomoea obscura* and *I. aquatica* demonstrated by pathogenicity tests, has been neotypified. The two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*, are found to be hosts of *E. aff. betae*. These results suggest that hosts in some plant families can be infected by more than one *Erysiphe* pathogen, e.g., Convolvulaceae by *E. ipomoeae* and *E. convolvuli* and Polygonaceae by *E. polygoni* and *E. aff. betae*, respectively. In addition, phylogenetic analyses of PMs on *Cardiospermum halicacabum* and tomato belonging to the *E. aquilegiae* complex are allocated under *E. neolycopersici* comb. nov. This extends the potential host range of *E. aquilegiae* complex to the plant family Sapindaceae. We conclude that awareness of the host associations of PMs can potentially benefit crop disease management.

**Keywords:** Ascomycota; *Pseudoidium ipomoeae*; *Erysiphe betae*; *Erysiphe aquilegiae*; *Pseudoidium neolycopersici*; molecular markers; taxonomy; host ranges; vegetables; crop production



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## 1. Introduction

Powdery mildews (PMs) are a group of obligate biotrophic plant pathogenic fungi in Erysiphaceae within Helotiales, Leotiomyces, and Ascomycota [1]. There are about 900 known species worldwide [2–4] and the estimated diversity of PMs would be far more than that number [5]. This group of fungi can affect around 10,000 species of angiosperms, including numerous economically important plants, such as crops, cereals, vegetables, fruits, and ornamentals [2,6]. The symptoms of the disease appear as conspicuous white, powdery mycelial and spore masses on the above-ground parts of the plants, e.g., the leaves, buds, stems, flowers, and fruits. Severe infections can cause leaf drop, withering, reduction in growth, and even death of plants, resulting in substantial economic losses [7,8].

*Erysiphe* is the largest genus comprising about half of all the powdery mildew species [2,9,10]. This genus has been classified into five practical morphological sections [2] and further research has divided *Erysiphe* into phylogenetic lineages, such as *Microsphaera* and *Uncinula* lineage [9,10]. The basic morphological characteristics of *Erysiphe* are the anamorph (asexual morph) of *Pseudoidium*-type conidiogenesis (conidia formed singly) and the teleomorph

(sexual morph) of polyascal chasmothecia [2,11]. The anamorphic genus name *Pseudoidium* is still in use where the teleomorph had not been found, however, these species could also be assigned under its teleomorphic genus name, *Erysiphe* [12].

Many investigations about *Erysiphe* have been carried out in different geographic regions. Limited by the obligatory parasitic, nonculturable nature of these fungi, exploration of the biodiversity of PMs in a region generally relies on local surveys. The first compilations of PMs in Taiwan are in the pioneer works of Sawada, Kaneyoshi [13,14]. Two pieces of literature in the 1910s recorded the currently known *Erysiphe* spp. on at least 15 plant species, e.g., wheat, pea, buckwheat, tomato, and grape, that revealed the earliest *Erysiphe* specimens in Taiwan, collected by Suzuki, Rikiji, could be dated back to 1907 [13,14]. Subsequent studies related to this group of PMs in Taiwan can be referred in Kuo [15], Braun and Cook [2], and the List of Plant Diseases in Taiwan [16]. Additional investigations in recent years are those in Kirschner and Liu [17], Kirschner [18], Wang et al. [19–21], Kirschner et al. [22], Yeh et al. [23], and Xiao et al. [24].

Presently, using both morphological and phylogenetic approaches is routine for accurate fungal identification and in taxonomic studies. The ribosomal DNA internal transcribed spacer (ITS) region is a standard sequence identifier for PMs [25–27]. However, the ITS marker might be insufficient for species discrimination [9,26]. In this study, specimens of *Erysiphe* in Taiwan were collected to clarify the species identities and phylogeny of PMs on the plant genus *Ipomoea*, *Fagopyrum*, and *Cardiospermum*. We obtained not only the ribosomal DNA sequences including the ITS and large subunit rRNA gene (28S rDNA) region but also the  $\beta$ -tubulin gene region (*TUB2*), another protein-coding gene region potentially useful in the phylogenetic analyses [26]. Our initial objective was to clarify the taxonomy of *Pseudoidium ipomoeae* (J.M. Yen and Chin C. Wang) U. Braun and R.T.A. Cook, a powdery mildew on obscure morning glory (*Ipomoea obscura* (L.) Ker Gawl.) occurring in Taiwan and Thailand [2,28,29], and resolve the taxonomic confusion associated with PMs on Convolvulaceae [27]. In addition, powdery mildew infections on buckwheats and herbaceous plants were found at high incidences (>50%) in an agricultural environment near the Taichung District Agricultural Research and Extension Station (TDARES) in Changhua County, Taiwan. These PMs were identified based on the morphology and molecular analyses. Pathogenicity tests were also conducted. Moreover, the host ranges and the implication on crop production were discussed in this study.

## 2. Materials and Methods

### 2.1. Sampling and Morphology

Diseased leaves bearing powdery mildew symptoms on obscure morning glory (*I. obscura*), water spinach (*I. aquatica* Forssk.), common buckwheat (*Fagopyrum esculentum* Moench, cv. Taichung No. 5), Tartary buckwheat (*F. tataricum* (L.) Gaertn., cv. Taichung No. 2) [30], and lesser balloon vine (*Cardiospermum halicacabum* L.) were collected in central Taiwan between 2021 and 2022. The samples were temporarily kept at 6 °C until morphological observations, extraction of nucleic acids, and pathogenicity tests were carried out. Voucher specimens were deposited at the herbarium of the National Museum of Natural Science (TNM) in Taichung, Taiwan. For light microscopical examination, fungal structures from the fresh leaf surfaces were mounted in distilled water and observed using a Leica DM2500 light microscope (Leica Microsystems, Wetzlar, Germany) under 400 $\times$  magnification. At least 10 conidiophores, foot cells, and 50 conidia were measured for each of the samples whenever possible. Photographs were taken using a Leica MC190 HD camera (Leica Microsystems, Wetzlar, Germany) equipped on the microscope.

### 2.2. Molecular Phylogeny

For molecular analysis, the total genomic DNA of the fungi was extracted from the mycelia with a Plant Genomic DNA Extraction Miniprep Kit (Viogene, New Taipei, Taiwan) following the manufacturer's instructions. The sequences of ITS, 28S rDNA, and *TUB2* were amplified using primer pairs ITS1/PM6 and PM5/ITS4 [31,32] for ITS, PM3/TW14 [31,33] for 3' half of ITS and 28S rDNA, and BtubF5/BtubR7a or BtubF5b/BtubR7a [26] for *TUB2*.

The PCR conditions had an initial denaturing step at 95 °C for 2 min, followed by 35 cycles of 95 °C for 30 sec, 55 °C for 30 sec, and 72 °C for 2 min, and a final step at 72 °C for 5 min. Alternative PCR conditions were used while the initial PCR amplification failed: denaturation at 95 °C for 5 min, followed by 37 cycles of 95 °C for 30 sec, 55 °C for 1 min, and 72 °C for 1.5 min, and final extension at 72 °C for 5 min. The amplicons were sequenced in both directions using the same primer sets at Tri-I Biotech, Inc., New Taipei, Taiwan. Additional sequences of the powdery mildew on tomato, other newly collected *Erysiphe* species, and those from our previous collections [24] were also obtained in this study. The resulting ITS and 28S rDNA sequences were combined (ITS + 28S), then the ITS + 28S and *TUB2* sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>, accessed on 28 January 2022).

The sequences of the PMs used in this study are listed in Table 1 [9,11,19,24–26,29,34–48]. To determine the phylogenetic relationships using ITS and concatenated sequences of ITS and *TUB2*, the sequences were aligned using the MAFFT v.7 online version (<https://mafft.cbrc.jp/alignment/software/>, accessed on 28 January 2022) with the L-INS-i strategy [49]. The best evolutionary models were estimated under the Akaike Information Criteria (AIC) by jModelTest v. 2.1.10 [50,51]. The phylogenetic trees were generated by the maximum-likelihood (ML) method. The ML analyses were performed by raxmlGUI v.2.0.6 [52] under general time-reversible model with gamma distribution plus invariant sites (GTR + G + I) for ITS and combined ITS and *TUB2* sequences with 1000 bootstrap replications. ML bootstrap values  $\geq$  70% were given at each node. Posterior probabilities (PPs) of Bayesian inference were determined by Markov Chain Monte Carlo sampling in MrBayes 3.2.7a [53]. Six chains with a temperature setting of 0.15 were run for 30 million generations, with trees being sampled every 1000 generations. The first 20% of the trees were discarded as part of the burn-in procedure. PPs  $\geq$  0.95 were indicated at each node.

**Table 1.** List of powdery mildew isolates used in the phylogenetic analyses.

Species	Host Family	Host Species	Voucher <sup>1</sup>	Accession Number <sup>2</sup>		Reference
				ITS	<i>TUB2</i>	
<i>Erysiphe alphitoides</i>	Convolvulaceae	<i>Ipomoea obscura</i>	HNIO-18	MN186769	n.a.	Pan et al. [34]
	Fabaceae	<i>Wisteria sinensis</i>	OE2014PM13	KY660754	KY786697	Ellingham et al. [26]
	Fagaceae	<i>Quercus robur</i>	OE2014PM103CS	KY660753	KY786753	Ellingham et al. [26]
	Fagaceae	<i>Q. robur</i>	MUMH1442	AB257430 *	n.a.	Takamatsu et al. [35]
	Fagaceae	<i>Q. robur</i>	MUMH631(t)	AB292708	n.a.	Takamatsu et al. [36]
<i>E. aquilegiae</i>	Ranunculaceae	<i>Aquilegia</i> sp.	BCRU00359	LC009883 *	n.a.	Takamatsu et al. [9]
	Ranunculaceae	<i>A. vulgaris</i>	OE2014PM147CS	KY653191	KY786773	Ellingham et al. [26]
	Ranunculaceae	<i>Clematis apiifolia</i>	MUMH277	LC009938 *	n.a.	Takamatsu et al. [9]
	Ranunculaceae	<i>Ranunculus repens</i>	OE2014PM109	KY653197	KY786756	Ellingham et al. [26]
<i>E. betae</i>	Amaranthaceae	<i>Beta vulgaris</i>	KUS F29140	KX574674	n.a.	Joa et al. [37]
	Amaranthaceae	<i>B. vulgaris</i>	WW-14	DQ164433	n.a.	Francis et al. [38]
	Amaranthaceae	<i>B. vulgaris</i> subsp. <i>cicla</i>	SE1R	KY399969	n.a.	Vakalounakis and Kavroulakis [39]
	Amaranthaceae	<i>Dysphania ambrosioides</i>	MUMH0395	LC009946 *	n.a.	Takamatsu et al. [9]
<i>E. aff. betae</i>	Polygonaceae	<i>Fagopyrum esculentum</i>	TNM F0034604	OM033347 *	OM056697	This study
	Polygonaceae	<i>F. esculentum</i>	TNM F0035414	OM368494 *	OM423597	This study
	Polygonaceae	<i>F. esculentum</i>	TNM F0035415	OM368495 *	OM423598	This study
	Polygonaceae	<i>F. tataricum</i>	TNM F0034605	OM033348 *	OM056698	This study

Table 1. Cont.

Species	Host Family	Host Species	Voucher <sup>1</sup>	Accession Number <sup>2</sup>		Reference
				ITS	TUB2	
<i>E. convolvuli</i>	Convolvulaceae	<i>Calystegia sepium</i>	MUMH7001	LC270835 *	n.a.	Abasova et al. [11]
	Convolvulaceae	<i>Ca. sepium</i>	OE2014PM62CS	KY660794	KY786726	Ellingham et al. [26]
	Convolvulaceae	<i>Ca. silvatica</i>	OE2014PM48CS	KY660793	KY786719	Ellingham et al. [26]
	Convolvulaceae	<i>Convolvulus arvensis</i>	UC1512307	AF011298	n.a.	Saenz and Taylor [40]
	Convolvulaceae	<i>C. arvensis</i>	VPRI 20227	AF154327	n.a.	Cunnington et al. [25]
	Convolvulaceae	<i>I. aquatica</i>	HMUT1009256	KJ885178	n.a.	Abasova et al. [11]
	Convolvulaceae	<i>I. tricolor</i>	n.a.	EU621391	n.a.	Takamatsu et al. [9]
<i>E. convolvuli</i> var. <i>convolvuli</i>	Convolvulaceae	<i>C. arvensis</i>	MUMH7048	LC328325	n.a.	Abasova et al. [11]
<i>E. heraclei</i>	Apiaceae	<i>Heracleum sphondylium</i>	OE2014PM52	KY660792	KY786720	Ellingham et al. [26]
	Apiaceae	<i>H. sphondylium</i>	OE2014PM65CS	KY660830	KY786728	Ellingham et al. [26]
<i>E. ipomoeae</i>	Convolvulaceae	<i>I. obscura</i>	TNM F0035015(t)	<b>OM033351</b> *	<b>OM056701</b>	This study
	Convolvulaceae	<i>I. obscura</i>	TNM F0035013	<b>OM033349</b> *	<b>OM056699</b>	This study
	Convolvulaceae	<i>I. obscura</i>	TNM F0035014	<b>OM033350</b> *	<b>OM056700</b>	This study
	Convolvulaceae	<i>I. obscura</i>	TNM F0035018	<b>OM033354</b> *	<b>OM056704</b>	This study
	Convolvulaceae	<i>I. obscura</i>	MUMH2978	LC163910	n.a.	Meeboon and Takamatsu [29]
	Convolvulaceae	<i>I. aquatica</i>	TNM F0034602	<b>OM033346</b> *	<b>OM056696</b>	This study
	Convolvulaceae	<i>I. aquatica</i>	TNM F0035410	<b>OM368491</b> *	<b>OM423594</b>	This study
<i>E. lespedezae</i>	Fabaceae	<i>Bauhinia variegata</i>	TNM F0033672	MT471985	<b>OM056688</b>	Xiao et al. [24] and this study
	Fabaceae	<i>B. variegata</i>	TNM F0033677	MT471988	<b>OM056693</b>	Xiao et al. [24] and this study
	Fabaceae	<i>B. variegata</i>	TNM F0033678	MT471989	<b>OM056694</b>	Xiao et al. [24] and this study
	Fabaceae	<i>B. blakeana</i>	TNM F0033679	MT471990	<b>OM056695</b>	Xiao et al. [24] and this study
	Fabaceae	<i>Desmodium caudatum</i>	TNM F0033671	MT471984	<b>OM056687</b>	Xiao et al. [24] and this study
	Fabaceae	<i>D. caudatum</i>	TNM F0033675	MT471986	<b>OM056691</b>	Xiao et al. [24] and this study
	Fabaceae	<i>D. caudatum</i>	TNM F0033676	MT471987	<b>OM056692</b>	Xiao et al. [24] and this study
<i>E. neolycopersici</i>	Caricaceae	<i>Carica papaya</i>	n.a.	GU358451	n.a.	Tsay et al. [41]
	Sapindaceae	<i>Cardiospermum halicacabum</i>	TNM F0035016	<b>OM033352</b> *	<b>OM056702</b>	This study
	Sapindaceae	<i>C. halicacabum</i>	TNM F0035412	<b>OM368492</b> *	<b>OM423595</b>	This study
	Sapindaceae	<i>C. halicacabum</i>	TNM F0035413	<b>OM368493</b> *	<b>OM423596</b>	This study
	Solanaceae	<i>Solanum lycopersicum</i>	Et-1(t)	AF229019	n.a.	Kiss et al. [42]
	Solanaceae	<i>S. lycopersicum</i>	UMSG2	KX776199 *	MCFK01008520	Wu et al. [43]
	Solanaceae	<i>S. lycopersicum</i>	MUMH66	LC009912 *	n.a.	Takamatsu et al. [9]
<i>E. pedaliacearum</i>	Pedaliaceae	<i>Sesamum indicum</i>	KUS F30128	LC342963 *	n.a.	Shin et al. [44]
	Polygonaceae	<i>Antigonon leptopus</i>	R. Kirschner 4701	MK685172	n.a.	Wang et al. [19]
<i>E. polygona</i>	Polygonaceae	<i>F. esculentum</i>	n.a.	KP076437	n.a.	Lu et al. [45]
	Polygonaceae	<i>Polygonum</i> sp.	OE2014PM85CS	KY660828	KY786741	Ellingham et al. [26]
	Polygonaceae	<i>P. aviculare</i>	OE2014PM120CS	KY660829	KY786760	Ellingham et al. [26]
	Polygonaceae	<i>P. aviculare</i>	MUMH7036	LC328322	n.a.	Abasova et al. [11]
	Polygonaceae	<i>P. aviculare</i>	MUMH7036	LC328322	n.a.	Abasova et al. [11]
<i>E. quercicola</i>	Anacardiaceae	<i>Mangifera indica</i>	TNM F0033673	<b>OM033344</b> *	<b>OM056689</b>	This study
	Fagaceae	<i>Q. phillyraeoides</i>	MUMH124	AB193591	n.a.	Limkaisang et al. [46]
	Lauraceae	<i>Cinnamomum camphora</i>	TNM F0033674	<b>OM033345</b> *	<b>OM056690</b>	This study
	Sapindaceae	<i>Nephelium lappaceum</i>	MUMH6769	MN081591 *	n.a.	Meeboon and Takamatsu [47]
<i>E. sedi</i>	Crassulaceae	<i>Sedum aizoon</i>	MUMH2575	LC010045 *	n.a.	Takamatsu et al. [9]
<i>E. takamatsui</i>	Nelumbonaceae	<i>Nelumbo nucifera</i>	TNS F-52102	AB916688 *	n.a.	Meeboon and Takamatsu [48]
<i>G. cichoracearum</i>	Asteraceae	<i>Sonchus oleraceus</i>	UMSG1	HM449077	MCBS01024998	Wu et al. [43]

<sup>1</sup> Type specimens are marked with (t) after the voucher names. <sup>2</sup> Sequences obtained in this study are shown in bold. Sequences of ITS + 28S are marked with asterisks.

### 2.3. Pathogenicity Tests

Pathogenicity tests were conducted by gently pressing each of the fresh, powdery mildew-infected leaves onto the leaves of approximately two-week-old healthy plants that had been sprayed with water. (1) Four plants of *I. obscura* were inoculated with an infected leaf of *I. obscura*. (2) Six plants of *I. aquatica* were inoculated with an infected leaf of *I. obscura*. (3) Ten plants of *I. aquatica* were inoculated with an infected leaf of *I. aquatica*. (4) Two pots of *F. esculentum* cv. Taichung No. 5 and two pots of *F. tataricum* cv. Taichung No. 2, containing at least fifteen plants in each pot, were inoculated with an infected leaf of *F. esculentum*. (5) Two plants of *C. halicacabum* were inoculated with an infected leaf of *C. halicacabum*. The same number of non-inoculated plants in each pathogenicity test served as controls, except that controls of *F. esculentum* and *F. tataricum* were one pot for each. The inoculation tests were performed in a greenhouse of the TDARES between March and June 2021 (test 1–4) and in January 2022 (test 5), with average temperatures of 29.4 °C, 25.2 °C, 21.1 °C, 22.9 °C, and 20.0 °C, respectively. A repeated experiment of test 1 was conducted with the same method under an average temperature of 23.7 °C in November 2021. The plants were inspected about every three days to note the dates when the symptoms appeared after the inoculations. While the symptoms of the powdery mildew clearly appeared on the leaf surfaces, the leaves were collected for morphological observations and subjected to ITS sequence characterization as previously mentioned.

## 3. Results

### 3.1. Morphology

Morphological characteristics of the PMs on the plants of Convolvulaceae, Polygonaceae, and Sapindaceae in this study were consistent with those of the anamorph in the genus *Erysiphe* [2,54]. The conidia, formed singly (*Pseudoidium* type) on conidiophores [2,54], were ellipsoid–ovoid to cylindrical in shape. Chasmothecia were absent in the collections. Voucher specimens were deposited under TNM numbers F0035013–15, F0035018, F0035401–3, and F0035409 (on *I. obscura*), F0034602 and F0035410 (on *I. aquatica*), F0034604 and F0035414–5 (on *F. esculentum*), F0034605 (on *F. tataricum*), and F0035016 and F0035412–3 (on *C. halicacabum*). Some details of the vouchers are shown in Table 1.

### 3.2. Phylogentic Analyses

The nucleotide sequences of the ITS + 28S and *TUB2* gene regions were determined for six specimens on the plant genus *Ipomoea*, four specimens on *Fagopyrum*, and three specimens on *C. halicacabum*. An additional three ITS sequences and ten *TUB2* sequences were obtained from the other *Erysiphe* specimens (Table 1). They were further aligned with the sequences retrieved from the DNA database. Sequences of *Golovinomyces cichoracearum* (DC.) V.P. Heluta [43] were used as outgroups.

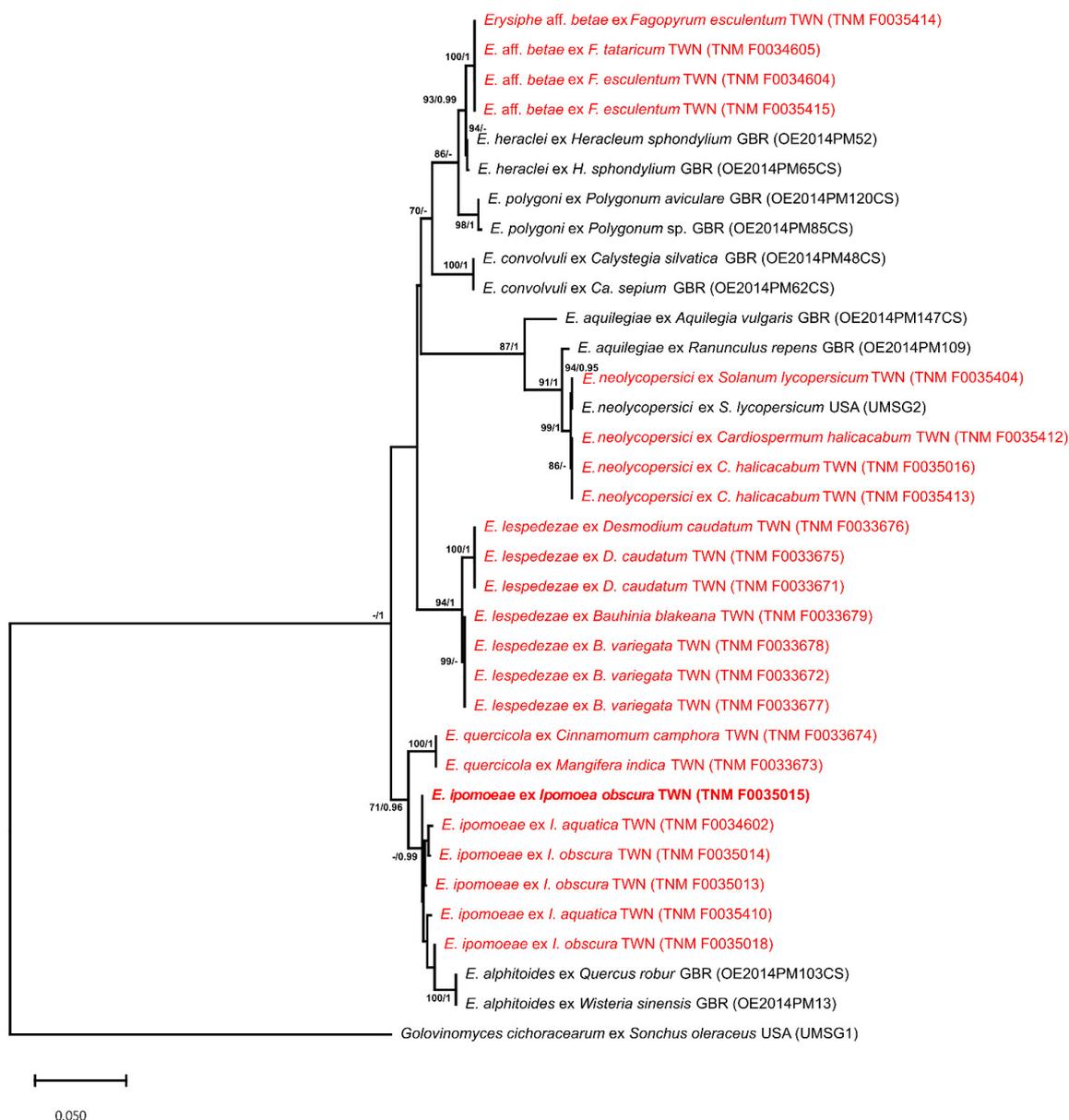
A best-scoring ML tree of ITS with a final optimization likelihood of  $-1646.264627$  is shown in Figure 1. The PMs on *I. obscura* and *I. aquatica* from Taiwan were clustered with *P. ipomoeae* on *I. obscura* (MUMH2978) from Thailand [29]. Our samples on *F. esculentum* and *F. tataricum* were grouped in a clade with *E. betae* (Vaňha) Weltzien on other host plants belonging to Amaranthaceae [9,37], distinguished from those in the clade of *E. heraclei* DC. and *E. polygoni* DC. [11,19,26,45]. Besides, the PMs on *C. halicacabum* were grouped with species in the *E. aquilegiae* complex [9,44,48].



**Figure 1.** RAxML tree based on ITS sequences from *Erysiphe*. *Golovinomyces cichoracearum* is used as an outgroup taxon. Maximum likelihood bootstrap values  $\geq 70\%$  and Bayesian posterior probabilities  $\geq 0.95$  are given at the nodes. Sequences obtained in this study are shown in red. Ex-type sequences are indicated in bold.

On the other hand, a best scoring ML tree inferred by the concatenated sequences of ITS and *TUB2* with a final optimization likelihood of  $-3606.639810$  is provided in Figure 2. In the phylogram, the PMs on *Ipomoea* in Taiwan were phylogenetically close to *E. alphitoides* (Griffon and Maubl.) U. Braun and S. Takam. and they were in a clade sister to *E. quercicola* S. Takam. and U. Braun; those on *Fagopyrum* clustered into a well-supported clade, clearly

distinct from *E. heraclei* and *E. polygoni*; and those on *C. halicacabum* were placed within a clade comprising *P. neolycopersici* (L. Kiss) L. Kiss (*Oidium neolycopersici* L. Kiss) on tomato.

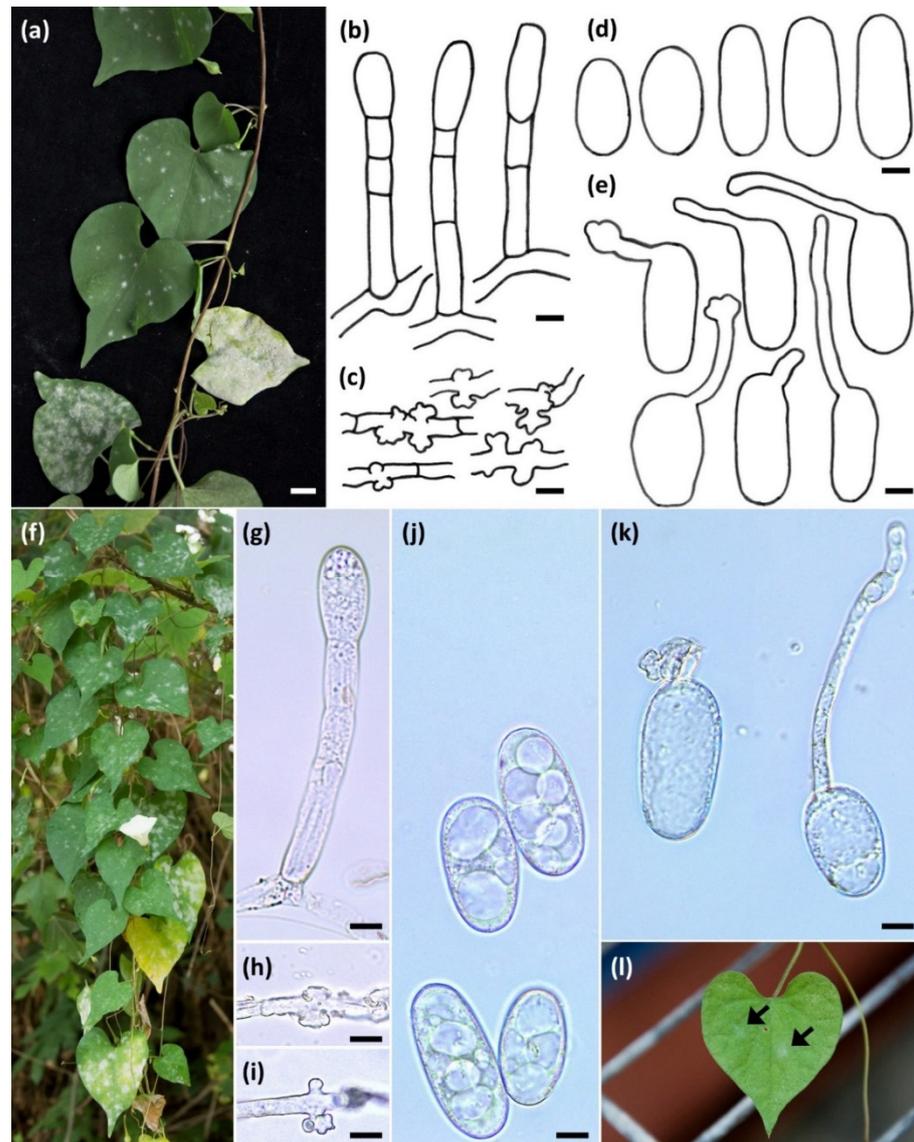


**Figure 2.** RAxML tree based on the concatenated sequences of ITS and *TUB2* from *Erysiphe*. *G. cichoracearum* is used as an outgroup taxon. Maximum likelihood bootstrap values  $\geq 70\%$  and Bayesian posterior probabilities  $\geq 0.95$  are given at the nodes. Sequences obtained in this study are shown in red. Ex-type sequences are indicated in bold.

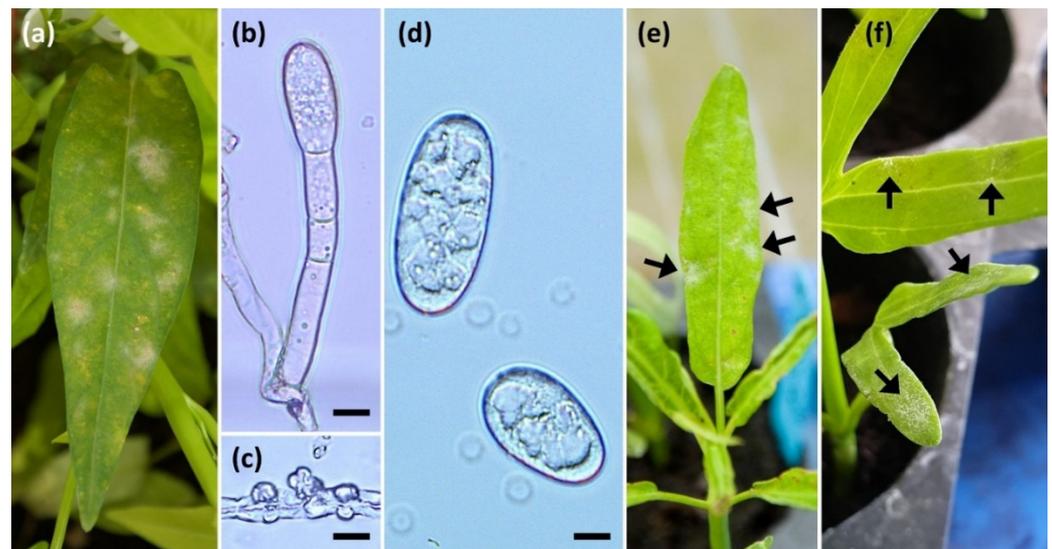
### 3.3. Pathogenicity Tests

PMs on *I. obscura* were successfully inoculated on *I. obscura* and *I. aquatica*, producing powdery mildew symptoms. White fungal colonies appeared on an inoculated leaf of *I. obscura* after three weeks post inoculation (wpi) (Figure 3I), whereas the mycelia were produced on leaves of all the treated *I. aquatica* at 1 wpi (Figure 4e). Using the powdery mildew on *I. aquatica* as an inoculum, white fungal patches were also produced on the leaves of *I. aquatica* at 2 wpi (Figure 4f). In the pathogenicity test of the powdery mildew on *Fagopyrum*, white colonies on inoculated leaves of *F. esculentum* and *F. tataricum* were observed on the fifth day post inoculation, as shown in Figure 5g,h. After 2 wpi, the

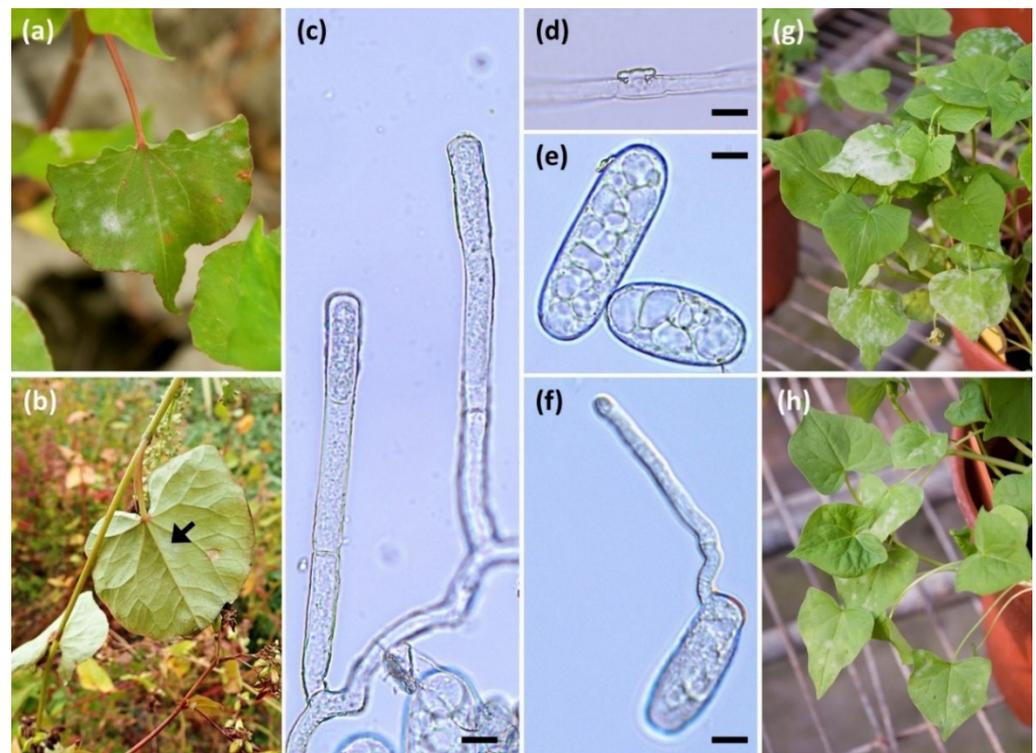
incidences in all the inoculated pots exceeded 85% and the controls were symptomless. In the experiment of *C. halicacabum*, white colonies on inoculated leaves appeared after 1 wpi (Figure 6g). In the repeated *I. obscura* experiment under a cooler temperature, mycelial colonies appeared on the inoculated leaves at 2 wpi. The morphological and molecular characteristics of the pathogen on inoculated plants were consistent with those of the originals. All the control plants in each pathogenicity test remained symptomless during the experimental period.



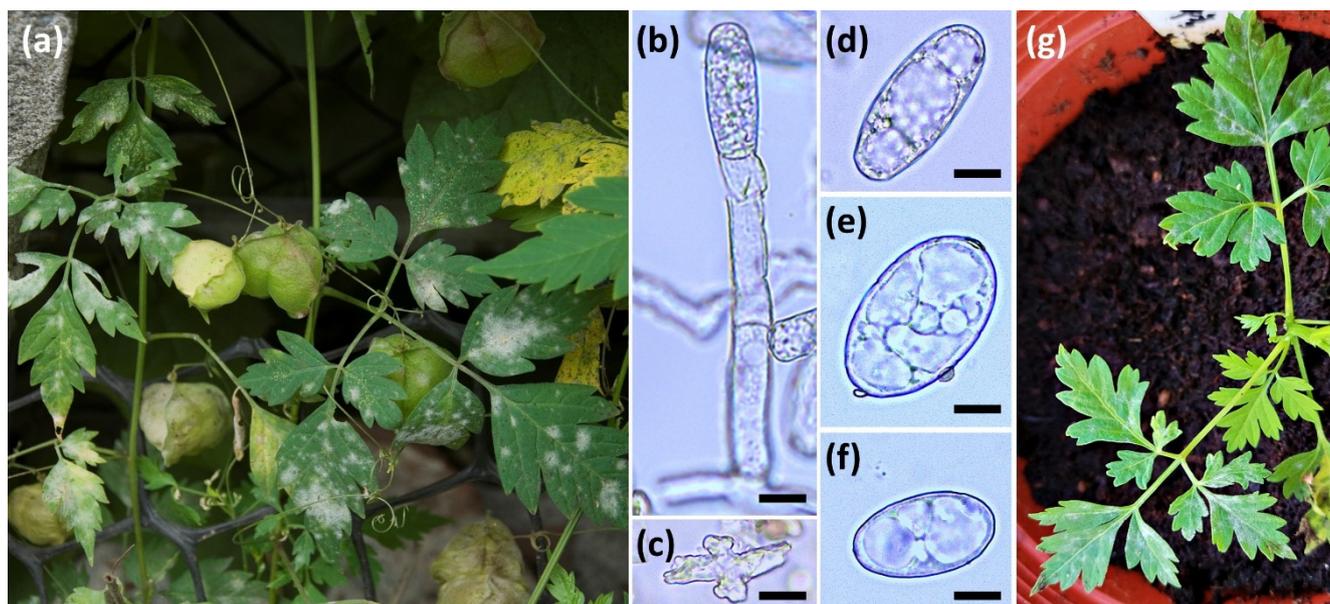
**Figure 3.** *Erysiphe ipomoeae* on *Ipomoea obscura*. (a) Symptoms of *E. ipomoeae* on *I. obscura*, TNM 0035015, neotype. (b–e) Drawings showing microscopic characteristics of TNM 0035015. (b) Conidiophores with conidia. (c) Hyphal appressoria. (d) Conidia. (e) Conidia with germ tubes. (f) Symptoms of the powdery mildew on naturally infected plant in field. (g–k) Micrographs of *E. ipomoeae* on *I. obscura* TNM 0035015. (g) Conidiophore with conidium. (h,i) Hyphal appressoria. (j) Conidia. (k) Conidia with germ tubes. (l) The symptoms on *I. obscura* inoculated with *E. ipomoeae* on *I. obscura*. Scale bars in (a) = 1 cm, in (b–e), and (g–k) = 10  $\mu$ m. Arrows indicate the colonies of the powdery mildew.



**Figure 4.** *Erysiphe ipomoeae* on *Ipomoea aquatica*. (a) Symptoms of the powdery mildew on naturally infected plant in greenhouse. (b–d) Micrographs of *E. ipomoeae* on *I. aquatica* TNM 0034602. (b) Conidiophore with conidium. (c) Hyphal appressoria. (d) Conidia. (e) The symptoms on *I. aquatica* inoculated with *E. ipomoeae* on *I. obscura*. (f) The symptoms on *I. aquatica* inoculated with *E. ipomoeae* on *I. aquatica*. Scale bars in (b–d) = 10 µm. Arrows indicate the colonies of the powdery mildew.



**Figure 5.** *Erysiphe* aff. *betae* on *Fagopyrum* spp. (a,b) Symptoms of the powdery mildew on naturally infected plant *F. esculentum* and *F. tataricum* in field, respectively. Arrow indicates the symptoms of the powdery mildew. (c–f) Micrographs of *E. aff. betae* on *F. esculentum* TNM 0034604. (c) Conidiophores with conidia. (d) Hyphal appressorium. (e) Conidia. (f) Conidium with germ tube. (g) The symptoms on *F. esculentum* inoculated with *E. aff. betae* on *F. esculentum*. (h) The symptoms on *F. tataricum* inoculated with *E. aff. betae* on *F. esculentum*. Scale bars in (c–f) = 10 µm.



**Figure 6.** *Erysiphe neolycopersici* on *Cardiospermum halicacabum*. (a) Symptoms of the powdery mildew on naturally infected plant in field. (b–f) Micrographs of *E. neolycopersici* on *C. halicacabum* TNM 0035016. (b) Conidiophore with conidium. (c) Hyphal appressoria. (d–f) Conidia. (g) The symptoms on *C. halicacabum* inoculated with *E. neolycopersici* on *C. halicacabum*. Scale bars in (b–f) = 10  $\mu$ m.

### 3.4. Taxonomy

*Erysiphe ipomoeae* (J.M. Yen and Chin C. Wang) H. Y. Hsiao and Y. M. Shen, comb. nov. Figures 3 and 4.

**Mycobank:** MB842410.

**Basionym:** *Oidium erysiphoides* f. *ipomoeae* J.M. Yen and Chin C. Wang, Rev. Mycol. 37(3): 138, [“1972”] 1973.

$\equiv$  *Oidium ipomoeae* (J.M. Yen and Chin C. Wang) U. Braun, Mycotaxon 25: 268, 1986.

$\equiv$  *Pseudoidium ipomoeae* (J.M. Yen and Chin C. Wang) U. Braun and R.T.A. Cook, CBS Biodiversity Series 11: 607, 2012.

**Typification:** (Holotype: TAIWAN, Fengshan, on *Ipomoea obscura* (L.) Ker Gawl., 5 May 1972, Yen and Wang (not preserved)) Neotype (designated here, MycoBank: MBT 10006013): Taiwan, Nantou, N23.921944, E120.697333, 90 m altitude, on *Ipomoea obscura*, 28 March 2021, H. Y. Hsiao and Y. M. Shen (TNM F0035015). Ex-neotype reference sequences: OM033351 (ITS); OM056701 (*TUB2*).

**Description:** (on *I. obscura*, TNM F0035015).

Mycelium amphigenous, mainly epiphyllous, white, effuse or in patches. Hyphae 4.3–8.8  $\mu$ m wide. Hyphal appressoria mainly lobed to multilobed, sometimes nipple-shaped, solitary or in opposite pairs. Conidiophores 50.0–75.0  $\mu$ m long, erect. Foot cells 27.5–40.0  $\times$  6.3–10.0  $\mu$ m, cylindrical, straight, followed by 1–2 shorter cells, forming conidia singly. Conidia 33.8–60.0  $\times$  12.5–25.0  $\mu$ m, ellipsoid–ovoid–subcylindrical, with a length-to-width ratio of 1.5–3.9. Chasmothecia absent.

**Description:** (on *I. aquatica*, TNM F0034602).

Mycelium amphigenous, mainly epiphyllous, white, effuse or in patches. Hyphae 4.8–9.5  $\mu$ m wide. Hyphal appressoria mainly lobed to multilobed, sometimes nipple-shaped, solitary or in opposite pairs. Conidiophores 52.5–82.5  $\mu$ m long, straight. Foot cells 28.8–45.0  $\times$  8.8–12.5  $\mu$ m, cylindrical, followed by 1–2 shorter cells, forming conidia singly. Conidia 30.0–58.8  $\times$  12.5–25.0  $\mu$ m, ellipsoid–ovoid–subcylindrical, with a length-to-width ratio of 1.6–3.4. Chasmothecia absent.

**Material Examined:** Taiwan, Nantou, on *I. obscura*, 28 March 2021, TNM F0035015 (neotype), GenBank: OM033351 (ITS), OM056701 (*TUB2*); Taiwan, Changhua, on *I. obscura*,

24 March 2021, TNM F0035013, GenBank: OM033349 (ITS), OM056699 (*TUB2*); Taiwan, Nantou, on *I. obscura*, 28 March 2021, TNM F0035014, GenBank: OM033350 (ITS), OM056700 (*TUB2*); Taiwan, Changhua, on *I. obscura*, 26 May 2021, TNM F0035018, GenBank: OM033354 (ITS), OM056704 (*TUB2*); Taiwan, Nantou, on *I. obscura*, 11 November 2021, TNM F0035401; Taiwan, Nantou, on *I. obscura*, 11 November 2021, TNM F0035402; Taiwan, Taichung, on *I. obscura*, 1 December 2021, TNM F0035403; Taiwan, Nantou, on *I. obscura*, 17 December 2021, TNM F0035409; Taiwan, Changhua, on *I. aquatica*, 22 February 2021, TNM F0034602, GenBank: OM033346 (ITS), OM056696 (*TUB2*); Taiwan, Nantou, on *I. aquatica*, 28 December 2021, TNM F0035410, GenBank: OM368491 (ITS), OM423594 (*TUB2*).

**Known Distribution:** Taiwan, Thailand [29], and India [2,55].

**Notes:** The powdery mildew on *I. obscura* was first discovered at Fengshan, Taiwan, on 5 May 1972 by Yen and Wang [28]. It was introduced under the name of *Oidium erysiphoides* f. *ipomoeae* J.M. Yen and Chin C. Wang and later replaced by the names *O. ipomoeae* (J.M. Yen and Chin C. Wang) U. Braun [56] and *P. ipomoeae* in Braun and Cook [2]. The morphology of our collections is generally in agreement with previous descriptions [2,28]. The teleomorph of the powdery mildew has never been found so far. Interestingly, Meeboon and Takamatsu [29] reported *P. ipomoeae* on two host plants, *I. obscura* and *I. aquatica*, in Thailand. A DNA sequence covering the ITS region of *P. ipomoeae* on *I. obscura* was determined (LC163910) [29] but that of the pathogen on *I. aquatica* was not available. The *P. ipomoeae* sequence from Thailand clustered with sequences from the PMs on *I. obscura* and *I. aquatica* in Taiwan in the phylogenetic analysis (Figure 1). Evidently, the newly obtained PMs on *Ipomoea* in this study are conspecific with *P. ipomoeae*, and moreover, the molecular phylogeny suggests that this powdery mildew should be allocated under *Erysiphe*. To the best of our knowledge, the holotype material may not be extant ([28] and personal communication with Uwe Braun) so that a neotype is needed. The powdery mildew is here neotypified by the specimen collected near the type locality with the name *Erysiphe ipomoeae*, and this may resolve the taxonomic confusion of *Erysiphe* on *Ipomoea*. In addition, the DNA sequences of *E. ipomoeae* on *I. aquatica* were generated in this study for the first time and this is the first report of the powdery mildew *E. ipomoeae* on *I. aquatica* in Taiwan.

***Erysiphe* aff. *betae*** Figure 5.

**Description:** (on *F. esculentum*, TNM F0034604).

Mycelium amphigenous, often covering the entire surface of the leaves, effuse or in patches. Hyphae 3.3–7.9 µm wide. Hyphal appressoria lobed, solitary or in opposite pairs. Conidiophores 43.8–105.0 µm long, straight. Foot cells 27.5–46.3 × 6.3–8.8 µm, cylindrical, occasionally slightly curved–sinuous, followed by a cell of approximately the same length or 1–2 shorter cells, forming conidia singly. Conidia 36.3–58.8 × 16.3–22.5 µm, cylindrical to ovoid, with a length-to-width ratio of 1.7–3.6. Chasmothecia not observed.

**Description:** (on *F. tataricum*, TNM F0034605).

Mycelium amphigenous, mainly hypophyllous, effuse or in patches. Hyphae 3.6–8.6 µm wide. Hyphal appressoria lobed, solitary or in opposite pairs. Conidiophores 42.5–118.8 µm long, straight. Foot cells 31.3–55.0 × 6.3–10.0 µm, cylindrical, occasionally slightly curved–sinuous, followed by 1–2 shorter cells, or one cell of equal or longer length, forming conidia singly. Conidia 37.5–55.0 × 17.5–27.5 µm, cylindrical to ovoid, with a length-to-width ratio of 1.6–3.1. Chasmothecia not observed.

**Material Examined:** Taiwan, Changhua, on *F. esculentum*, 3 March 2021, TNM F0034604, GenBank: OM033347 (ITS), OM056697 (*TUB2*); Taiwan, Changhua, on *F. esculentum*, 12 January 2022, TNM F0035414, GenBank: OM368494 (ITS), OM423597 (*TUB2*); Taiwan, Changhua, on *F. esculentum*, 12 January 2022, TNM F0035415, GenBank: OM368495 (ITS), OM423598 (*TUB2*); Taiwan, Changhua, on *F. tataricum*, 3 March 2021, TNM F0034605, GenBank: OM033348 (ITS), OM056698 (*TUB2*).

**Notes:** PMs on buckwheats in Taiwan were reported on *F. esculentum* and *F. tataricum* as *Microsphaera polygona* (DC.) Sawada [13,14] and *Ischnochaeta polygona* (DC.) Sawada [57], respectively, and the fungal names have been changed to *E. polygona*. Although the morphology of the PMs on *Fagopyrum* in this study was similar to previous descriptions of

*E. polygona*, the morphological and molecular characteristics showed a close relationship between these recent collections and *E. betae*. *E. betae* in Taiwan, first recorded under the anamorphic name *O. cylindricum* Sawada, was found on *Dysphania ambrosioides* (L.) Mosyakin and Clemants (*Chenopodium ambrosioides* L.) in the northern part of the island [57]. Our newly obtained ITS + 28S sequences of the PMs on *Fagopyrum* shared more than 99.7% sequence identities over a 1356 bp alignment to that of *E. betae* MUMH0395 (LC009946) on *D. ambrosioides* from Japan [9]. However, the ITS analyses may not be sufficient to resolve the complex around *E. betae* and *E. heraclei* and *TUB2* sequences for *E. betae* on *Beta* spp. are currently not available, therefore, the powdery mildew on *Fagopyrum* in this study is herein named as *E. aff. betae*. Analogous to the case to compare the ITS sequences of sugar-beet PMs previously known as *E. betae* and *E. polygona* and given the conclusion that they are supposed to be *E. betae* [38], the result of the phylogenetic analyses (Figures 1 and 2) indicated that the powdery mildew diseases of buckwheats in this study were caused by *Erysiphe* species closely related to *E. betae*. To the best of our knowledge, this is the first report of the powdery mildew *E. aff. betae* on *F. esculentum* and *F. tataricum* in Taiwan.

***Erysiphe neolycopersici* (L. Kiss) H. Y. Hsiao and Y. M. Shen, comb. nov.** Figure 6.  
**Mycobank:** MB843164.

**Basionym:** *Oidium neolycopersici* L. Kiss, Mycological Research 105 (6): 695, 2001.

(Typus: France, Aigue Mortes, on *Lycopersicon esculentum*, 1989, P. C. Nicot Et1 (BPI 747013-holotypus, HAL-isotypus). Living material maintained at INRA, Unité de Pathologie Végétale, Avignon, France.)

≡ *Pseudoidium neolycopersici* (L. Kiss) L. Kiss, CBS Biodiversity Series 11: 612, 2012.

**Description:** (on *C. halicacabum*, TNM F0035016, TNM F0035412-3).

Mycelium amphigenous, also on stems and capsules, effuse or in patches. Hyphae 4.3–8.3 µm wide. Hyphal appressoria nipple-shaped to lobed, solitary or in opposite pairs. Conidiophores 38.8–72.6 µm long, straight. Foot cells 21.3–50.0 × 7.1–12.5 µm, cylindrical, followed by 1–2 shorter cells, or one cell of equal or longer length, forming conidia singly. Conidia 25.0–50.0 × 12.5–25.0 µm, ellipsoid–ovoid–subcylindrical, with a length-to-width ratio of 1.5–3.6. Chasmothecia absent.

**Material Examined:** Taiwan, Changhua, on *C. halicacabum*, 14 April 2021, TNM F0035016, GenBank: OM033352 (ITS), OM056702 (*TUB2*); Taiwan, Nantou, on *C. halicacabum*, 1 January 2022, TNM F0035412, GenBank: OM368492 (ITS), OM423595 (*TUB2*); Taiwan, Nantou, on *C. halicacabum*, 2 January 2022, TNM F0035413, GenBank: OM368493 (ITS), OM423596 (*TUB2*); Taiwan, Nantou, on *Solanum lycopersicum*, 9 December 2021, TNM F0035404, GenBank: OM368490 (ITS), OM423593 (*TUB2*).

**Notes:** Phylogenetic analyses of the PMs on *C. halicacabum* and tomato revealed that they should be allocated to *Erysiphe*. They are assignable to *E. neolycopersici*, which has priority over the previous anamorph-typified names. The morphological characteristics of the powdery mildew on *C. halicacabum* generally matched those of the powdery mildew on tomato (*P. neolycopersici*) [2]. The phylogenetic relationships inferred by the ITS sequences showed the powdery mildew on *C. halicacabum* nested together with PMs on tomato in the clade of *E. aquilegiae* complex [9] (Figure 1) and differed by only one base from the type sequence (AF229019) of *O. neolycopersici* Et1 [42]. In addition, the ITS and *TUB2* sequences of the powdery mildew on *C. halicacabum* showed high sequence identities with those of PMs on tomato (differ by only two bases in the aligned dataset) and they formed a monophyletic clade in the phylogenetic tree (Figure 2). Consequently, the powdery mildew on *C. halicacabum* is here identified as *E. neolycopersici*. *E. neolycopersici* was originally found on leaves and stems of tomato [2,42], further recorded on other solanaceous plants [9,58–61], and on hosts in a variety of plant families such as Caricaceae [41,62], Euphorbiaceae [63,64], Moringaceae [65], and Fabaceae [66]. There are only a few records of PMs on the family Sapindaceae, mainly on woody plants [67]; and the recorded PMs on the herbaceous plant genus *Cardiospermum* were *Oidium* spp. on *C. microcarpum* Kunth and *C. velutinum* Hook. and Arn. (synonym of *C. grandiflorum* Sw.) in Jamaica and Argentina, respectively [6].

To the best of our knowledge, this is the first report of *C. halicacabum* as the host of *E. neolycopersici*.

#### 4. Discussion

##### 4.1. *Erysiphe ipomoeae* and *E. convolvuli*, the Two Distinct Species Causing Powdery Mildews on Convolvulaceae

In addition to *E. ipomoeae* (previously *Pseudoidium ipomoeae*), another species in the same genus, *E. convolvuli* DC., is commonly known to cause the powdery mildew disease on the plant family Convolvulaceae [2,11,27,54]. Bolay et al. [27] observed *E. convolvuli* on *I. lobata* (Cerv.) Thell. in Switzerland and doubted that *P. ipomoeae* and *E. convolvuli* may be conspecific. Probably due to the unclear relationships of the anamorph of PMs on *Ipomoea* [2], this study further noted that sequence analyses of PMs on *Ipomoea* are urgently necessary [27]. In this perspective, the new powdery mildew collections on *I. obscura* and *I. aquatica* in Taiwan, where the fungus on *I. obscura* was first discovered, provided valuable information to this issue.

Our phylogenetic analyses confirmed that *E. ipomoeae* is obviously distinguished from *E. convolvuli* in the phylogenetic trees (Figures 1 and 2). The results revealed that at least two *Erysiphe* spp., *E. ipomoeae* and *E. convolvuli*, were able to infect *Ipomoea* in the plant family Convolvulaceae, supporting the speculation that more than one powdery mildew species may occur on *Ipomoea* spp. [27]. Recently, a study reported the powdery mildew *E. alphitoides* on *I. obscura* in China [34] but the sequence of their sample (HNIO-18) was closer to *E. ipomoeae* (Figure 1). It appears that *E. ipomoeae* may occupy a wider geographic range in East and Southeast Asia. In addition, other *Erysiphe* spp. have been reported to occur on plants of the Convolvulaceae, such as *E. cruciferarum* Opiz ex L. Junell and *E. heraclei* [6,25,68], and identifications of other collections on convolvulaceous hosts remained unclear and could only be referred to as *Erysiphe* sp. or *Oidium* sp. [69].

*Erysiphe ipomoeae* has already been confirmed on *I. obscura* and *I. aquatica* in Taiwan and Thailand [29], but it may well be that this species also occurs on other hosts in Convolvulaceae in India, Myanmar, and other parts of Asia [2,55,70]. On the other hand, *E. convolvuli* has hitherto been reported on the plant genus *Calystegia*, *Convolvulus*, and *Ipomoea* of Convolvulaceae in Asia, Africa, Europe, and America [2,27,54,67,71–73]. In regards to the geographic ranges of the main convolvulaceous plant-infecting PMs, *E. ipomoeae* is known to be distributed in tropical to subtropical regions in Asia, whereas *E. convolvuli* has a worldwide distribution, especially in the temperate regions.

##### 4.2. Powdery Mildews on Buckwheat and the Host Range of *Erysiphe betae*

The present study reports the first occurrence of *E. aff. betae* associated with the powdery mildew diseases of *F. esculentum* and *F. tataricum*. Previously, PMs recorded on buckwheats were referred to as *E. polygoni* (including *E. polygoni* var. *fagopyri*, *E. polygoni* var. *kailashi*, and *E. polygoni* var. *rumicis*) and *Oidium* sp. [2,54,67]. The identifications were mainly based on morphological traits and the host association, however, Lu et al. [45] acquired an ITS fragment of *E. polygoni* on *F. esculentum*, confirming the pathogen–host relationship molecularly. That ITS sequence (KP076437) was grouped with those of *E. polygoni* on other polygonaceous hosts, whereas the collections of PMs on buckwheats in this study are apparently separated from this group (Figure 1). The result revealed that in the case of *Fagopyrum*, more than one powdery mildew species of *Erysiphe* may infect species of this genus, and this scenario is analogous to those on *Ipomoea* (host of *E. ipomoeae* and *E. convolvuli*), *Bauhinia* (host of *E. lespedezae* R.Y. Zheng and U. Braun and *E. quercicola*) [24,74,75], *Quercus* and *Mangifera* (host of *E. quercicola*, *E. alphitoides*, and other species) [2,67,76,77], etc. The discovery of *E. aff. betae* on buckwheats raised the question whether some of the previous regional records of *E. polygoni* on *Fagopyrum* have to be reidentified as powdery mildew species other than *E. polygoni*, similar to that in Francis et al. [38]; and if *E. betae* and *E. polygoni* could occupy an overlapping niche on the same host in a limited spatial range, however, what is the proportion of each of the species?

The occurrence frequency of *E. quercicola* and *E. alphitoides* on infected mango [76] and oak [78] provided examples of the possible distribution of the PMs. Various proportions of powdery mildew species may be detected on the same host according to different locations, sampling dates, infected organs, host developmental stages, and environmental factors at multi-scales [76,78]. It is, therefore, worthwhile to obtain more samples of PMs on buckwheats of a wider range for detailed characterization in future research.

The recorded host range of *E. betae* covers the plant genera *Beta* [2,37,38,54,79], *Dysphania* (= *Chenopodium p.p.*) [2,80,81], and *Spinacia* [2,81] in Amaranthaceae, *Euphorbia* of Euphorbiaceae, *Phaseolus*, *Pisum*, and *Vigna* of Fabaceae [82,83]. However, the latter host references are doubtful and not confirmed by sequence analyses. The finding of *E. aff. betae* on *Fagopyrum* of Polygonaceae lends support to the idea that *E. betae* might have a wider host range than that of our previous understanding. Thus, the host range of *E. betae* requires further validation through additional molecular analyses and cross-inoculation studies. It is likely that the host-range breadths of the PMs could ideally fit in the pattern of modularity (but not strict nestedness) in the infection matrices in Morris and Moury [84].

#### 4.3. *Erysiphe aquilegiae* Complex Needs Further Exploration

The phylogenetic analyses in this study verify that the powdery mildew on *C. halicacabum* in Taiwan is a member of the *E. aquilegiae* complex, a group comprising many closely allied species that are indistinguishable by the ITS data [9,44,69]. The type hosts of *E. aquilegiae* DC. (var. *aquilegiae*) and *E. aquilegiae* var. *ranunculi* (Grev.) R.Y. Zheng and G.Q. Chen are the ranunculaceous species *Aquilegia vulgaris* L. and *Ranunculus cf. muricatus* L., respectively [2], whereas the *E. aquilegiae* clade [9] encompasses many species, i.e., *E. neolycopersici*, *P. hortensiae* (Jørst. ex S. Blumer) U. Braun and R.T.A. Cook, *E. sedi* R.Y. Zheng and G.Q. Chen, *E. pileae* U. Braun, *E. hommae* U. Braun, *E. takamatsui* Y. Nomura, *E. chloranthi* (Golovin and Bunkina) U. Braun, *E. macleayae* R.Y. Zheng and G.Q. Chen 1981, *E. circaeae* L. Junell, *E. knautiae* Duby, *E. euphorbiae* Peck, *P. boroniae* (Crooks) U. Braun and R.T.A. Cook, and *E. catalpae* Simonyan, on a wide range of hosts. More recently, additions to species belonging to the *E. aquilegiae* complex, such as *E. pedaliacearum* (H.D. Shin) H.D. Shin on sesame [44], *E. asclepiadis* U. Braun and V. Kumm. on *Asclepias tuberosa* L., *E. tortilis* (Wallr.) Link on *Cornus* spp., and two *Erysiphe* spp. on *Astilbe* × *arendsii* H.Hara and *Calystegia* sp. [69], provided insight into the discussions of this group. One of the viewpoints that an increasing number of new collections which pertain to the *E. aquilegiae* complex could be found [69] is compatible with our finding of *E. neolycopersici* on *C. halicacabum* in Taiwan. This extends the understanding of the potential host range of *E. neolycopersici* and the *E. aquilegiae* complex to the plant family Sapindaceae. Previous studies have demonstrated that the powdery mildew on tomato (*E. neolycopersici*) could cause infections on solanaceous hosts and alternative hosts within the other 12 plant families [85] and *Sedum alboroseum* Baker (synonym of *Hylotelephium erythrostictum* (Miq.) H. Ohba) (Crassulaceae) [86] through artificial inoculation. Well-designed cross-inoculation tests should be carried out to validate the pathogen–host relationship of this polyphagous powdery mildew. Beside the biological approach, using additional phylogenetic markers may provide better resolutions in the phylogenetic trees [44,69]. Our result supported the use of *TUB2*, a DNA marker offering additional diagnostic utility to powdery mildew [26], to distinguish species within the *E. aquilegiae* clade. However, it also revealed that *TUB2* sequences had limitations in resolving the *E. alphitoides* complex [36] (Figure 2). It is suggested that the increasing availability of multiple independent DNA barcodes [26] and the announcement of genome resources [43,87,88] will help the species delimitation and facilitate the exploration of the evolutionary history of the PMs.

#### 4.4. Perennation of Powdery Mildews in the Subtropics and the Impact on Crop Production

This study highlights three PMs on several herbaceous wild plants and crops around the agricultural environment in the subtropical region of Taiwan. The existence of the pathogens on the alternative hosts may play a key role in perennation, the process of surviving from

one season to another, in this group of obligatory parasites. Perennation of PMs under unfavorable conditions such as cold winter and hot summer temperatures may occur by the sexual reproduction of chasmothecia, infection in dormant buds, and persistence as mycelia [89]. Examples include overwintering of hop and cucurbit PMs through bud perennation [90,91] and chasmothecia [92], respectively, and over summering of wheat powdery mildew through chasmothecia [93]. In the present study, the occurrence periods of the PMs in the winter and spring imply they prefer mild weather instead of excessively high temperature (up to 35 °C) in summer, and it is suggested that the PMs in the subtropical regions may stay in a quiescent state in their hosts during hot summers. However, chasmothecia are rarely formed in subtropical and tropical environments [23,47,77,94]. Thus, the reservoirs of the PMs on all their possible hosts as mycelia or other structures are crucial for their survival and for the infection in the next season.

Considering the crop disease management related to the PMs in this study, if there exist essential reservoirs of the pathogen for each of the powdery mildews, the presence of alternative hosts in the vicinity may pose a significant impact on the disease development of the target crops. Taking water spinach as an example, the vegetable is fast growing [95], can be cultivated year round (up to 12–13 times a year), and the growing period is 2–4 weeks in Taiwan [96]. The harvest of the vegetable in short terms may interrupt the buildup of *E. ipomoeae* populations on the leaves, and this may explain why the powdery mildew disease on water spinach was not noticed in Taiwan [16]. However, an overlooked flourish of *I. obscura* nearby the vegetable field may serve as additional reservoir of the inocula according to our study results. The effect of lengthening the presence time of hosts is comparable with lengthening the growing season for plants, which would promote severe powdery mildew infections [97]. The conclusion is also in line with Mulpuri et al. [98], who state that continuous cultivation of crop, and even the existence of collateral hosts and weeds, will lead to increased inoculum load of PMs. It is suggested that more comprehensive knowledge of the PMs with a wide host range would be beneficial to management of crop diseases, e.g., awareness of the potential host associations of *E. ipomoeae*, *E. betae*, and *E. neolycopersici* may bring about improvements in cultural practices to reduce the inoculum. Finally, accurate recognition of the pathogen species and their hosts could minimize the risk of cryptic invasion [78] of PMs in a regional scale and in agricultural systems.

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