

ORIGINAL ARTICLE

First report of phyllode rust on *Acacia crassicaarpa* outside its native range

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Abstract

Acacia crassicaarpa is a tropical tree species native to Australia, West Papua and Papua New Guinea, which has been widely used to establish plantations in the lowland humid tropics of Sumatra and Kalimantan. These trees, able to grow on sites having relatively poor nutrition, have been relatively free of serious disease problems. A rust disease infecting the phyllodes of *A. crassicaarpa* has recently been encountered in plantations in various areas of Indonesia and Malaysia where they are not native. In this study, the rust was collected and identified as *Endoraecium violae-faustiae* using DNA sequence analysis based on the internal transcribed spacer (ITS) region of the rDNA. This is the first record of the rust outside its native range. Damage at present appears to be relatively mild but the pathogen could become important in the future.

KEYWORDS

acacia, fungal pathogen, introduced pathogen, plantation forestry, rust disease, Southeast Asia

1 | INTRODUCTION

Various Australian *Acacia* spp. have been utilized to establish plantations in countries of the tropics and Southern Hemisphere. Of these, *Acacia mearnsii* has been planted in temperate areas such as in parts of South Africa and Brazil, where it tolerates relatively low winter temperatures (Moreno Chan et al., 2015; Moreno Chan & Isik, 2021; Richardson et al., 2015). Two other species, *Acacia mangium* and *A. crassicaarpa*, have been planted over much greater areas with tropical climates and particularly in the humid tropics of Southeast Asia (Griffin et al., 2011; Harwood et al., 2015; Midgley & Turnbull, 2003).

In all areas of the world where tree species are planted outside their native range, they have increasingly been challenged by diseases (Burgess & Wingfield, 2016; Wingfield et al., 2011, 2015). These include those that are native to the areas where the trees

have been established and others that have been gradually introduced over time (Burgess & Wingfield, 2016; Wingfield et al., 2015). This is equally true for *Acacia* spp. as it is for other trees widely planted in the tropics and Southern Hemisphere such as *Eucalyptus*, *Pinus* and *Populus* (Burgess & Wingfield, 2016; Hurley et al., 2023; Roux & Wingfield, 2009; Wingfield et al., 2011). Broadly, the situation in all cases is that diseases as well as insect pests are some of the most economically important factors threatening the long-term sustainability of plantation forestry utilizing non-native tree species internationally (Healy et al., 2022; Payn et al., 2015; Wingfield et al., 2015).

Rust diseases are amongst those that have caused serious damage to non-native trees such as *Eucalyptus* and *Acacia* grown over relatively short rotations. The best known of these is myrtle rust caused by *Austropuccinia psidii* (Sphaerophragmiaceae, Pucciniales),

which has a wide host range in the Myrtaceae and can seriously damage plantation-grown *Eucalyptus* trees (Coutinho et al., 1998; Glen et al., 2007). In the case of *Acacia* spp., phyllode rust caused by *Endoraecium digitatum* (Endoraeciaceae, Pucciniales) is a well-known disease of *A. mangium* in Southeast Asian countries including Indonesia, Malaysia, and Vietnam (Berndt, 2011; Doungsa-ard et al., 2018; Mohd Farid et al., 2023; Old et al., 2000). In recent years, rust caused by *Uromycladium acaciae* (Raveneliaceae, Pucciniales) has emerged as a threat to *A. mearnsii* in South African plantations (Fraser et al., 2021; McTaggart, Doungsa-ard, Wingfield, & Roux, 2015; Morris et al., 1988) and most recently also in Ethiopia (Pham et al., 2023). In all cases, these *Acacia* rust pathogens, *Endoraecium* and *Uromycladium*, are known on their native hosts in Australia (Doungsa-ard et al., 2018).

Acacia crassicarpa, native to Australia, West Papua and Papua New Guinea, is amongst the most widely established plantation tree species in Southeast Asia, where it is well suited to grow on nutrient-poor sites (Griffin et al., 2011; Harwood et al., 2015). Relatively little work has been conducted on the pests and pathogens of these trees outside their native range, despite their importance to the commercial forestry sector. One of the first serious diseases to appear on *A. crassicarpa* was caused by the leaf and shoot pathogen *Pleopassalora perplexa* (syn. *Passalora perplexa*) (Beilharz et al., 2004). These trees can also be infected by *Ceratocystis manginecans* that has devastated plantations of *A. mangium* in Southeast Asia (Hurley et al., 2023; Tarigan et al., 2011, b; Wingfield et al., 2023), although they have substantially lower levels of susceptibility to that pathogen (Barnes et al., 2023; Tarigan, Roux, et al., 2011). Most recently, it has been recognized that these trees, particularly where they are under stress, can be severely infested and damaged by the wood-boring ambrosia beetle *Euwallacea perbrevis* (Lynn et al., 2020, 2021).

Lesions reminiscent of rust infections have been observed on the phyllodes (modified petioles) of *A. crassicarpa* trees in Indonesia (Riau, Kalimantan) and Malaysia since 2019. The aim of this study was to identify the pathogen using DNA sequence data and morphological characteristics.

2 | MATERIALS AND METHODS

2.1 | Sample collections

Infected *A. crassicarpa* leaves showing symptoms of rust (Figure 1) were collected from Kalimantan and Riau in Indonesia, and Sabah in Malaysia (Table 1), and stored in paper bags. These samples were kept in a fridge before they were brought into the laboratory for investigation or dried at room temperature for storage. Additionally, sori on the leaves were either scraped off or added directly to cryovials containing RNAlater (Thermo Fisher Scientific, Waltham, MA, USA), or pieces of leaf material with the sori were placed in these vials for downstream analyses. The specimens were deposited in the H.G.W.J. Schweickerdt Herbarium (PRU), University of Pretoria, South Africa (Table 1).

2.2 | DNA sequencing, PCR amplification and sequencing

DNA was extracted from spore masses or infected plant material using DNeasy® Plant Pro Kit (QIAGEN, Hilden, Germany) following the manufacturer's protocols. The internal transcribed spacer regions 1 and 2 (ITS), including the 5.8S rRNA region, were amplified using primers ITS5u and ITS4rust (Beenken et al., 2012; Pfunder et al., 2001). DNA was amplified by PCR with FastStart™ Taq DNA Polymerase (Sigma-Aldrich, St. Louis, MO, USA). The thermal cycling included an initial denaturation at 95°C for 5 min followed by 10 primary amplification cycles of 30s at 95°C, 30s at 53°C, and 60s at 72°C, then 30 additional cycles of the same reaction sequence, with a 5 s increase in the annealing step per cycle, and the reactions were completed with a final extension at 72°C for 10 min. Amplified fragments were purified using ExoSAP-IT™ PCR Product Cleanup Reagent (Thermo Fisher Scientific, Waltham, MA, USA). Amplicons were sequenced in both directions using the BigDye Terminator v 3.1 Cycle Sequencing kit (Thermo Fisher Scientific, Waltham, MA,

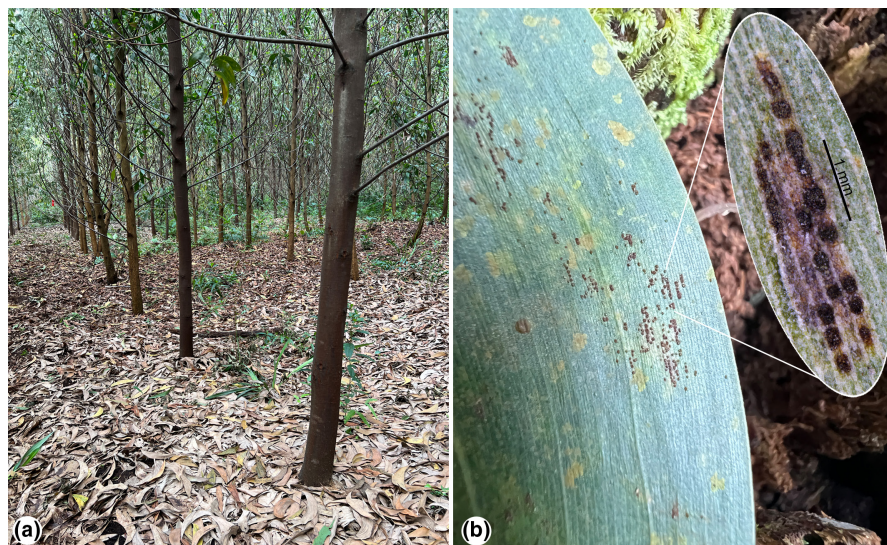


FIGURE 1 *Acacia crassicarpa* infected with *Endoraecium violae-faustiae* in Riau, Indonesia, resulted in heavy defoliation of lower branches seen below these trees (a), and a phyllode with sori (scale bar: 1 mm) (b).

TABLE 1 Collection details for the *Endoraecium* specimens and GenBank accessions included in the phylogenetic analysis.

Species	Specimen	Host	Country	ITS accession number	Reference
<i>E. auriculiformis</i>	BRIP 56548 ^a	<i>A. auriculiformis</i>	Australia	KJ862355	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 56549	<i>A. auriculiformis</i>	Australia	KJ862356	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 57926	<i>A. dealbata</i>	Australia	KJ862357	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. disparriimae</i>	BRIP 55626 ^a	<i>A. disparriima</i>	Australia	KJ862358	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 55632	<i>A. disparriima</i>	Australia	KJ862359	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. falciformis</i>	BRIP 57583 ^a	<i>A. falciformis</i>	Australia	KJ862360	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 57279	<i>A. irrorata</i>	Australia	KJ862365	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. irroratae</i>	BRIP 57286 ^a	<i>A. irrorata</i>	Australia	KJ862366	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 57872 ^a	<i>A. daphnifolia</i>	Australia	KJ862367	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. parvum</i>	BRIP 57524	<i>A. leiocalyx</i>	Australia	KJ862369	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 57631	<i>A. leiocalyx</i>	Australia	KJ862373	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. peggii</i>	BRIP 55602 ^a	<i>A. holoserica</i>	Australia	KJ862361	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 55631	<i>A. holoserica</i>	Australia	KJ862362	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. phyllodiorum</i>	BRIP 57516	<i>A. aulacocarpa</i>	Australia	KJ862378	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 57578	<i>A. aulacocarpa</i>	Australia	KJ862381	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. podalyriifoliae</i>	BRIP 57294	<i>A. podalyriifolia</i>	Australia	KJ862386	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 57576 ^a	<i>A. podalyriifolia</i>	Australia	KJ862387	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. tierneyi</i>	BRIP 27880	<i>A. harpophylla</i>	Australia	KJ862389	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 27887	<i>A. harpophylla</i>	Australia	KJ862390	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. tropicae</i>	BRIP 56555	<i>A. tropica</i>	Australia	KJ862391	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 56557 ^a	<i>A. tropica</i>	Australia	KJ862392	McTaggart, Doungsa-ard, Geering, et al. (2015)
<i>E. violae-faustiae</i>	BRIP 55601	<i>A. aulacocarpa</i>	Australia	KJ862393	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 55629	<i>A. aulacocarpa</i>	Australia	KJ862394	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 56544	<i>A. difficilis</i>	Australia	KJ862395	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 55616	<i>A. difficilis</i>	Australia	KJ862396	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 55611	<i>A. difficilis</i>	Australia	KJ862397	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 56539	<i>A. difficilis</i>	Australia	KJ862398	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 56540	<i>A. difficilis</i>	Australia	KJ862399	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 56545	<i>A. difficilis</i>	Australia	KJ862400	McTaggart, Doungsa-ard, Geering, et al. (2015)
	BRIP 56547	<i>A. difficilis</i>	Australia	KJ862401	McTaggart, Doungsa-ard, Geering, et al. (2015)
	PRU(M) 4555	<i>A. crassicaarpa</i>	Sabah, Malaysia	OR481949	This study
	PRU(M) 4556	<i>A. crassicaarpa</i>	Riau, Indonesia	OR481950	This study
	PRU(M) 4557	<i>A. mangium</i> × <i>auriculiformis</i>	Riau, Indonesia	OR481951	This study
	PRU(M) 4558	<i>A. crassicaarpa</i>	Kalimantan, Indonesia	OR481952	This study
<i>Diorchidium woodii</i>	ZT Myc 582	<i>Milletia grandis</i>	South Africa	KM217352	Beenken and Wood (2015)

Note: Specimens collected in this study are represented in bold. BRIP: Queensland Plant Pathology Herbarium, Queensland, Australia; PRU(M): H.G.W.J. Schweickert Herbarium, University of Pretoria, Pretoria, South Africa. ZT Myc: Zürich Herbaria Z + ZT, ETH Zürich, Switzerland.

^aHolotype.

USA). Sequences were obtained by running the products on an ABI PRISM™ 3100 DNA sequencer (Applied Biosystems, Waltham, MA, USA) at the Sequencing Facility of the Faculty of Natural and Agricultural Sciences, University of Pretoria, South Africa. Geneious Prime 2023.0.1 was used to assemble and edit the raw sequences (<https://www.geneious.com>). All sequences generated in this study were deposited in GenBank (<http://www.ncbi.nlm.nih.gov>) (Table 1).

2.3 | Phylogenetic analyses

Reference sequences for species closely related to those emerging from this study were downloaded from GenBank database (Table 1). All sequences were aligned using MAFFT v. 7 (<http://mafft.cbrc.jp/alignment/server/>) (Kato & Standley, 2013) and then confirmed manually in MEGA v. 7 (Kumar et al., 2016), where necessary. Maximum likelihood (ML) analysis was performed using RaxML v. 8.2.4 on the CIPRES Science Gateway v. 3.3 (Stamatakis, 2014) with default GTR substitution model and 1000 rapid bootstraps. Sequence data for *Diorchidium woodii* (ZT Myc 255) was used as the outgroup taxon. The resulting tree was viewed using MEGA v. 7.

2.4 | Morphology

Cut pieces of the phyllodes containing sori were boiled for a few seconds. Spore masses were scraped from the surface of phyllodes using a hypodermic needle or with an agar piece at the tip of the needle. The spores were mounted on a microscope slide in water that was replaced with 85% lactic acid, in which measurements and micrographs were made. Nikon microscopes (SMZ18, Eclipse Ni, Tokyo, Japan) and cameras (Nikon DS-Ri2, Japan) mounted on the microscopes, and an image processing program (NIS Elements, Nikon, Japan) were used to capture images, make measurements and examine morphological structures.

The colonization of the rust within the phyllode tissues was studied in vertically sectioned tissues. The boiled phyllodes containing lesions infected with rust were cut into small pieces (5 mm²) and mounted in a freezing medium (Tissue freezing medium, Leica, UK). These tissues were cut into sections of 10–12 µm thickness using a Leica Cryomicrotome (Leica Biosystem, Germany) and mounted in 85% lactic acid for observation. Up to fifty measurements were made for characteristic structures when available and are presented as minimum–maximum (average ± standard deviation). The nomenclature used to describe spores and sori followed the suggestions of Laundon (1967) and McTaggart, Doungsa-ard, Geering, et al. (2015).

For Scanning Electron Microscopy (SEM), tissues containing lesions were cut into 1 cm² and fixed in 2.5% glutaraldehyde/

formaldehyde (50% v/v) for 24 h. Samples were dehydrated using a graded ethanol series at 30%, 50%, 70% and 90% for 15 min each, followed by four dehydration steps in 100% ethanol, three times for 15 min each and once for 30 min. The dehydrated samples were placed in hexamethyldisilazane (HMDS) and subsequently mounted on aluminium stubs. Samples were coated with carbon using a Quorum Q150T Coating Unit (Quorum, UK) and were observed using a 540 Gemini Ultra Plus FEG SEM (Zeiss, Germany) at the Laboratory for Microscopy and Microanalysis, University of Pretoria, South Africa.

3 | RESULTS

3.1 | Phylogenetic analysis

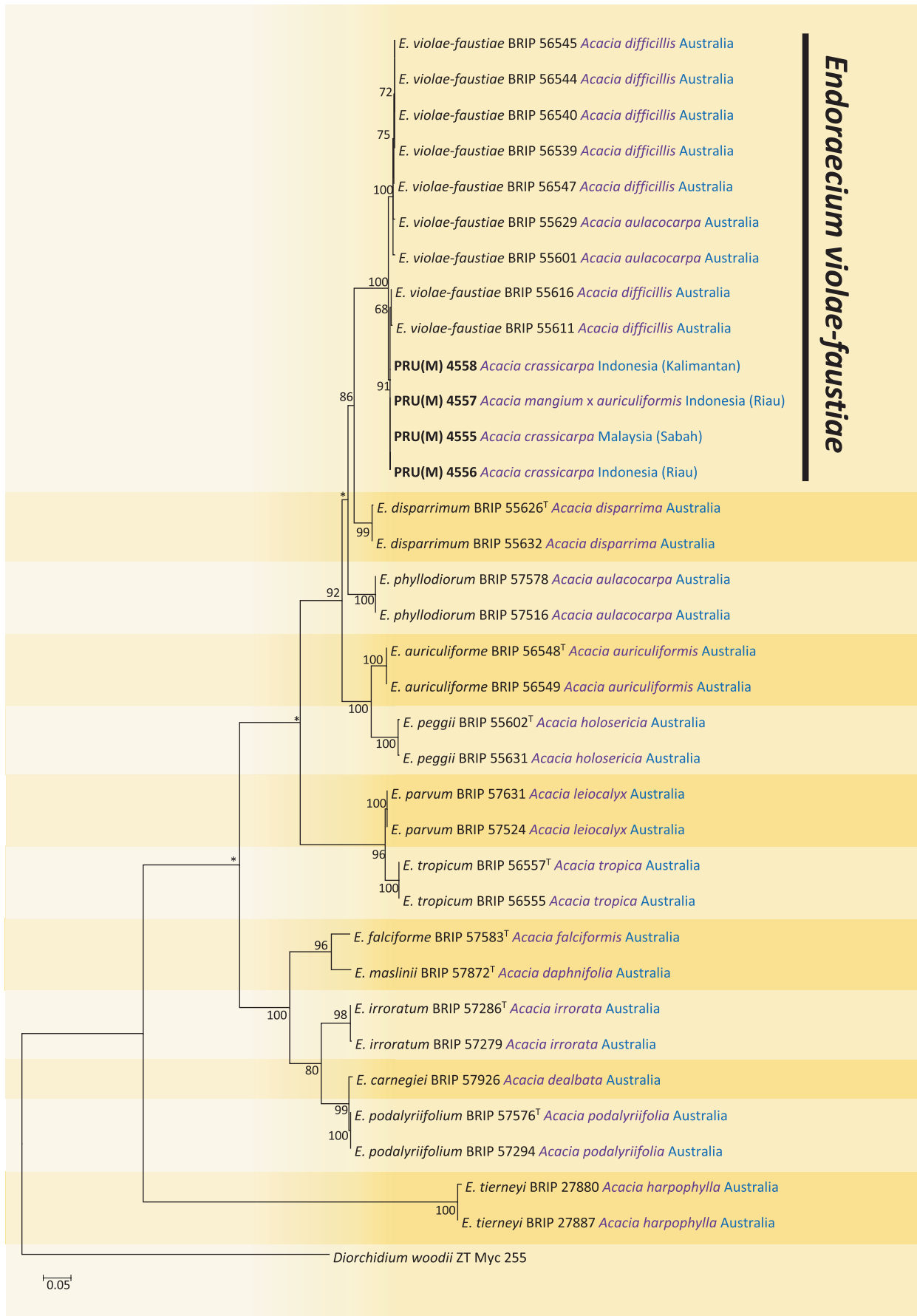
For all collected specimens, amplicons of approximately 780 bp were generated for the ITS region. The dataset used in the phylogenetic analysis included 34 ingroup taxa and contained 926 characters including alignment gaps. The four specimens from Indonesia (PRU(M) 4556, 4557, 4558) and Malaysia (PRU(M) 4555) had identical sequences and formed a well-supported (100%) monophyletic clade in the ML tree (Figure 2) that included all representative specimens of *Endoraecium violae-faustiae* from Australia. These specimens were thus identified as *E. violae-faustiae*.

3.2 | Morphology

Hyphae started to colonize under epidermis cells, occupied the palisade mesophyll cells and eventually grew towards the central parenchyma (Figure 3a). *Uredinia* were present on both the upper and underside of phyllodes, were ferruginous, scattered singly or in groups and became erumpent (Figure 3a,b,h). *Paraphyses* were present amongst urediniospores, hyaline to pale yellow, cylindrical, with apical knob-like structures similar to that of teliospores (Figure 3d,h). *Urediniospores* were yellowish brown, foveolate, sub-globose to oval or nearly cylindrical (length: width = 1.2–2.6:1, 33–48 × 17.5–30 (41 ± 4.09 × 24 ± 2.29) µm; walls were 3–5 (4 ± 0.43) µm thick at sides; apex acute or apiculate, 2–7 (5.4 ± 1.05) µm thick; bases were occasionally tapering to a point or truncated; 3–5 germ-pores were lined more or less equatorially; pedicels were mostly present, central or off-central, hyaline, tubular-shaped or trapezoid, and ranged in 1–20 (3.1 ± 2.7) µm long and 3–10.5 (7.6 ± 1.42) µm wide (Figure 3b,f–j). *Telia* were borne inside a uredinium or separately on the upper surface (Figure 3a,c). *Teliospores* were sub-hyaline to pale yellow, obovoid or cylindrical with the inflated upper part and 38–57 × 16–28 (21.8 ± 2.41) µm; walls were 1–2.5 (1.7 ± 0.38) µm thick at the sides;

FIGURE 2 Phylogenetic tree based on maximum likelihood (ML) analysis of ITS sequences for *Endoraecium* species. Specimens sequenced in this study are presented in bold. *Acacia* host species are highlighted in purple, and the countries of origin of the specimens are in blue. Bootstrap values (≥60%) for ML analyses are indicated at the nodes. Specimen representing the holotypes are marked with a 'T'. Sequence for *Diorchidium woodii* (ZT Myc 255) represents the outgroup taxon.

Endorhacium violae-faustiae



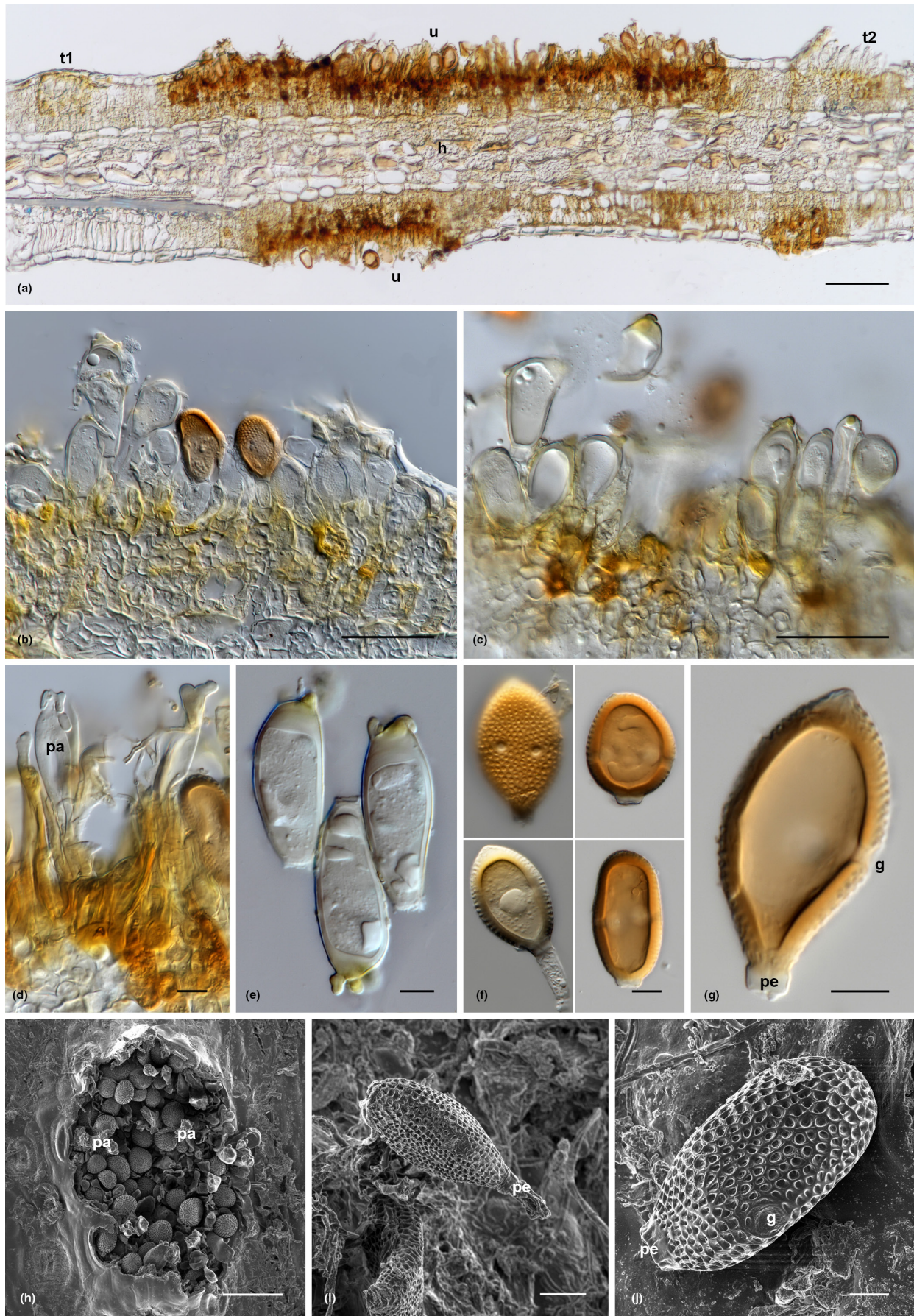


FIGURE 3 Micrographs of *Endoraecium violae-faustiae* infecting phyllodes of *Acacia crassicaarpa*. (PRU(M) 4556: a–d, g; PRU(M) 4558 e, f, h–j). (a) Cross-section of a phyllode infected with *E. violae-faustiae* on both the upper and underside of phyllode (h: vegetative hyphae invading central parenchyma, t1: innate telium, t2: erumpent telium, u: uredinium). (b) Urediniospores and teliospores borne in a uredinium. (c) Teliospores borne in a telium. (d) Paraphyses (pa) with apical ornaments similar to that of teliospores. (e) Teliospores with apical ornaments (knob-like) (f) Various shapes of urediniospores in optical section: young spore (left below) and focused on surface (left top). (g) Urediniospore in optical section showing germ-pore (g), pedicel (pe) and acute apex. (h) Erumpent uredinium producing urediniospores and paraphyses (pa). (i, j) Urediniospore. Scale bars: a = 100 μ m; b, c, h = 50 μ m; d–g, i = 10 μ m; j = 5 μ m.

apices were round, thickened with 1–4 knob-like structures; pedicels were hyaline, tubular-shaped, 3–15 (7.6 ± 5.06) μ m long (Figure 3b,c,e).

4 | DISCUSSION

The results of this study have shown that the phyllode rust disease found on *A. crassicaarpa* in Indonesia and Malaysia is caused by *Endoraecium violae-faustiae*. This is the first record of the rust on this tree species in plantations outside its area of origin. Although extensive surveys have not been carried out, collections included in this study were from relatively widely distributed locations. It is thus probable that *E. violae-faustiae* occurs more widely on *A. crassicaarpa* in Southeast Asian plantations than is known from the present study.

Endoraecium violae-faustiae was described by Berndt (2011) in a detailed study of *Endoraecium digitatum*, which he separated into a number of discrete taxa. Prior to the present study, *E. violae-faustiae* was known only from the northern parts of Australia where it occurs on *A. crassicaarpa*, *A. aulacocarpa* and *A. difficillis* (McTaggart, Doungsa-ard, Geering, et al., 2015). These species are well-adapted to tropical conditions, which accounts for the fact that *A. crassicaarpa* has been extensively propagated in the humid tropics of Southeast Asia (Griffin et al., 2011; Midgley & Turnbull, 2003; Moran et al., 1989). Specifically, *A. aulacocarpa* is of interest for hybridization with *A. crassicaarpa* (Griffin et al., 2011; Harwood et al., 2015) and future studies should consider the susceptibility of the former species and hybrids to infection by *E. violae-faustiae*. This could provide opportunities to avoid the disease in situations where it might cause significant defoliation.

Phyllode rust caused by *E. violae-faustiae* appears to be a relatively new disease on *A. crassicaarpa* in Indonesia and Malaysia. This view is based on the fact that disease surveys have been conducted regularly in plantations of this tree since the early 1990s. It might, however, have occurred at sufficiently low levels so as not to be detected until relatively recently, when it first became obvious. Damage caused by the rust appears to be relatively mild at present, but it has become increasingly visible during the last year (Wingfield, personal observation).

The most likely pathway of entry of *E. violae-faustiae* into Southeast Asian plantations of *E. crassicaarpa* would have been with infected plant material, accidentally introduced into some part of this large area, and after which air-borne dispersal would easily have occurred locally. Although various pathogens of trees widely utilized for plantation forestry, such as species of *Pinus* and *Eucalyptus*, are

commonly seed-borne and have likely entered into new environments with such germplasm (loos et al., 2009; Jimu et al., 2015), rust pathogens would be unlikely to move in this way. The emergence of rust caused by *E. violae-faustiae* in plantations of *A. crassicaarpa* emphasizes the need for adequate quarantine measures to prevent the accidental introduction of new pathogens into areas where non-native trees are being propagated for plantation forestry (Burgess & Wingfield, 2002, 2016; Healy et al., 2022).

It would be interesting to determine whether *E. violae-faustiae* in the present study, originated from a single introduction into one of the *A. crassicaarpa* areas sampled, from which it then spread further. Rust fungi have powdery spores that are easily wind dispersed, which would have allowed for a single introduction of the pathogen to spread more widely. Alternatively, there could have been multiple introductions into different areas. Knowledge of this pathway of introduction and the diversity of the pathogen would require more extensive collections and a population genetic study, the value of which would lie in understanding patterns of resistance to the disease.

Acacia crassicaarpa is one of the most important plantation-grown tree species in lowland areas of Indonesia, where it is extensively propagated. These trees have been relatively free of serious disease problems in the past. The appearance of a phyllode rust disease is thus of concern. Surveys should now be undertaken to assess the incidence and severity of the disease and to develop strategies to reduce its impact.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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