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Pseudoidium peltophori on the ornamental tropical tree legume *Peltophorum pterocarpum*: a new competing synonym of *Erysiphe quercicola*, and a new host record for Taiwan

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Abstract

An anamorphic powdery mildew fungus was observed on the leaves of two individual trees of *Peltophorum pterocarpum* (Fabaceae) for several years in Taiwan. The host and morphology initially suggested *Pseudoidium peltophori*. While the morphology of some conidiophores showed atypical long foot cells, sequences of the internal transcribed spacer ribosomal DNA and beta-tubulin genes identified the species as *Erysiphe quercicola*. Based on morphology and phylogeny, *Pseudoidium peltophori* is considered a synonym of *E. quercicola*, in addition to the older *E. cinnamomi*, originally described from *Cinnamomum camphora* in Taiwan.

Keywords – 1F1N – Erysiphaceae – fungal nomenclature – plant pathogenic fungi – powdery mildews

Introduction

During the study of powdery mildews on oak trees using molecular methods, it was revealed that the species complex of *Erysiphe alphitoides* (Griffon & Maubl.) U. Braun & S. Takam. comprises several teleomorph-based species, particularly *E. alphitoides sensu stricto*, *E. epigena* S. Takam. & U. Braun, *E. hypogena* S. Takam. & U. Braun, and *E. quercicola* S. Takam. & U. Braun. Additionally, mainly anamorphic taxa in the genera *Oidium* or *Pseudoidium* (*Ps.*) from predominantly tropical woody plants were found to be conspecific with *E. quercicola* (Limkaisang et al. 2006, Takamatsu et al. 2007, Siahaan et al. 2016). Due to the dual nomenclature for anamorphic and teleomorphic fungi, *Pseudoidium anacardii* (F. Noack) U. Braun & R.T.A. Cook emerged as the name with the oldest species epithet for the anamorph (Braun & Cook 2012). Since the dual nomenclature was abandoned in 2012, competition arose between the previously strictly separated names of anamorph and teleomorph stages of the same fungal species for priority. Braun (2013), therefore, proposed to conserve the teleomorph name *E. quercicola* against the oldest known name of the anamorph, *Oidium anacardii* Noack (= *Ps. anacardii*). This conservation was approved and included in Appendix IV of the International Code of Nomenclature for algae, fungi, and plants (Wiersema et al. 2018). However, this conservation did not affect other names that are also potential competing synonyms of *E. quercicola*.

Sawada (1919) described the powdery mildew on camphor trees, *Cinnamomum camphora* (L.) J. Presl in Taiwan as *Erysiphe cinnamomi* Sawada based on anamorph material. In 1959, he

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considered *E. cinnamomi* to be identical to the oak powdery mildew *E. alphitoides* (as *Microsphaera alphitoides* Griffon & Maubl.).

Braun & Cook (2012), when shifting the species name under the older dual nomenclature from *Erysiphe* to the anamorph genus *Pseudoidium* as *Ps. cinnamomi*, confirmed that this taxon was similar to the anamorph of *E. quercicola* and suggested resolving the relationship by molecular analyses or infection experiments.

Kirschner & Liu (2014) provided the first DNA data of *Ps. cinnamomi* and suggested the conspecificity of *Erysiphe cinnamomi* (= *Ps. cinnamomi*). *Erysiphe cinnamomi* and its synonyms from camphor tree hosts were tentatively listed as synonyms of *E. quercicola* (Kirschner & Liu 2014). The question posed by Kirschner & Liu (2014, p. 193), "Would *E. cinnamomi* have precedence over the younger name *E. quercicola* and its corresponding anamorph names, though *E. cinnamomi* is itself anamorph-typified?", however, has remained without discussion or answer. Since then, the name *E. quercicola* has been widely used in numerous publications (Siahaan et al. 2016, Qiu et al. 2017, Abasova et al. 2018, Dorneles et al. 2018, Fonseca et al. 2019, Meeboon & Takamatsu 2020, Afshan et al. 2022). The conspecificity of the fungus on the camphor tree with *E. quercicola* has never been challenged but has been confirmed (Dorneles et al. 2018, Bradshaw et al. 2022).

Among the powdery mildew species described in the anamorph genera *Oidium* and *Pseudoidium*, there might be further names potentially conspecific with *E. quercicola*. For example, *Pseudoidium peltophori* (J.M. Yen) U. Braun & R.T.A. Cook was described from the ornamental tropical legume tree *Peltophorum pterocarpum* (*Pe.*) (DC.) K. Heyne (Braun & Cooke 2012). In Taiwan, the tree was introduced in 1898 as ornamental (Hsueh & Yang 2008). For several years, we observed powdery mildew on the same trees, but the development of the colonies was weak, morphological characteristics varied, and attempts to extract DNA failed several times. Finally, the internal transcribed spacer region of the ribosomal RNA gene (ITS) and the gene coding for the beta-tubulin could be successfully amplified and sequenced. The ITS sequence suggested another host and synonym for *E. quercicola*.

Materials & Methods

Specimens of powdery mildew on *Pe. pterocarpum* were collected from two trees planted at Taichung High-Speed Railway station in March or April of 2020, 2022, 2023, and 2024. Searching for material from May to November was not successful. The collection site was not checked from December to February. The methods for preservation, morphology, and DNA analysis were applied as in Yeh et al. (2021) and yielded an ITS sequence (GenBank PP479113). Freshly collected anamorphic powdery mildews on leaves of *C. camphora* from National Taiwan University, Taipei City, Taiwan, collected on November 25, 2023, with voucher Yu-Wei Yeh AKII0191 (TNM), and on leaves of *Pe. pterocarpum* (R. Kirschner 5983-B) were used for amplification of the beta-tubulin gene (*TUB*) with the primers BtubF5b and BtubR7a (Ellingham et al. 2019) using the FailSafe™ PCR PreMix Selection Kit (Hoddesdon, UK). The resulting sequences were deposited in the DNA Databank of Japan (accession numbers LC804709 and LC810625, respectively). The *TUB* and ITS sequences were subjected to searches for sequences with the highest identities in GenBank using BLAST.

For the phylogenetic analysis, published ITS sequences were chosen from GenBank through BLAST searches (Kirschner et al. 2023) and through consulting the most recent and comprehensive sampling in Bradshaw et al. (2022), with *Erysiphe izuensis* (Y. Nomura) U. Braun & S. Takam. as the outgroup. The alignment was done using MUSCLE, implemented in MEGA version X (Kumar et al. 2018). After trimming the ends of the alignment without manual manipulation within the block, the alignment comprising 24 sequences with a total length of 577 characters (10.5281/zenodo.10867722) was subjected to a maximum likelihood analysis using the Kimura-2-parameter model with gamma distribution and 1000 bootstrap replications.

Results

The powdery mildew was observed on the two individuals of *Pe. pterocarpum*. The symptomatic leaves showed small and thin white colonies. The micromorphology differed slightly between the first and following collections. DNA was extracted and amplified from the second and fifth collections (R. Kirschner 5549 and 5983-B, respectively).

Phylogenetic analyses

The *TUB* sequences of *E. quercicola* from *C. camphora* and *Pe. pterocarpum* (both over 750 bp long) differed by a single base. The *TUB* sequence of *E. quercicola* from *C. camphora* in BLAST searches showed the highest similarities with those labeled as *E. quercicola* and *Oidium heveae* B.A. Steinm. from diverse host plants in GenBank with 0–2 base pair differences, while other species differed by at least nine base pairs.

BLAST searches with the ITS sequence from a specimen on *Pe. pterocarpum* (GenBank PP479113) showed high identities with those of *E. quercicola*, exceeding 600 bp with 0–5 base pair differences (99–100% identity). An exception was GenBank LC128428, which differed by 11 base pairs and had a 98% identity. Sequences labelled as *E. alphitoides* differed by at least 12 base pairs and had a maximum identity of 98%.

The dataset of the ITS phylogeny (Fig. 1) comprises 24 sequences with a length of 577 characters. The clade comprising samples of *E. quercicola* on different hosts from different countries is confirmed with solid support. The sequence from our specimen on *Pe. pterocarpum* formed a weakly supported subclade with a sequence from *E. quercicola* on *C. camphora* from Brazil. *Erysiphe alphitoides* formed a polytomy in the maximum likelihood analysis (Fig. 1), but formed a discrete subclade with 85% support in the neighbor joining analysis (not shown).

Taxonomy

Erysiphe quercicola S. Takam. & U. Braun, in Takamatsu, Braun, Limkaisang, Kom-un, Sato & Cunnington, Mycol. Res. 111(7): 819 (2007), nom. cons. [against *Oidium anacardii* Noack in Bol. Inst. Estado São Paulo 9(2): 77. 1898, nom. rej.] Figs 2–3

Synonyms - see Bradshaw et al. (2022).

Additional synonyms from Kirschner & Liu (2014):

= *Erysiphe cinnamomi* Sawada, Rep. Dept Agric., Govern. Res. Inst. Formosa, Spec. Bull. Agric. Exp. Station Formosa 19: 144 (1919).

= *Oidium erysiphoides* f. *cinnamomi* J.M. Yen, Cahiers Pacif. 11: 96 (1967)

≡ *Oidium cinnamomi* (J.M. Yen) U. Braun, Mycotaxon 25(1): 266 (1986)

≡ *Pseudoidium cinnamomi* (Sawada) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 601 (2012)

New synonyms:

= *Oidium erysiphoides* f. *peltophori* J.M. Yen, Revue Mycol., Paris 31(4): 289 (1966) [not page 290 as in Braun & Cook (2012)]

≡ *Oidium peltophori* (J.M. Yen) Boesew. Bot. Rev. 42(2): 172 (1980)

[not the authors (J.M. Yen) Hosag., Vijay., Udaiyan & Manian as in Braun & Cook (2012)]

≡ *Pseudoidium peltophori* (J.M. Yen) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 615 (2012)

? = *Oidium peltophori* var. *indicum* Hosag., Vijay., Udaiyan & Manian, Indian J. For. 15(2): 161 (1992), not seen

Colonies predominantly epiphyllous, scattered and sparse on leaf blades, white. *Hyphae* hyaline, smooth to verruculose, 3–8 µm wide. *Appressoria* nipple-shaped or lobed, exceptionally elongate, solitary or in opposite pairs. *Conidiophores* arising from the center or near a septum of the hyphal mother cell, erect, straight or slightly curved at the base, finely verruculose, (40–)54–81(–90)

× (6–)6.5–9(–11) µm (n = 30; R. Kirschner 4924); in youngest colonies on youngest leaf pinnules occasionally presumably underdeveloped without conidium production, consisting of 2–3 cells; terminal cell cylindrical or slightly wider than the basal cell, apex pointed or broadly rounded, 88–130 × 6–8 µm (only in R. Kirschner 4924). Foot cell cylindrical, straight or curved at base, basal septum at level with the upper surface of hyphal mother cell or shifted distally for up to 3 µm (R. Kirschner 5549) or up to 7 µm (R. Kirschner 4924), (15–)20–30(–43) × (7–)8–9.5(–10) µm (n = 30; R. Kirschner 5549) or (22–)27.5–49(–57) × 5–8(–10) µm (n = 30; R. Kirschner 4924), followed by 0–2 shorter cells. *Conidia* solitary, ovoid, doliiform to cylindrical, with fine longitudinal striation on surface, (26–)30–39(–45) × 15–22(–23) µm (n = 30; R. Kirschner 5549) or (25–)27.5–36(–41) × (12–)14–17(–20) µm (n = 30; R. Kirschner 4924), germination at one end with single hypha.

Known distribution – Widespread in temperate, subtropical and tropical regions (Bradshaw et al. 2022).

Material examined – Taiwan, Taichung City, Wuri District, Taiwan High-Speed Rail Taichung Station, 24.110416 N, 120.615104 E, ca. 30 m, on leaves of *Peltophorum pterocarpum* (DC.) K. Heyne, 27 Apr 2020, R. Kirschner 4924 (TNM); *ibid*., 22 Apr 2022, R. Kirschner 5549 (TNM; ITS GenBank PP479113), *ibid*., 24 Mar 2023, R. Kirschner 5720 (TNM); *ibid*., 22 Mar 2024, R. Kirschner 5983 (TNM); *ibid*., 29 Mar 2024, R. Kirschner 5983-B (*TUB* GenBank LC810625).

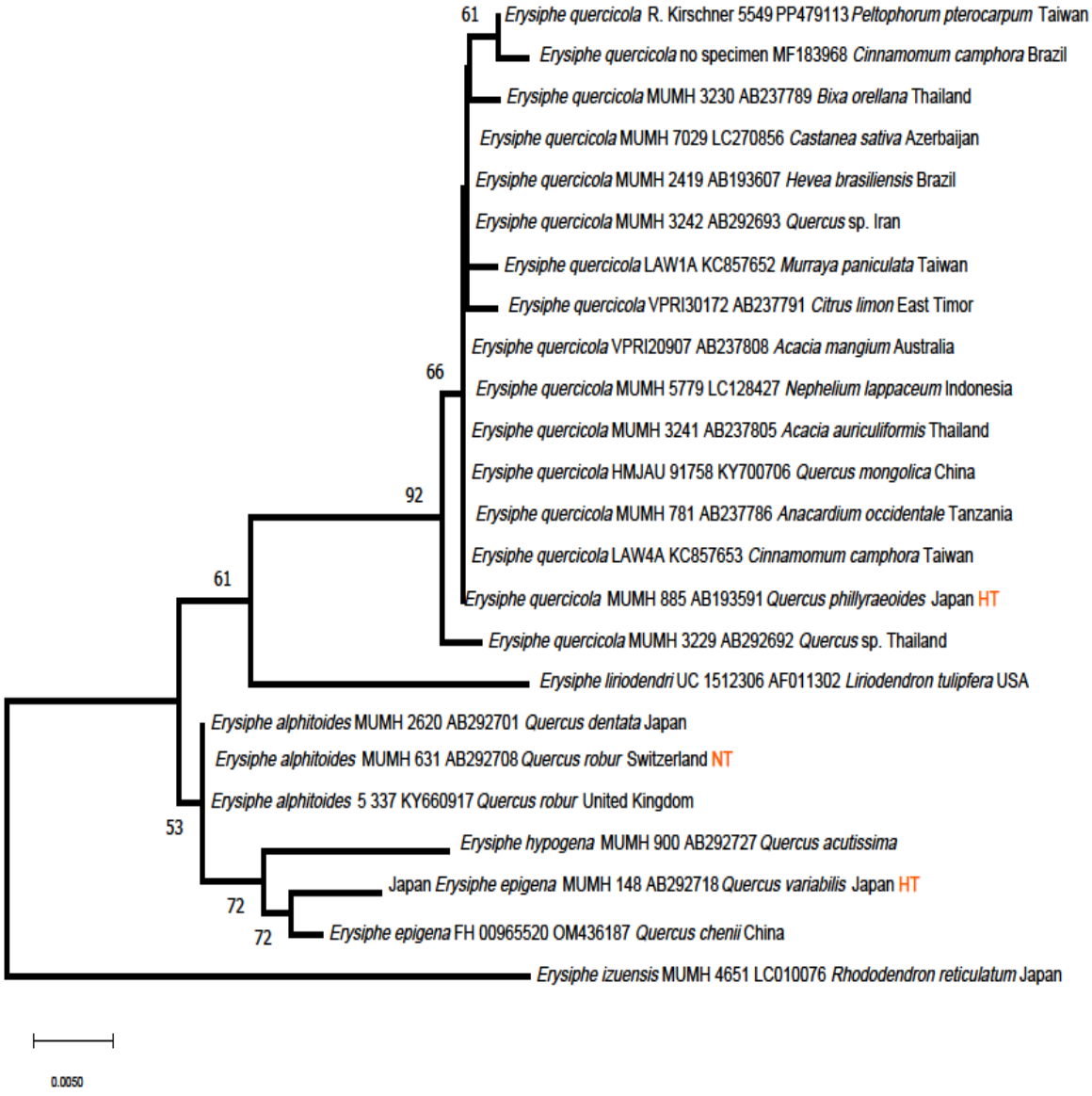

Fig 1 – Unrooted maximum likelihood analysis of ITS sequences of *Erysiphe quercicola* and related

Erysiphe species, with *E. izuensis* as outgroup and 1000 bootstrap replications. After the scientific name, the specimen and GenBank accession numbers are given, followed by the host name and country. **HT** and **NT** denote the holotype or neotype, respectively.

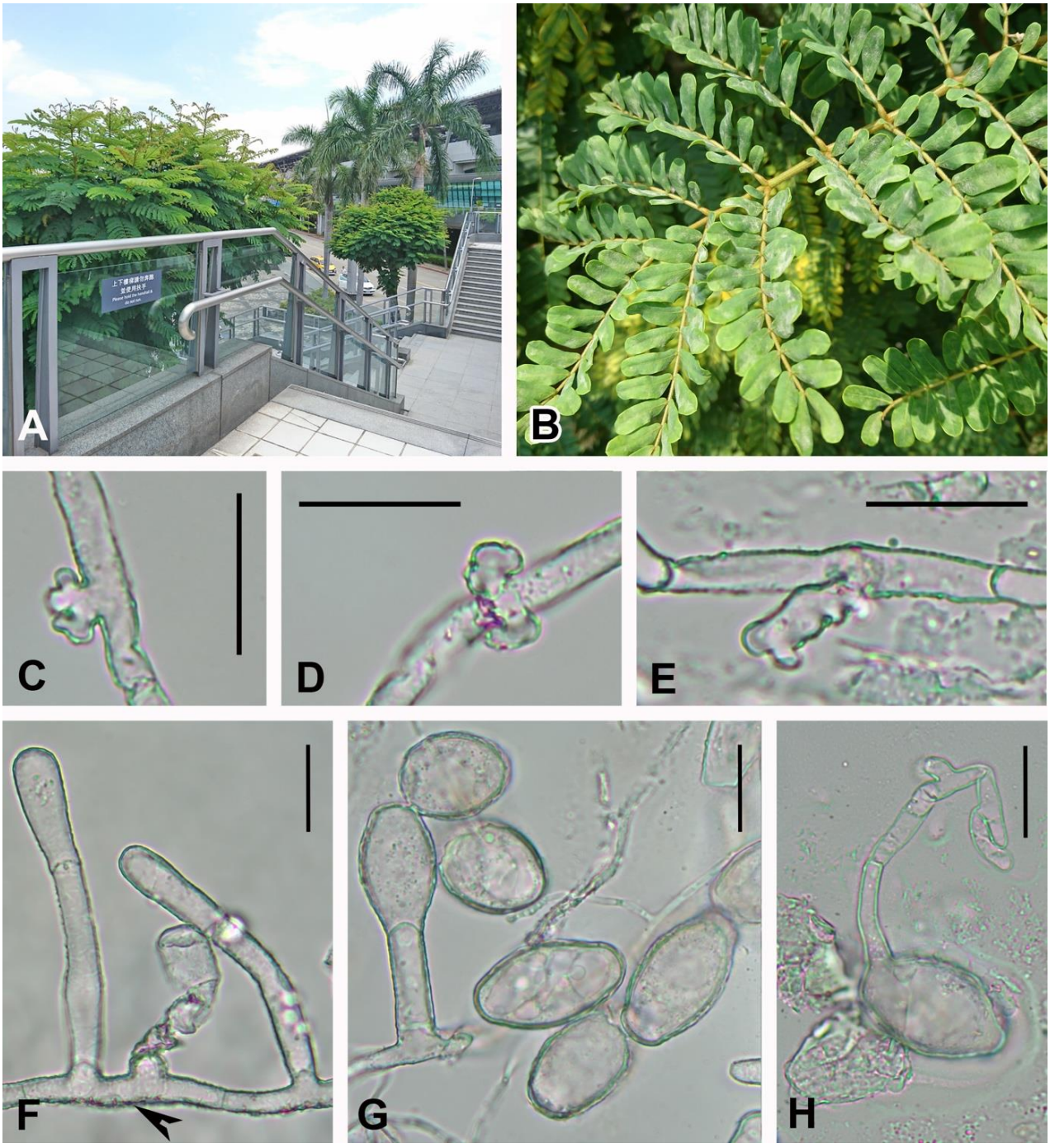

Fig 2 – *Erysiphe quercicola* on *Peltophorum pterocarpum* (R. Kirschner 5549, except B: R. Kirschner 5720). A Habitat photo of the two tree crowns of *Pe. pterocarpum*. B Young leaf with powdery mildew symptoms. C–E Hyphal appressoria. C Solitary, lobed appressorium. D Pair of opposite, lobed appressoria. E Exceptionally elongated appressorium. F Three conidiophores, two of them arising from the same hyphal mother cell (pointed by arrowhead). G Short conidiophore and conidia. H Germinating conidium. Scale Bars = 20 µm.

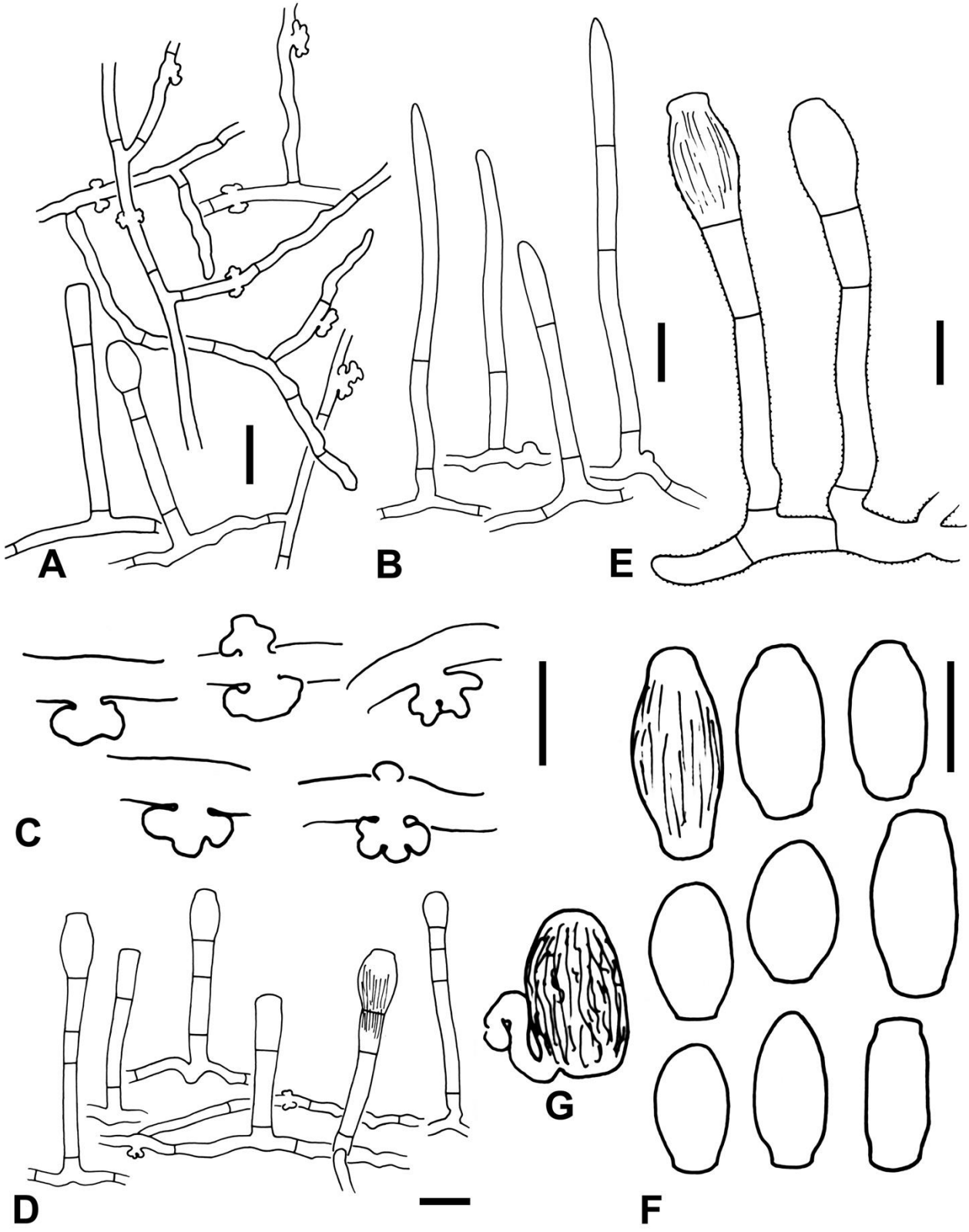

Fig 3 – *Erysiphe quercicola* on *Peltophorum pterocarpum* (R. Kirschner 4924). A Hyphae with appressoria and two conidiophores. B Underdeveloped conidiophores from the young colony. C Solitary and opposite lobed appressoria. D Conidiophores arising from hyphae with appressoria (verruculose surface not indicated). E Two conidiophores with verruculose surface. F Conidia (striate surface indicated in uppermost left conidium). G Germinating conidium. Scale Bars = 20 µm, except in C = 10 µm.

Discussion

In the phylogenetic analysis, the ITS sequences of *E. alphitoides* formed a polytomy, consistent with the results of Kirschner & Liu (2014) and Dorneles et al. (2018). As Bradshaw et al. (2022) pointed out, sequences of the ribosomal RNA gene region do not allow for sufficient resolution of *E. alphitoides* and closely related species. However, the clade comprising sequences of *E. quercicola* could be reproduced with sufficient support. This clade of *E. quercicola* included the sequences from the camphor tree host (Kirschner & Liu 2014, Dorneles et al. 2018), as confirmed by Bradshaw et al. (2022) as well as the new host *Pe. pterocarpum*.

In Taiwan, *E. quercicola* on camphor tree is one of the most common powdery mildews, mostly infecting young leaves and, therefore, being obvious on suckers and seedlings (Chang et al. 1999). Another common host throughout Taiwan is *Murraya paniculata* (L.) Jack (Rutaceae; Chang et al. 1999, Kirschner & Liu 2014). The teleomorph has not been found on either of these hosts (Chang et al. 1999, Kirschner & Liu 2014). Although *E. cinnamomi* was proposed by Sawada (1919) for the anamorphic stage on camphor trees in Taiwan, this species' name anticipated the unified nomenclature effective since 2012. As outlined above, *E. cinnamomi* competes with the later *E. quercicola* S. Takam. & U. Braun (2007). Hitherto, only *Oidium anacardii* has been rejected, but not the other synonyms of *E. quercicola* (Braun 2013). Conserving teleomorph-based names against old anamorph-based names has the advantage of more convenient morphological identification of the teleomorph compared to the anamorph (Braun 2013). Many new records of *E. quercicola* were based on anamorphic specimens and DNA sequence data (e.g., Qiu et al. 2017, Abasova et al. 2018, Dorneles et al. 2018, Fonseca et al. 2019, Afshan et al. 2022). Since the younger synonym, *E. quercicola* has become widely used, it will be proposed for protection or conservation in another publication.

As shown by the powdery mildew on *Pe. pterocarpum*, there might be further older names synonymous with *E. quercicola*. The conidial width is very narrow (9–19 µm) in Braun & Cook (2012), but given as 14–19(–21.5) µm in the original description of *Oidium erysiphoides* f. *peltophori* by Yen (1966). The conidium width found in our specimens fits that described by Yen (1966). Sizes of foot cells were variable in the specimens on *Pe. pterocarpum*, with the longer ones conforming to the description of *Ps. cinnamomi* and *Ps. peltophori*, and the shorter ones to *E. quercicola* in Braun & Cook (2012). Considerable variation in the sizes of foot cells was demonstrated for *E. quercicola* on diverse hosts in Thailand (Meeboon & Takamatsu 2020). Such differences, in some cases, are diagnostic for species, but in others, they seem to depend on the environment (Wang et al. 2020). For several old names of powdery mildews, new collections, DNA sequence data, and morphological analyses are still necessary to clarify further potential synonymies (Yeh et al. 2021). Another powdery mildew on *C. camphora* is hitherto only known as the type in the USA, *Erysiphe cinnamomicola* U. Braun & S. Takam., i.e., outside the native range of distribution of the host tree (Braun & Cook 2012). It is known only as a teleomorph which has rather diffusely branched ascomatal appendages, differing from the densely forked tips of appendages of *E. quercicola* (Braun & Cook 2012). Further study of the powdery mildew on camphor trees in America in the teleomorph stage should clarify whether the hitherto single gathering represents a distinct species or an atypically developed specimen of *E. quercicola*.

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Accessibility of data

For identifiers of material and data deposited in public collections (TNM), databases (GenBank) and data repositories (zenodo), see Materials & Methods and Results.

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