Mycological Progress (2026) 25:27
https://doi.org/10.1007/s11557-026-02137-z

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ORIGINAL ARTICLE

A unique ecological role of the entomopathogenic fungus *Metarhizium koreanum* in infecting plant peltate glands

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Received: 9 January 2026 / Revised: 9 March 2026 / Accepted: 16 March 2026
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Abstract

Metarhizium koreanum, a known entomopathogenic fungus previously reported only from insect hosts, was discovered colonizing the peltate glands on the abaxial leaf surface of *Clerodendrum japonicum* var. *japonicum* in Taiwan. Field surveys consistently showed that the fungus was exclusively associated with sand-colored glands, whereas uninfected glands remained transparent. The transition from transparent to yellow–brown coloration was found to result from fungal infection. This phenomenon had previously been misinterpreted as an inherent trait of the host plant. Morphological examination and multilocus phylogenetic analyses (ITS, *TUB*, *TEF-1α*, and *RPB1*a) confirmed the identity of the isolates as *M. koreanum*. Endophyte isolation assays did not recover the fungus from surface-sterilized leaf lamina segments lacking infected peltate glands, indicating that *M. koreanum* does not occur as an endophyte. Pathogenicity tests further confirmed the ability of *M. koreanum* to infect the foliar glands. This study represents the first report of a *Metarhizium* species infecting a flowering plant, although colonization appears limited to external glandular structures. This unique association raises intriguing questions about potential plant–fungus–insect interactions, especially given the overlapping geographic distribution of *C. japonicum* var. *japonicum* and *M. koreanum* in Japan, South Korea, Taiwan, and Thailand.

Keywords *Clerodendrum japonicum* var. *japonicum* · Entomopathogen · Phytopathogen · Gland-specific

Introduction

Clerodendrum japonicum var. *japonicum* (*Lamiaceae*) is a shrub native to lowland to mid-elevation regions across Taiwan. It typically grows along forest edges, roadsides, and in secondary woodlands. The species is characterized by large opposite leaves and terminal inflorescences bearing predominantly red flowers, with occasional white-flowered individuals reported. Historically referred to as *Clerodendrum kaempferi* (Yang et al. 1998), it is currently treated as *C. japonicum* var. *japonicum* following taxonomic revision (World Flora Online 2025).

Clerodendrum japonicum var. *japonicum* is also characterized by the presence of peltate glands on the abaxial leaf surface, which are transparent but often coated with a sand-colored (yellow–brown) secretion (World Flora Online 2025). During field surveys in Taiwan, we observed that the sand-colored peltate glands were consistently permeated by fungal growth, whereas the other glands that appeared transparent were uncolonized. Notably, only the peltate glands were colonized by the fungus, while the surrounding leaf tissue remained unaffected. This pattern suggests that the sand-colored appearance is due to fungal colonization rather than plant secretion. The fungus was morphologically consistent with species of the genus *Metarhizium*.

Metarhizium species are best known as entomopathogens, although some species have also been reported as saprophytes, pathogens of lizards and mushrooms, and most notably, as plant endophytes (Tang et al. 2025). Despite their ecological versatility, there have been no reports of *Metarhizium* species acting as plant pathogens. Given that the only known plant-associated behavior of *Metarhizium* is endophytism, the consistent colonization of the peltate glands on *Clerodendrum japonicum* var. *japonicum* raises the question of whether the fungus originates from internal plant tissues or whether it exhibits pathogenicity by infecting from an external inoculum. To explore whether the fungus was endophytic,

Section Editor: Marco Thines

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Published online: 13 April 2026

leaves were thoroughly surface-sterilized prior to fungal isolation. To determine whether the fungus was pathogenic to the plant, inoculation experiments were conducted. In addition, morphological and molecular analyses were performed to precisely determine the identity of the fungus.

In this study, we report the discovery of an entomopathogenic fungus, *Metarhizium koreanum*, colonizing the peltate glands of *Clerodendrum japonicum* var. *japonicum*. This is the first documentation of a *Metarhizium* species exhibiting apparent pathogenicity toward a plant. The findings presented here raise intriguing questions about the ecological and evolutionary significance of *Metarhizium*–plant interactions.

Materials and methods

Sample collection and fungal isolation

Leaves of *Clerodendrum japonicum* var. *japonicum* exhibiting discolored glands were collected across Taiwan during 2020 and 2024. Single-spore isolations were performed. A sterile inoculation loop was used to pick up conidia on the surface of glands. The conidia were then streaked onto 2% water agar (WA). After incubation at room temperature (~25 °C) for approximately 24 h, plates were observed under a stereomicroscope to locate germinated conidia. Agar blocks containing single germinated conidia were then transferred to potato dextrose agar (PDA; Difco, USA) and incubated at 25 °C to establish pure cultures. All isolates obtained in this study are preserved at the Mycology Laboratory, Department of Plant Pathology, National Chung Hsing University (NCHU), Taichung, Taiwan. Selected strains have also been cryopreserved at the Bioresource Collection and Research Center (BCRC), Hsinchu, Taiwan.

Morphological characterization

Fungal strains were cultured on potato dextrose agar (PDA) and SDAY (1/4 strength) media [SDAY: 10 g bacto peptone, 40 g dextrose, 2.5 g yeast extract, 20 g agar per liter] and incubated at 25 °C under ambient light/dark conditions. Colony morphology was assessed after 7 and 14 days of incubation. Microscopic characteristics were examined in situ on the peltate glands, and from cultures grown on PDA and SDAY media. Observations and measurements were conducted using slide preparations with water as the mounting medium, and representative images were captured for documentation.

Histological examination of peltate glands

To examine internal colonization of peltate glands by *Metarhizium koreanum*, cross-sections of both transparent (non-infected) and yellow (infected) glands were prepared. Leaf segments containing peltate glands were excised and sectioned by using a freezing microtome. Sections were cut at approximately 20 µm thickness and mounted in water without staining.

Fungal DNA extraction, PCR, and sequencing

Genomic DNA was extracted from fungal colonies grown on PDA for one week using the commercial Plant Genomic DNA Purification Kit (Biokit, Taiwan), following the manufacturer's instructions. The PCR reactions were performed using PowerPol 2X PCR Mix (ABclonal Inc., Massachusetts, USA) under the thermocycling conditions listed in Table 1.

Partial sequences of four loci were amplified by PCR: the internal transcribed spacer (ITS) regions using primer

Table 1 Primer pairs, sequences, and PCR reaction conditions used in the present study

Locus	Primer	Orientation	Primer sequence (5'- 3')	PCR amplification procedures	Reference
ITS	ITS5	Forward	GGAAGTAAAAGTCGTAACAAGG	95 °C 5 min; 35 cycles of 95 °C 30 s, 55 °C 30 s, 72 °C 60 s; 72 °C 10 min	White et al. (1990)
	ITS4	Reverse	TCCTCCGCTTATTGATATGC		White et al. (1990)
TUB	Bt1F	Forward	GGTCCCTTCGGTCAGCTCTTCC	95 °C 5 min; 35 cycles of 95 °C 30 s, 54 °C 30 s, 72 °C 60 s; 72 °C 10 min	Bischoff et al. (2009)
	Bt1R	Reverse	CAGCCATCATGTTCTTAGGGTC		Bischoff et al. (2009)
*RPB1*a	MzR1-1328F	Forward	GACTGYCCYGGTCAYTTTGGAC	95 °C 5 min; 35 cycles of 95 °C 30 s, 58 °C 30 s, 72 °C 90 s; 72 °C 10 min	Designed in the present study
	MzR1-2822R	Reverse	GGCACCCARAGCATCATGTTCAT		Designed in the present study
EF-1α	EF1-983F	Forward	GCYCCYGGHCAYCGTGAYTTYAT	95 °C 5 min; 35 cycles of 95 °C 30 s, 53 °C 30 s, 72 °C 90 s; 72 °C 10 min	Rehner and Buckley (2005)
	EF1-2218R	Reverse	ATGACACCRACRGCRACRGTYTG		Rehner and Buckley (2005)

ITS5 and ITS4 (White et al. 1990); beta tubulin (*BTUB*) with primer BT1F and BT1R (Bischoff et al. 2009); translation elongation factor 1 alpha (*TEF-1α*) with primers EF1-983F and EF1-2218R (Rehner and Buckley 2005); and the largest subunit of RNA polymerase II (*RPB1*a) with primers MzR1-1328F (5'-GACTGYCCYGGTCAYTTTGGAC-3') and MzR1-2822R (5'-GGCACCCARAGCATCATGTTCAT-3') (designed in the present study).

PCR products were visualized by agarose gel electrophoresis, and target bands were subsequently purified. The same primers used in PCR amplification were employed for sequencing reactions. Sequencing was carried out on an ABI PRISM 377 DNA sequencer at the Biotechnology Center of National Chung Hsing University. All resulting sequences have been deposited in the NCBI GenBank database (Table 2).

Table 2 List of sequences used in the phylogenetic analyses. Type strains are indicated by superscript T

Strain	Species	Host	Geography	GenBank accession no.				Reference
				ITS	*TUB*	*TEF-1α*	*RPB1a*	
CBS 218.56^T	*Metarhizium flavoviride*	*Coleoptera*	Czech Republic	-	KJ398555	KJ398787	KJ398598	Kepler et al. (2014)
ARSEF 4124^T	*Metarhizium frigidum*	*Coleoptera*	Australia	-	EU248828	DQ464002	DQ468361	Bischoff et al. (2006, 2009)
ARSEF 2038^T	*Metarhizium koreanum*	*Hemiptera: Delphacidae*	Korea	-	KJ398577	KJ398805	KJ398615	Kepler et al. (2014)
ARSEF 2039	*Metarhizium koreanum*	*Hemiptera: Delphacidae*	Korea	-	KJ398578	KJ398806	KJ398616	Kepler et al. (2014)
BCC 27998	*Metarhizium koreanum*	*Hemiptera: Fulgoromorpha*	Thailand	MN781903	-	MN781700	-	Mongkolsamrit et al. (2020)
BCC 30455	*Metarhizium koreanum*	*Hemiptera: Fulgoromorpha*	Thailand	MN781904	-	MN781701	MN781750	Mongkolsamrit et al. (2020)
SX01 (FU31599)	*Metarhizium koreanum*	*Clerodendrum japonicum* var. *japonicum*	Taiwan	PV444756	PV461176	PV461173	PV461170	The present study
SX02 (FU31600)	*Metarhizium koreanum*	*Clerodendrum japonicum* var. *japonicum*	Taiwan	PV444757	PV461177	PV461174	PV461171	The present study
SX03 (FU31601)	*Metarhizium koreanum*	*Clerodendrum japonicum* var. *japonicum*	Taiwan	PV444758	PV461178	PV461175	PV461172	The present study
SX05	*Metarhizium koreanum*	*Clerodendrum japonicum* var. *japonicum*	Taiwan	PV533905	PV540748	PV540751	PV540749	The present study
SX08	*Metarhizium koreanum*	*Clerodendrum japonicum* var. *japonicum*	Taiwan	PV533906	-	PV540752	PV540750	The present study
ARSEF 2037^T	*Metarhizium minus*	*Hemiptera*	Philippines	-	KJ398576	DQ522353	DQ522400	Bischoff et al. (2006); Kepler et al. (2014)
ARSEF 6569	*Metarhizium pemphigi*	*Hemiptera*	United Kingdom	-	KJ398586	KJ398813	KJ398624	Kepler et al. (2014)
ARSEF 7491	*Metarhizium pemphigi*	*Hemiptera*	United Kingdom	-	KJ398591	KJ398819	KJ398629	Kepler et al. (2014)
ARSEF 13510^T	*Metarhizium argentinense*	*Blaberidae: Epilamprinae*	Argentina	-	MF966623	MF966624	MF966625	Gutierrez et al. (2019)
BCC 51812^T	*Metarhizium biotecense*	*Hemiptera: Delphacidae*	Thailand	MN781878	-	MN781693	MN781745	Mongkolsamrit et al. (2020)
ARSEF 12850^T	*Metarhizium blattodeae*	*Blattodea*	Brazil	KU182915	KU182914	KU182917	KU182918	Montalva et al. (2016)
BCC 28246^T	*Metarhizium fusoideum*	*Lepidoptera*	Thailand	MN781893	-	MN781699	MN781749	Mongkolsamrit et al. (2020)
BCC 7600^T	*Metarhizium culicidarum*	*Diptera: Culicidae*	Thailand	MN781889	-	MN781707	MN781754	Mongkolsamrit et al. (2020)
BCC 25948^T	*Metarhizium nornnoi*	*Coleoptera:* adult beetle	Thailand	MN781892	-	MN781697	MN781748	Mongkolsamrit et al. (2020)
CCTCC M 2016588^T	*Metarhizium gaoligongense*	Soil	China	KY087808	-	KY087820	KY087824	Chen et al. (2018)
NBRC 112661^T	*Metarhizium bibionidarum*	*Diptera: Bibionidae*	Japan	-	LC126066	LC126076	LC125908	Nishi and Sato (2017)
CBS 464.88^T	*Metapochonia rubescens*	Nematode eggs	Scotland	-	KJ398552	EF468797	EF468903	Kepler et al. (2014); Sung et al. (2007)
CBS 101433^T	*Metapochonia microbactrospora*	Bdelloid rotifers	Japan	-	KJ398562	KJ398794	KJ398605	Kepler et al. (2014)

Molecular phylogenetic analysis

For the phylogenetic analyses, sequences of the *Metarhizium flavoviride* species complex, which *Metarhizium koreanum* belongs to, were retrieved from GenBank. Sequences of *Metapochonia microbactrospora* CBS 101433 and *Metapochonia rubescens* CBS 464.88 were selected as outgroups (Table 2). Each gene region was aligned individually using MAFFT v7.407 through the NGPhylogeny.fr platform (Lemoine et al. 2019), and alignments were manually adjusted where necessary. Ambiguously aligned regions were trimmed using Gblocks (for ITS) or BMGE (for *TEF-1α*, *TUB*, and *RPB1*a) with default parameters.

Maximum likelihood (ML) analysis was performed using IQ-TREE v2.4.0 (Minh et al. 2020) on the concatenated dataset comprising ITS, *TEF-1α*, *TUB*, and *RPB1*a sequences. The best-fit substitution model for each gene partition was selected using ModelFinder (Kalyaanamoorthy et al. 2017). Branch support was evaluated using both SH-like approximate likelihood ratio test (SH-aLRT; 1,000 replicates) and ultrafast bootstrap approximation (UFBoot; 1,000 replicates). Node support values in the consensus tree represent the more conservative of the two (i.e., the minimum of SH-aLRT and UFBoot), as automatically output by IQ-TREE.

Bayesian phylogenetic inference was conducted using MrBayes v3.2.7a (Ronquist et al. 2012) with the same partition scheme and substitution models inferred from the ML analysis (TN + F + G4 for all regions). Each partition was assigned a transitional model (nst = 2) with a gamma-distributed rate variation and empirical nucleotide frequencies. Two independent MCMC runs were executed for 2,000,000 generations, each with four chains, sampling every 1,000 generations. Convergence was confirmed in Tracer v1.7.2 (Rambaut et al. 2018), with all parameters showing effective sample sizes (ESS) > 200. A 50% majority-rule consensus tree was generated after discarding the first 25% of trees as burn-in.

Branch support values in the resulting phylogenetic tree are displayed as posterior probabilities/SH-aLRT support/UFBoot support.

Survey of herbarium specimens for *Metarhizium koreanum*

To assess the prevalence of *Metarhizium koreanum* associated with the peltate glands on *Clerodendrum japonicum* var. *japonicum*, examination of herbarium specimens was conducted. Specimens of this plant species preserved at the Herbarium of the Department of Forestry, National Chung Hsing University, were examined.

Endophyte isolation

To determine whether *Metarhizium koreanum* is endophytic within the tissues of *Clerodendrum japonicum* var. *japonicum*, three types of leaf material were examined:

1. Whole leaves without infected glands (no visible yellow–brown glands);
2. Leaves with visibly infected glands, from which segments were excised directly from infected gland areas;
3. Leaves with partially infected glands, from which isolation was performed exclusively on areas lacking infected glands.

Treatment (1) was designed to test whether *M. koreanum* is endophytic within leaf tissues in the absence of visible gland infection. If the fungus were capable of systemic or latent endophytic colonization, it would be expected to be recoverable from such asymptomatic leaves. Treatment (2) was included as a sterilization control, to verify that the surface-sterilization protocol did not eliminate *M. koreanum* when present in leaf tissue. Treatment (3) was designed to examine whether *M. koreanum* could be present endophytically in leaf lamina tissue adjacent to infected glands. If the fungus were capable of endophytic colonization, recovery would be expected from asymptomatic areas of partially infected leaves.

Leaves were first rinsed with sterile reverse osmosis (RO) water to remove surface debris. Leaf blades were cut into approximately 0.5 × 0.5 cm segments. In treatment (3), segments were carefully excised only from areas without visible infected glands, avoiding direct contact with colonized gland structures. Segments were surface-sterilized by immersion in 2% sodium hypochlorite for 2, 5, 10, or 15 min, followed by sequential immersion in 70% ethanol for 1 min and 95% ethanol for 1 min. The segments were then rinsed twice with sterile RO water (1 min each), air-dried under sterile conditions, and plated onto oatmeal agar (OA) amended with 0.6 g/l CTAB (Posadas et al. 2012).

For each sterilization duration, four leaf segments were placed on each plate, and three plates were prepared, resulting in a total of 12 segments per sterilization duration (2, 5, 10, and 15 min) for each tissue condition. Fungal growth was assessed after 7 days of incubation at 25 °C under ambient light/dark conditions. Isolation frequency was calculated as the percentage of segments (out of 12) from which *M. koreanum* was recovered for each sterilization duration.

Pathogenicity test

To evaluate whether *Metarhizium koreanum* is pathogenic to peltate glands, a pathogenicity assay was conducted on three young leaves of *Clerodendrum japonicum* var. *japonicum*

that exhibited no visible signs of infection (i.e., all glands were transparent and lacked yellow–brown pigmentation). Each leaf represented one biological replicate. On each leaf, six 1 × 1 cm squares were delineated on the abaxial surface using a fine-tip marker. Two inoculation treatments were applied: (1) inoculation following wounding of the peltate glands, and (2) inoculation without wounding. Wounding was performed within the marked squares using a No. 00 insect pin to gently scratch the surface of the peltate glands, mimicking minor physical damage. The area within each square represented the wounded treatment, whereas the area immediately adjacent to the right side of each square served as the unwounded treatment.

A conidial suspension of *Metarhizium koreanum* (isolate SX05) was prepared at a concentration of 1×10^5 conidia/ml in 0.5% (w/v) water agar solution supplemented with 0.05% (v/v) Tween 20. A total of 60 µl of this suspension was carefully applied to each square and its adjacent unwounded area. As a negative control, one square per leaf was treated with sterile 0.5% water agar containing 0.05% Tween 20 but without fungal spores. Following inoculation, the petioles of leaves were wrapped by moist tissue paper, and then incubated in moist chambers at 25 °C in the dark for 14 days. An inoculation site was considered positive if more than 15 peltate glands within the wounded square or within the adjacent unwounded area exhibited visible symptom with fungal colonization attributable to *M. koreanum*, the area of inoculation was considered positive for infection. Colonies on the infected glands were examined microscopically to confirm their identity.

Results

During the survey *of Clerodendrum japonicum* var. *japonicum* across Taiwan, eleven locations were found (Supplementary Table S1). It was ascertained that a species of *Metarhizium* is consistently found on the peltate glands. This species is identified as *Metarhizium koreanum* based on morphological features and phylogenetic analyses.

Ecological observations about the occurrence of the *Metarhizium* species on *Clerodendrum japonicum* var. *japonicum*

Comprehensive observations revealed a consistent pattern in the colonization of peltate glands by the *Metarhizium* fungus on individual plants of *Clerodendrum japonicum* var. *japonicum* (Fig. 1a–b). Newly emerged young leaves were free from fungal infection, and their peltate glands appeared transparent. As leaves matured, some of the peltate glands gradually developed a sand-colored appearance, indicating the onset of fungal colonization. With increasing leaf age, the number of sand-colored glands increased, suggesting progressive spread of the fungus. This trend was evident within individual leaves and across the plant, as older leaves exhibited a higher proportion of infected glands. Since *C. japonicum* var. *japonicum* is a deciduous species, its leaves are shed during the dry season or winter. After seasonal leaf shedding, newly emerged leaves were initially uninfected, resulting in a temporary absence of sand-colored glands. However, fungal colonization reappears and gradually intensifies as the foliage matures.

There were no symptoms on the leaf blades, with the glands showing variable extents of infection (Fig. 1c). Healthy peltate glands were typically full, translucent, and glistening (Fig. 1d). Once infected, they gradually changed from transparent to pale yellow, becoming turbid and opaque (Fig. 1e–g). The fullness of the peltate glands decreased as their colour shifts. Fungal hyphae emerged progressively from the edge of the opaque yellow glands, eventually giving rise to visible conidial masses (Fig. 1h–j), namely sporodochia. As hyphal growth and conidiation proceeded, the underlying peltate glands began to shrink and wither, with their colour gradually turning brown (Fig. 1h–j). Sporodochia initially appeared white and turned green as they mature. Occasionally, the sporodochia on the glands were dislodged (Fig. 1k) from the severely infected peltate glands.

Internal colonization of peltate glands

To determine whether fungal colonization occurred within glandular tissues prior to visible surface sporulation, microtome cross-sections of peltate glands were prepared and examined microscopically (Fig. 2).

In transparent glands lacking visible discoloration, tissues appeared intact, and no fungal hyphae were observed (Fig. 2a). In contrast, cross-sections of yellow glands revealed hyphae within the tissue even in the absence of external sporodochia (Fig. 2b), indicating internal colonization preceding surface conidiation. In addition to hyphal presence, yellow intracellular granular deposits were observed within cells of infected glands (Fig. 2b). These deposits were absent in transparent glands and may represent a host-associated tissue response associated with fungal invasion.

Phylogenetic analyses

Five strains of *Metarhizium* obtained from the glands of *Clerodendrum japonicum* var. *japonicum* were used. Based on the analyses of both maximum-likelihood (ML) and Bayesian inference (BI), all these 5 strains were nested within the clade composed exclusively of *Metarhizium koreanum* strains from insects (Fig. 3).

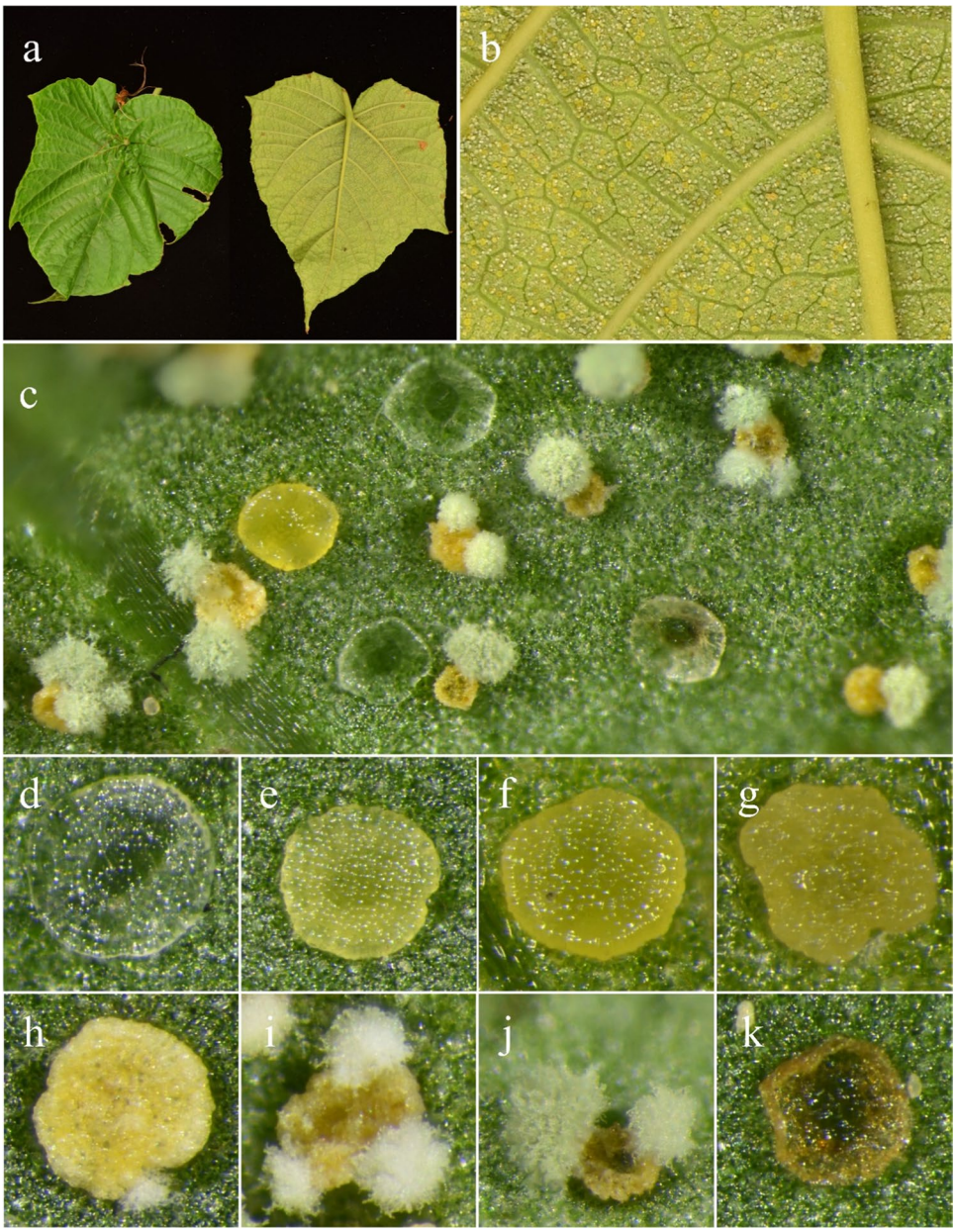


Fig. 1 Features of *Metarhizium koreanum* on peltate glands of *Clerodendrum japonicum* var. *japonicum* observed in nature and the infection process. **a** Adaxial and abaxial surfaces of infected leaves. **b** Close-up of the abaxial surface showing infected peltate glands. **c** Peltate glands showing varying degrees of infection and associated conidial masses. **d**–**k** Sequential stages of peltate gland infection (refer to text)

Taxonomy

Metarhizium koreanum: Kepler, S. A. Rehner & Humber, in Kepler, Humber, Bischoff & Rehner, Mycologia 106(4): 823 (2014). Fig. 4.

Obvious white to greenish sporodochial masses (Fig. 4a) were observed on the peltate glands of leaf, with up to three sporodochia on each gland. Sporodochia (Fig. 4b–c) composed of strongly adpressed conidiophores. Conidiophores macronematous, hyaline, smooth-walled, the primary axis terminating in one phialide which is subtended by two lateral phialides, usually bearing 1 whorl of compact branches terminating on 1–3 phialides at top. Phialides cylindrical, with papillate apices, hyaline, smooth-walled, 3.7–11.0 × 1.0–2.5 µm (av. 7.4 × 1.7 µm, $n = 20$). Conidia (Fig. 4d) pale green, formed in chains, unicellular, oblong, with rounded apices, hyaline, 3.6–5.3 × 1.7–2.2 µm (av. 4.4 × 1.9 µm, $n = 20$).

Cultural characteristics: On SDAY colonies attaining approximately 3.8 cm in diameter after 14 days at 25 °C. Colony (Fig. 4e) yellow to brownish yellow, exhibiting distinct concentric zonation and prominent radial fissures extending from the centre toward the periphery, margin entire, white, surrounded by a floccose halo. On PDA colonies attaining approximately 4.2 cm diam after 14 days at 25 °C. Colony (Fig. 4f) green, diffuse, with a velvety to powdery texture, appearing evenly concentric zonation, without radial fissures. Reverse pale yellow to light cream, with distinct concentric rings reflecting the surface zonation.

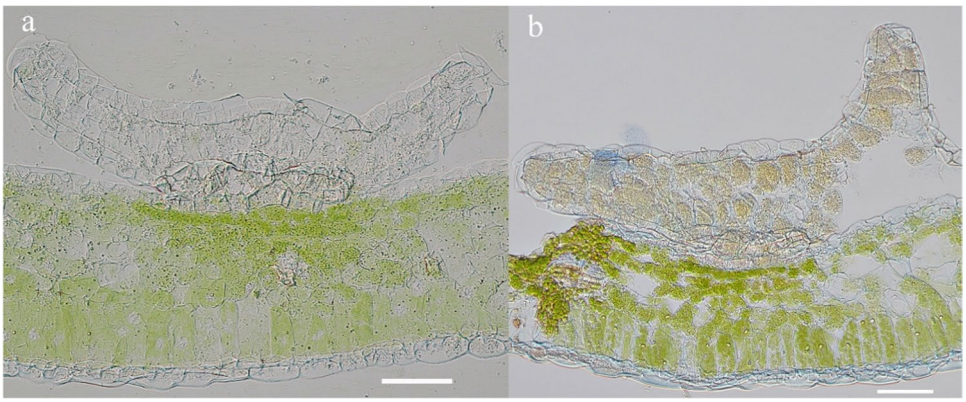


Fig. 2 Cross-sections of peltate glands of *Clerodendrum japonicum* var. *japonicum*. **a** Transparent gland without visible infection, showing intact glandular tissue and absence of fungal hyphae. **b** Yellow gland exhibiting internal colonization by *Metarhizium koreanum*, with hyphae present within tissue prior to surface sporulation. Yellow intracellular granular deposits are visible in infected gland cells. Scale bars = 50 μm

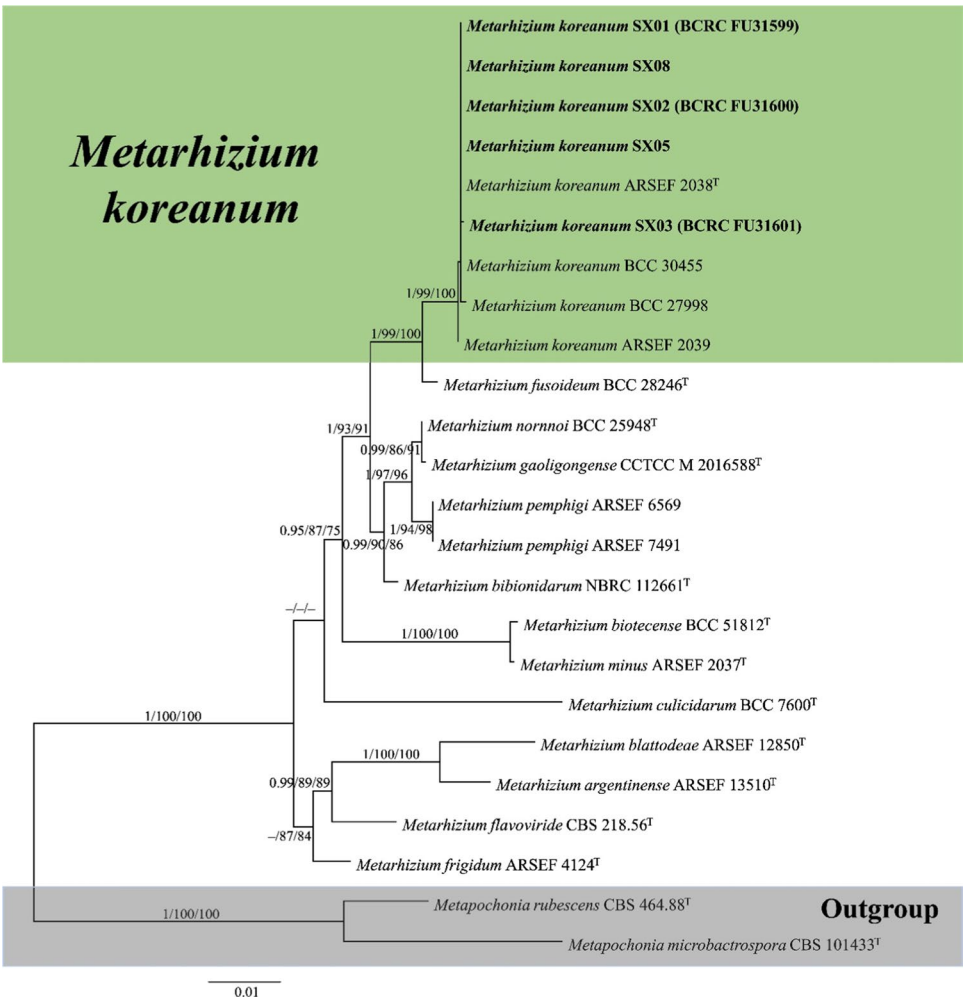
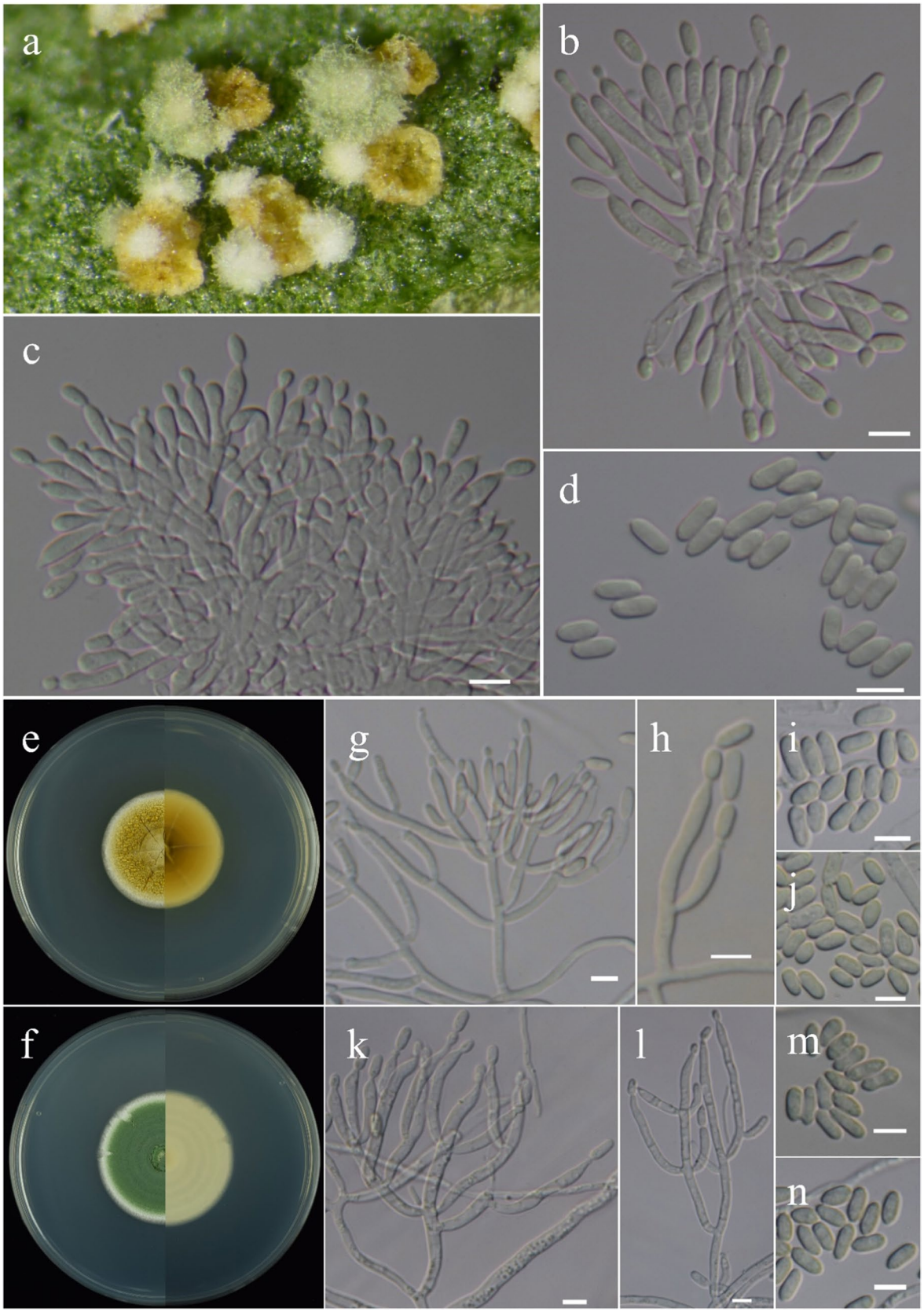


Fig. 3 Maximum likelihood (ML) phylogeny of the *Metarhizium flavoviride* species complex based on concatenated ITS, *TUB*, *TEF-1α*, and *RPB1*a sequences. The ML tree was constructed using IQ-TREE, with branch supports estimated using SH-aLRT and ultrafast bootstrap (UFBoot). Bayesian posterior probabilities (PP) were calculated using MrBayes. Node values are shown as PP/SH-aLRT/UFBoot, with only values ≥ 0.95 (PP) and ≥ 80% (SH-aLRT, UFBoot) displayed. *Metapochonia rubescens* CBS 464.88 and *M. microbactrospora* CBS 101433 were used as outgroup taxa. Strains SX01, SX02, SX03, SX05, and SX08 were obtained in this study. Superscript T denotes ex-type strains

Abundant mucilaginous exudates were present across the colony surface. Reverse yellow to brownish, with intensified pigmentation at the centre and radiating cracks extending outward.

Sporodochia not observed. Conidiophores (Fig. 4g–h, k–l) mononematous, macronematous, simple, arising from aerial mycelium, hyaline, smooth-walled. Conidiophores terminating on 1–3 phialides, bearing 1–3 layers of branches, each layer composed of a lateral branch or 2–3 verticillately arranged branches, with the branches arising at wide angles from the main axis of conidiophore, usually bearing 1–3 phialides on top, tertiary branches occasionally


a
b
c
d
e
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j
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k
l
m
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◂**Fig. 4** Morphological characteristics of *Metarhizium koreanum* (SX01) observed in nature and in culture. **a** Natural infection structures on the abaxial leaf surface, with dense white to greenish conidial masses on peltate glands. **b–c** Sporodochia bearing branched conidiophores, phialides, and conidia. **d** Conidia. (**e**, **g–j**) Growth on SDAY. **e** Colony with reverse view shown on the right. **g–h** Conidiophores and phialides. **i–j** Conidia on SDAY. **f**, **k–n** Growth on PDA. **f** Colony with reverse view shown on the right. **k–l** Conidiophores and phialides. **m–n** Conidia. Scale bars: b–d, g–j, k–n = 5 µm

present. Branches occasionally reduced to a phialide. Phialides cylindrical, with papillate apices, hyaline, smooth-walled, 9.0–20.1 × 1.1–2.5 µm (av. 14.9 × 1.8 µm, *n* = 40). Conidia (Fig. 4i–j, m–n) pale green, unicellular, oblong, with rounded apices, smooth-walled, 4.1–6.4 × 1.7–2.9 µm (av. 5.3 × 2.3 µm, *n* = 40).

Known distribution: South Korea, Japan, Thailand, and Taiwan.

Specimens examined: TAIWAN: Tainan city, Xinhua Forest Station, on leaf of *C. japonicum* var. *japonicum*, 07 Nov 2020, Seet, S. X. (SX01 = BCRC FU31599); Taichung City, Beitun District, Dakeng Trail, on leaf of *C. japonicum* var. *japonicum*, 06 Feb 2021, Seet, S. X. (SX02 = BCRC FU31600); Taichung City, Taiping District, Poisonous Woodnettle Trail, on leaf of *C. japonicum* var. *japonicum*, 14 Feb 2021, Seet, S. X. (SX03 = BCRC FU31601); Taichung City, South District, National Chung Hsing University, Medicinal Garden, on leaf of *C. japonicum* var. *japonicum*, 04 Aug 2021, Seet, S. X. (SX05); Nantou County, Ren'ai Township, Huisun Forest Recreation Area, on leaf of *C. japonicum* var. *japonicum*, 28 May 2023, Seet, S. X. (SX08).

Notes: The fungi obtained in the present study conform to the protologue description of *Metarhizium koreanum* (Kepler et al. 2014). *M. koreanum* is a member of the *M. flavoviride* species complex, and was previously reported only on insects (Mongkolsamrit et al. 2020). The finding of *M. koreanum* on the plant is exclusive, and particularly only peltate glands of leaves were infected.

Survey of herbarium specimens for *Metarhizium koreanum*

Herbarium specimens of *Clerodendrum japonicum* var. *japonicum* deposited at the Herbarium of the Department of Forestry, National Chung Hsing University were examined to assess the historical occurrence of infected peltate glands (Table 3). These specimens represent dried plant materials collected between 1974 and 2023.

In multiple specimens, peltate glands exhibiting the characteristic sand-colored to brown discoloration consistent with fungal infection were observed. No fungal isolation was attempted from these dried materials. The presence of infected glands on historical specimens indicates that colonization of *C. japonicum* var. *japonicum* by *M. koreanum* is not a recent phenomenon and has likely occurred for several decades.

Specimens consisting exclusively of fresh young leaves lacked infected glands and were therefore not included in Table 3, which documents only herbarium specimens exhibiting infected peltate glands. This pattern is consistent with field observations that newly emerged leaves are initially free of infection.

Endophytism of *Metarhizium koreanum*

Isolation outcomes differed among the three tissue conditions (Table 4).

From leaves bearing visibly infected glands (treatment 2), *M. koreanum* was successfully recovered after all tested sterilization durations (2–15 min), with isolation frequencies ranging from 25.0% to 41.7%. Recovery of the fungus even after 15 min of sodium hypochlorite treatment

Table 3 Herbarium specimens of *Clerodendrum japonicum* var. *japonicum* examined to assess the historical occurrence of infected peltate glands. The specimens represent deposited dried plant materials and were evaluated only for the presence of infection

Collection Date	Locality	Observer/Collector
25-Apr-1974	Zhushan Township, Nantou County	Lin
06-Dec-1980	Madou District, Tainan City	Huang
02-Jan-1986	Eight Trigram Mountains Buddha Landscape, Changhua City, Changhua County	Chan; Lin
11-May-1986	Dakeng, Beitun District, Taichung City	Wang
22-Oct-1986	Mingjian Township, Nantou County	Wu, J. S.
29-Apr-2011	Dakeng No. 2 Trail, Beitun District, Taichung City	Chang, C. H.
30-May-2015	Beikeng Industrial Road, Wufeng District, Taichung City	Chen, Guan-Ru
14-May-2016	No. 148, County Road, Yuanlin City, Changhua County	Chou, Tzu-Ching
27-Apr-2019	Dakeng No. 9 Trail, Beitun District, Taichung City	Zheng, H. H.
18-Mar-2022	Jiji Township, Nantou County	Sun, C. H.
11-Apr-2023	Nankeng Industry Rd, Wufeng District, Taichung City	Yang, H. H.
21-Mar-2023	Nankeng Industry Rd, Wufeng District, Taichung City	Chuang, P. Y.

Table 4 Effect of surface sterilization duration on isolation frequency of *Metarhizium koreanum* from different leaf tissue conditions

Tissue condition	2 min	5 min	10 min	15 min
1. Whole leaf without infected glands	0% (0/12)	0% (0/12)	0% (0/12)	0% (0/12)
2. Leaf with infected glands (segments excised from infected gland areas)	25.0% (3/12)	33.3% (4/12)	33.3% (4/12)	41.7% (5/12)
3. Leaf with partially infected glands (segments excised from areas without infected glands)	0% (0/12)	0% (0/12)	0% (0/12)	0% (0/12)

confirms that the surface-sterilization protocol did not eliminate *M. koreanum* when present in leaf tissue. In contrast, no colonies of *M. koreanum* were recovered from whole leaves lacking visible gland infection (treatment 1). Likewise, no colonies were recovered from visually asymptomatic areas excised from partially infected leaves (treatment 3). Across all sterilization durations (2, 5, 10, and 15 min), isolation frequency from these two tissues remained 0% (0/12 segments).

The absence of fungal recovery from leaf segments without infected glands indicates that *M. koreanum* does not colonize internal leaf lamina tissue. Taken together, these results demonstrate that *M. koreanum* is not endophytic within the leaf tissues of *C. japonicum* var. *japonicum*, and that its occurrence is confined to externally infected peltate glands.

Pathogenicity test

Symptoms of fungal infection developed in both wounded and unwounded inoculation treatments (Fig. 5). On each inoculated leaf, peltate glands within five of the six marked squares and their adjacent unwounded areas exhibited visible fungal colonization, with at least 15 glands per treatment area showing infected. In contrast, no infection was observed in the control.

The same infection pattern was consistently observed across all three replicates. Microscopic examination of

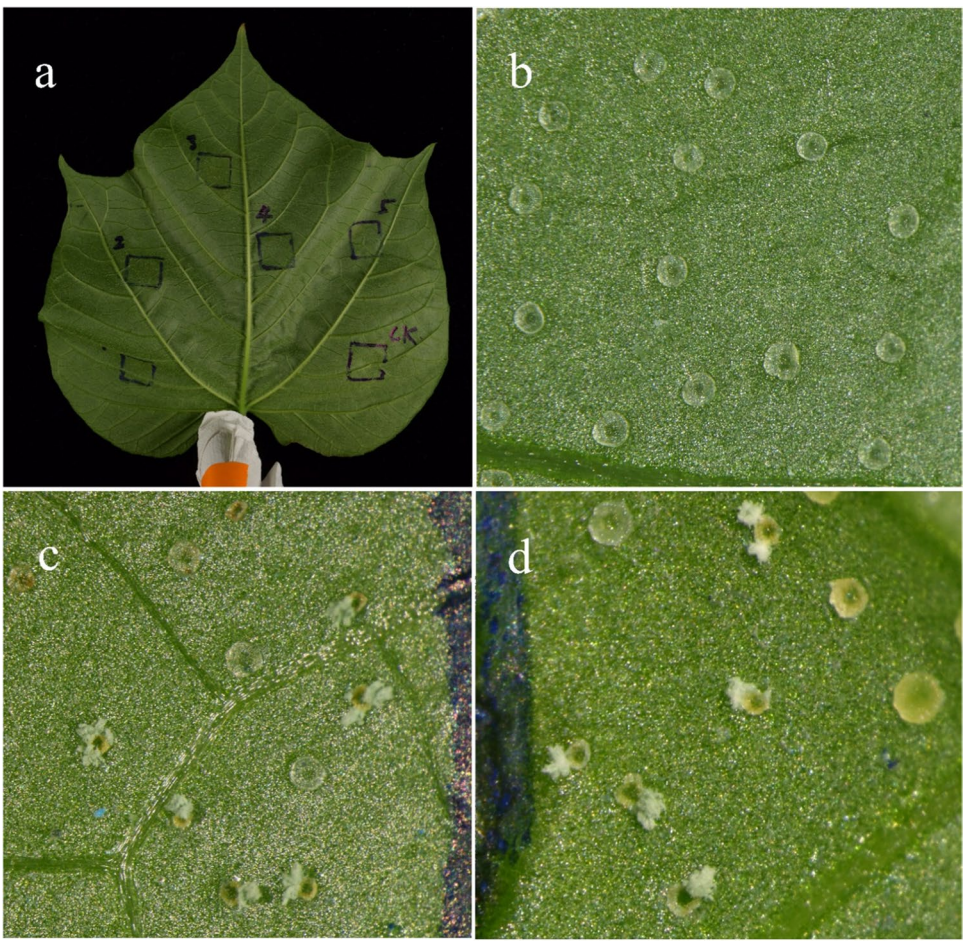


Fig. 5 Pathogenicity test on detached leaves of *Clerodendrum japonicum* var. *japonicum*. **a** Macroscopic view of a detached leaf showing the inoculation layout, with six 1 × 1 cm squares delineated on the abaxial surface. **b** Control (CK) square, showing no discoloration of peltate glands. **c** Wounded treatment, showing discoloration and sporulation on peltate glands. **d** Unwounded treatment, also showing discoloration and sporulation on peltate glands

sporodochia formed on infected peltate glands revealed morphological characteristics consistent with *Metarhizium koreanum*. Re-isolated fungi from infected glands matched the inoculated strain, thereby fulfilling Koch's postulates.

Discussion

The yellow–brown coloration of the peltate glands has long been misinterpreted in botanical studies as an inherent trait of *C. japonicum* var. *japonicum*, without recognizing that it is actually a consequence of infection by *M. koreanum*. Histological examination (Fig. 2) demonstrated that glands exhibiting yellow–brown discoloration already contained internal fungal hyphae, even in the absence of visible surface sporulation. Thus, the transition from transparent to yellow–brown represents an early sign of colonization occurring within the gland tissue prior to the emergence of superficial sporodochia. In infected glands, intracellular yellow–brown granular deposits were consistently observed. These deposits were absent in transparent glands and appear to accumulate as a host response to fungal invasion. The yellow–brown appearance of infected peltate glands is therefore attributable to the accumulation of these intracellular deposits. Notably, hyphal presence was restricted to peltate glands, with no evidence of invasion into adjacent leaf lamina tissues, supporting a highly tissue-specific mode of colonization.

Given that colonization appears to initiate at glands following external inoculum, the mechanism by which *M. koreanum* reaches these sites remains unclear. Because *M. koreanum* has consistently been recorded from insects—particularly members of the infraorder *Fulgoromorpha*—in multiple countries, insect-mediated transmission remains a plausible hypothesis. To date, all known records of *M. koreanum* have been confined to insects of the *Fulgoromorpha*. In Thailand, the fungus was isolated from unidentified planthoppers belonging to this group (Mongkolsamrit et al. 2020). In South Korea, *M. koreanum* was reported from the family *Delphacidae* (Kepler et al. 2014), and in Japan, from the family *Tropiduchidae* (Nishi and Sato 2017); both families are part of the *Fulgoromorpha*. These records, spanning diverse geographic regions, suggest a degree of host specificity toward this insect lineage. Notably, the natural distribution of *C. japonicum* var. *japonicum* includes South Korea, Japan, and Thailand (EPPO 2025; Leeratiwong et al. 2011)—the same countries where *M. koreanum* has been reported from *Fulgoromorpha* insects. This spatial overlap raises the possibility that insect vectors may play a role in fungal dispersal to the foliar surfaces of this plant species. Although *M. koreanum* is here reported for the first time in Taiwan, it is reasonable to assume that its putative insect host is also present, even though it has not yet been observed or identified. In the present study, no *Fulgoromorpha* insects were seen on *C. japonicum* var. *japonicum*, leaving the mechanism of transmission unresolved.

The nature of the colonized peltate structures adds further complexity. Metcalfe and Chalk (1979) classified the peltate hairs in the Squamata section of *Clerodendrum* as non-glandular, and *C. japonicum* var. *japonicum* is taxonomically assigned to this section (Steane et al. 1997). Our anatomical observations support this interpretation, as the structures lack secretory tissues and consist of multiple layers of non-secretory cells (Fig. 2). Nevertheless, we retain the commonly used term "glands" for continuity, while acknowledging that their precise functional identity remains unresolved.

In many *Lamiaceae* species, glandular trichomes produce lipophilic secondary metabolites with deterrent or antimicrobial properties (Werker 2000). If the peltate structures in *C. japonicum* var. *japonicum* are indeed glandular, their chemical content may theoretically repel insects and inhibit fungal colonization, thereby challenging the notion of insect-mediated transmission or surface colonization. Conversely, if these structures are non-glandular hairs, they may lack such chemical defenses, rendering them more accessible to fungal infection. Indeed, there are reports of fungi that exclusively infect non-glandular plant hairs (Dornelo-Silva and Dianese 2004; Pereira-Carvalho et al. 2009), though, to our knowledge, no fungal species have previously been reported to colonize true foliar glands.

While *Metarhizium* species are widely recognized as entomopathogens, several species have also been reported to colonize plant tissues as endophytes, in some cases conferring benefits such as enhanced pest resistance and abiotic stress tolerance (Sasan and Bidochka 2012; Vega 2018). Importantly, endophytic and pathogenic lifestyles are not mutually exclusive (Schulz and Boyle 2005). Under the framework of the endophytic continuum, fungi may persist within host tissues asymptomatically for extended periods and subsequently transition to pathogenic or saprotrophic phases when the balance between host defense and fungal antagonism is disturbed (Schulz and Boyle 2005). Such shifts may be influenced by environmental conditions (e.g., nutrient availability, light, or climate) as well as by the genetic constitution of both host and fungus. The colonization of peltate glands by *M. koreanum* therefore raises the possibility that the fungus might initially occur as a latent endophyte within leaf tissues before becoming pathogenic and visible through gland discoloration and fungal sporulation. However, our isolation experiments did not recover *M. koreanum* from surface-sterilized leaf lamina segments lacking infected peltate glands, including segments taken from partially infected leaves. Notably, the absence of fungal recovery from lamina segments taken from leaves already bearing infected glands, but sampled from areas

free of infected glands, provides further evidence against endophytic colonization, as an endophytic fungus would be expected to occur elsewhere within the same leaf. These results indicate that the fungus does not colonize the leaf lamina tissues and therefore does not occur as an endophyte in the host plant. Instead, fungal occurrence appears to be spatially restricted to the infected peltate glands. This pattern is consistent with the possibility that fungal propagules arrive on the leaf surface from external sources—for example via insect visits, wind dispersal, or rain splash—and subsequently establish infection at the gland structures. However, because the present study did not directly investigate dispersal or transmission mechanisms, this interpretation remains speculative.

Fungi exhibiting multifunctional lifestyles are well documented in plant–microbe–invertebrate systems. For example, the nematophagous fungus *Pochonia chlamydosporia* parasitizes eggs of plant-parasitic nematodes, including root-knot nematodes, while also colonizing plant roots and inducing plant-dependent systemic resistance (Kerry 2000; Ghahremani et al. 2019). Similarly, *Purpureocillium lilacinum* functions as a biological control agent against root-knot nematodes and has been reported to promote plant growth under nematode pressure (Kerry 2000; Khan and Tanaka 2023). These examples demonstrate that antagonism toward invertebrate pests and intimate association with plant tissues, including endophytic colonization, can coexist within a single fungal species, emphasizing that fungal ecological roles often span multiple biological interactions rather than fitting strict categorical boundaries. In this broader context, the highly tissue-specific colonization of peltate glands by *M. koreanum* may represent another form of ecological specialization within a multifunctional spectrum of fungal lifestyles.

The pathogenicity assay revealed that both wounded and unwounded treatments resulted in fungal infection of the peltate glands, suggesting that *M. koreanum* is capable of infecting these structures even in the absence of wounding. The wounded treatment was designed to simulate physical damage caused by insects, under the hypothesis that insect-mediated transmission might facilitate fungal colonization. While infection following wounding was expected, the ability of *M. koreanum* to infect unwounded peltate glands was unexpected and indicates that physical injury is not a prerequisite for infection. This finding raises important ecological questions regarding the route of fungal entry—specifically, whether insect vectors are involved in the deposition or facilitation of fungal spores, and, if not, how *M. koreanum* comes into contact with the peltate structures in the absence of wounding or insect activity. Furthermore, during the pathogenicity assay, spore suspensions were applied broadly to both the peltate structures and surrounding leaf tissue. Notably, infection symptoms developed only in the peltate glands, whereas the adjacent leaf lamina remained symptomless, highlighting a remarkable tissue specificity in pathogenicity.

Although some variability in infection rates on peltate glands was observed during each inoculation—likely due to differences in peltate gland maturity or inoculation technique—most glands within each treated area became infected. We used a threshold of ≥ 15 infected glands to score a treatment as positive, based on an estimated 30 glands per square.

Taken together, our findings suggest that *M. koreanum* exploits a previously unrecognized ecological niche. The fungus appears to infect peltate structures externally, without affecting surrounding tissues. Whether this reflects a specialized adaptation facilitated by unknown insect vectors or environmental conditions remains an open question for future investigation.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s11557-026-02137-z.

Acknowledgements We thank Professor Hsy-Yu Tzeng, curator of the Herbarium at the Department of Forestry, National Chung Hsing University, for granting access to herbarium specimens.

Author contribution Siaw Xuan Seet Conceptualization, methodology, sample collection, morphological and molecular analyses, phylogenetic analysis, pathogenicity assays, manuscript preparation; Chi-Yu Chen Conceptualization, supervision, taxonomic decision, manuscript revision.

Funding Open access funding provided by National Chung Hsing University. This study was supported by the National Science and Technology Council, Taiwan (Grant No. NSTC 113–2621-B-005–006).

Data availability The sequences obtained in the present study are available in GenBank, with accession numbers shown in Table 2.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interests The authors declare no conflicts of interest. All the experiments undertaken in this study comply with the current laws of the country where they were performed.

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