A co-evolutionary relationship exists between *Endoraecium* (*Pucciniales*) and its *Acacia* hosts in Australia

A.R. McTaggart¹,²,³, C. Doungsa-ard¹,⁴, A.D.W. Geering¹, M.C. Aime⁵, R.G. Shivas²

**Key words**

Atelocauda 
eンドロキサル
Mimosoideae
Racemosperms
Ravenelaceae
Uredinales

**Abstract**  *Endoraecium* is a genus of rust fungi that infects several species of *Acacia* in Australia, South-East Asia and Hawaii. This study investigated the systematics of *Endoraecium* from 55 specimens in Australia based on a combined morphological and molecular approach. Phylogenetic analyses were conducted on partitioned datasets of loci from ribosomal and mitochondrial DNA. The recovered molecular phylogeny supported a recently published taxonomy based on morphology and host range that divided *Endoraecium* digitatum into five species. Spore morphology is synapomorph and there is evidence *Endoraecium* co-evolved with its *Acacia* hosts. The broad host ranges of *E. digitatum*, *E. parvum*, *E. phyllidiolum* and *E. violae-faustiae* are revised in light of this study, and nine new species of *Endoraecium* are described from Australia based on host taxonomy, morphology and phylogenetic concordance.

**Article info**  Received: 10 June 2014; Accepted: 18 December 2014; Published: 13 February 2015.

**INTRODUCTION**

*Endoraecium* (*Pucciniales*, *Ravenelaceae*) was established for two endocyclic species of rust fungi with pedicellate spores, *E. acaciae* (the type species) and *E. hawaiense*, which were found on *Acacia koa* (*Fabaceae*, subfamily *Mimosoideae*) in Hawaii (Hodges & Gardner 1984). There are over 1 000 species of *Acacia s.str.* (hereafter referred to as *Acacia*) known in Australia (Murphy et al. 2010, Maslin 2013). The classification of *Acacia* has moved from a traditional morphological one based on sections, to a molecular phylogenetic one based on clades (Murphy et al. 2010, Miller et al. 2013). At the commencement of this study, 20 species of *Acacia* were recorded as hosts of seven species of *Endoraecium* in Australia (Berndt 2011). These 20 host species fall within three clades of the plurinerved, uninnervated and Botrychpaleae (p.u.b.) group of *Acacia* (Murphy et al. 2010), namely the i) Botrychpaleae subclade (Murphy et al. 2010); ii) Juliflorae p.p. clade (Miller et al. 2013); and iii) Pliurinerves p.p. clade (Miller et al. 2013), hereafter referred to as Botrychpaleae, Juliflorae and Pliurinerves, respectively.

Species of *Endoraecium* produce a range of symptoms on *Acacia* that include bulate swellings or pellite nari on phyllodes, or galls and witches’ brooms on stems. These rust fungi produce spores of three types: i) spormogonia; ii) pedicellate spores, which have reticulate to foveolate ornamentations and were variously called aecial urediniospores (Walker 2001), uredo-like aeciospores (Berndt 2011) or teliospores in the endocyclic species (Hodges & Gardner 1984); iii) teliospores, which are single celled, subhyaline and smooth walled. The teliospores are morphologically similar to those of *Uromyces* s.l. and several species of *Endoraecium* were at one time classified in that genus, including *U. digitatus* (Winter 1886), *U. bicinctus* (McAlpine 1906), *U. phyllidiolum* (McAlpine 1906), *U. hyalosporus* (Sawada 1913) and *U. koae* (Stevens 1925). On the basis of morphology, some species currently considered as *Endoraecium* were previously placed in other genera, including *Pileolaria* (Dietel 1921), *Maravalia* (Dietel 1924), *Poliotelium* (Mains 1939), *Atelocauda* (Cummins & Hiratsuka 1983, Ony 1984, Gardner 1991), and *Racemosperms* (Walker 2001).

Gardner (1991) proposed that *Endoraecium* may be closely related to *Uromycladium* (*Pileolariaeae*), another genus of rust that occurs on *Acacia* in Australia. However, in combined analyses of the Large Subunit (LSU) and Small Subunit (SSU) regions of ribosomal DNA (rDNA), the systematic position of *Endoraecium* was shown by Scholler & Aime (2006) and Aime (2006) to have an affinity with mimosoid rusts in the *Raveneliaeae* rather than with the *Pileolariaeae*.

In this study, the systematic relationships of *Endoraecium* on *Acacia* in Australia were investigated with freshly collected field material and herbarium specimens. Currently, *Endoraecium* contains 13 species, all on *Acacia*, with seven endemic to Australia, one to South-East Asia and five to Hawaii (McAlpine 1906, Sawada 1913, Hodges & Gardner 1984, Berndt 2011). The species are *E. acaciae* (type on *A. koa*, Hawaii), *E. angustiphyllodium* (type on *A. koa*, Hawaii), *E. bicinctum* (type on *A. fasciculifera*, Australia), *E. digitatum* (type on *A. notabilis*, Australia), *E. hawaiense* (type on *A. koa*, Hawaii), *E. hyalosporum* (type on *A. confusa*, Taiwan), *E. kauaiianum* (type on *A. koa*, Hawaii), *E. koae* (type on *A. koa*, Hawaii), *E. parvum* (type on *A. leiocalyx*, Australia), *E. phyllidiolum* (type on *Acacia* sp., Australia), *E. tierneyi* (type on *A. harphophylla*, Australia), *E. violae-faustiae* (type on *Acacia* sp., Australia) and *E. walkerianum* (type on *A. penninervis*, Australia). The SSU, Internal Transcribed Spacer (ITS) and LSU regions of rDNA, and cytochrome c oxidase subunit 3 (CO3) of mitochondrial DNA, were used for phylogenetic reconstruction to determine
| Taxon                  | Accession number | Subclade1 of Host | GenBank accession |
|-----------------------|------------------|-------------------|-------------------|
| **E. acaciae**        | BPI 871098       | Plurinerves       |                   |
|                       |                  |                   |                   |
| **E. auriculiforme**  | BRIP 55690       | Juliflorae        |                   |
|                       |                  |                   |                   |
| **E. carnegiei**     | BRIP 57926       | Botrycephala      |                   |
|                       |                  |                   |                   |
| **E. dispensatum**    | BRIP 55659       | Juniflorae        |                   |
|                       |                  |                   |                   |
| **E. falciforme**     | BRIP 57583*      | Botrycephala      |                   |
|                       |                  |                   |                   |
| **E. hawaiiense**     | BRIP 87106       | Plurinerves       |                   |
|                       |                  |                   |                   |
| **E. irroratum**      | BRIP 55671       | Juliflorae        |                   |
|                       |                  |                   |                   |
| **E. maslinii**       | BRIP 57872*      | Botrycephala      |                   |
|                       |                  |                   |                   |
| **E. parvum**         | BRIP 57514       | Juliflorae        |                   |
|                       |                  |                   |                   |
| **E. peggi**          | BRIP 55602*      | Juliflorae        |                   |
|                       |                  |                   |                   |
| **E. phyllodiorum**   | BRIP 57310       | Juliflorae        |                   |
|                       |                  |                   |                   |
| **E. podalyriformium**| BRIP 57294       | Botrycephala      |                   |
|                       |                  |                   |                   |
| **E. tierneyi**       | BRIP 27071*      | Plurinerves       |                   |
|                       |                  |                   |                   |
| **E. tropicum**       | BRIP 56555       | Juliflorae        |                   |
|                       |                  |                   |                   |
| **E. violae-faustiae**| BRIP 55601       | Juliflorae        |                   |
|                       |                  |                   |                   |
| Kernkampella breyniae | BRIP 56909       | NA                |                   |
| Ravenella neocaledoniensis | BRIP 56907 | NA                |                   |
| Ravenella sp.          | BRIP 56904       | NA                |                   |
| Sphaerothrichium sp.   | BRIP 56910       | NA                |                   |
| Uromycladium simplex   | BRIP 57571       | Botrycephala      |                   |

1. Holotype
2. Botrycephala = Botrycephala subclade (Murphy et al. 2010); Juliflorae = Juliflorae p.p. clade (Miller et al. 2013); Plurinerves = Plurinerves p.p. clade (Miller et al. 2013).
3. Doungsa-ard et al. (2014).
whether the current taxonomy of Australian species was supported by molecular data and if further diversity existed within *Endoraecium*.

**MATERIALS AND METHODS**

**Taxon selection**

Fresh specimens were collected from New South Wales, the Northern Territory, Queensland, Victoria and Western Australia, representing a broad diversity of *Acacia* (Table 1). Species from representative genera of *Raveneliaceae*, namely *Diorchidium*, *Kernkampella*, *Ravenelia* and *Sphaerophragmium*, were selected as outgroup taxa for the phylogenetic analyses.

**Morphology**

Spores were scraped from leaf material, mounted in lactic acid and gently heated to boiling. Preparations were examined with a Leica DMLB microscope and images were taken with a Leica DFC500 camera. Measurements were made digitally from photographed spores. All previous taxonomic studies of *Endoraecium* have adopted an ontogenic approach to spore classification (Hodges & Gardner 1984, Walker 2001, Scholler & Aime 2006, Berndt 2011). Aeciospores, urediniospores and urediniospores of *Endoraecium* were mapped on to the topology.

**Uromycladium simplex** (*Pileolariciaceae*) was included as an outgroup to the *Raveneliaceae*, as it represented another Australian endemic rust on *Acacia*.

---

Fig. 1 Phylogram obtained in a maximum likelihood search in RAxML of the SSU, ITS, LSU and CO3 gene regions. Bootstrap support (≥ 70 %) values from 1 000 replicates above nodes. Posterior probabilities (≥ 0.95) from 4 200 trees in a Bayesian search are shown below nodes. Synapomorphic characters, namely host subclade and morphology of urediniospores, are mapped on to the topology.
in some cases teliospores, are often indistinguishable with this approach. For this reason, we used a morphological approach to classify spores (Laundon 1967), which recognises urediniospores of *Endoraecium* as spores with reticulate ornamentation, pedicels and germ pores.

**DNA extraction, PCR and sequencing**

DNA was extracted from fresh or archived material. Spores were obtained from leaf material according to the protocol in McTaggart et al. (2014), and then extracted with the UltraClean Microbial DNA Isolation Kit (MoBio Laboratories Inc., Solana Beach, CA, USA).

The ITS region was amplified with ITS1/ITS4B (Gardes & Bruns 1993). The ITS2-LSU region was amplified with Rust2inv (Aime 2006) / LR7 (Vilgalys & Hester 1990) and nested with LROR/LR6 (Vilgalys & Hester 1990). The LSU region was amplified with the primers CO3_F1/CO3_R1 (Viale et al. 2009). All PCRs were performed with high fidelity Phusion enzyme (New England Biolabs Inc.) according to the manufacturer’s instructions. The PCRs were performed with the following annealing temperatures: SSU, ITS and nested LSU at 62 °C, the initial LSU at 60 °C, and CO3 at 55 °C. PCR products were sent to Macrogen Korea for direct sequencing. Sequences were uploaded to GenBank under the accession numbers listed in Table 1.

**Phylogenetic analyses**

The SSU (19), ITS (47), LSU (51) and CO3 (29) sequences were aligned separately in MAFFT (Katoh et al. 2009) (available: http://www.ebi.ac.uk/Tools/msa/mafft/). Non-homologous regions in the ITS alignment were removed using GBlocks (Castresana 2000). The sequences from each locus were concatenated in MAFFT (Katoh et al. 2009) (available: http://mafft.cbrc.jp/alignment/server/). Non-homologous regions in the alignment were removed using GBlocks (Castresana 2000). The sequences from each locus were concatenated in MAFFT (Katoh et al. 2009) (available: http://mafft.cbrc.jp/alignment/server/). Non-homologous regions in the alignment were removed using GBlocks (Castresana 2000).

The topologies recovered by Bayesian inference and maximum likelihood were identical (Fig. 1). No differences were recovered in the tree topologies between nucleotide and amino acid coding sequences of CO3. *Endoraecium* was recovered as a mono-phyletic group sister to other members of the *Raveneliaceae*.

Three major clades of *Endoraecium* corresponded to three clades in *Acacia*, namely Plurinerves, Juliflorae and Botrycephalae. The clade of *Endoraecium* that diversified on Plurinerves contained the Hawaiian species of *Endoraecium* and the Australian species, *E. tierneyi*. Rust taxa formed well-supported clades corresponding to host species. This is contrary to the current broad host ranges proposed for *E. digitatum, E. parvum, E. phyliliorum* and *E. violae-faustiae* (Berndt 2011).

Morphology of the urediniospores was a synapomorphic character for the two large clades on Juliflorae and Botrycephalae (Fig. 1). Urediniospores of species on Juliflorae were golden brown with reticulate to foliolate ornamentation. Urediniospores of those on Botrycephalae were subhyaline to pale yellow with reticulate ornamentation.

**TAXONOMY**

*Endoraecium auriculiforme* McTaggart & R.G. Shivas, sp. nov.

— MycoBank MB808980; Fig. 2

**Etymology.** Name refers to the host, *Acacia auriculiformis*, on which it was found.

_Type. Australia_, Northern Territory, Darwin, Howard Springs (-12.4564, 131.0522), on *A. auriculiformis*, 15 Apr. 2012. C. Dougsa-ard, A.R. McTaggart, R. Berndt, V. Faust-Berndt, M.D.E. & R.G. Shivas (holotype BRIP 56548).

**Uredinia** on both phylloide surfaces, subepidermal, erumpent, on bullate swellings up to 1 cm long, or pulverulent on phylloide surface, linear to round, yellowish brown; paraphyses intrasoral, cylindrical, apex 6–9-digitate, subhyaline to yellow, 35–70 × 10–14 µm, thickened at apex, pedicel up to 40 µm. **Urediniospores** obovoid, oval to fusiform, apex acute, yellowish brown, 31–46 × 16–20 µm; wall 3–5 µm thick at sides and

![Fig 2 Endoraecium auriculiforme. a. Bullate sori on leaf (BRIP 56550); b, c. urediniospores (BRIP 55609); d. teliospores (BRIP 56550); e. germinating teliospore (BRIP 56549). — Scale bars: a = 1 cm; b–e = 10 µm.](image)
5–9 μm thick at apex, foveolate, with 3–4 equatorial germ pores; pedicel 3–5 μm, or absent. Telia formed from uredinia, erumpent, reddish brown. Teliospores cylindrical to fusiform, apex rounded, 2–4-digitate, hyaline to subhyaline, 36–54 × 13–25 μm; wall 1.5–2.5 μm thick at sides, 6–8 μm thick at apex; pedicel persistent, up to 38 μm. Basidia cylindrical, 3-septate, up to 35–40 × 8–12 μm. Basidiospores globose, hyaline, 4–6 μm, smooth-walled.

On phyllodes of Acacia auriculiformis (Juliflorae).

Additional specimens examined. AUSTRALIA, Northern Territory, Howard Springs, on A. auriculiformis, 9 May 2012, C. Dounga-sa-ard, A.R. McTaggart, R. Berndt, V. Faust-Berndt, M.D.E. & R.G. Shivdas, BRIP 55689; 15 Apr. 2012, C. Doungsa-ard, A.R. McTaggart, R. Berndt, R.G. Shivdas, BRIP 56580; Northern Territory, Darwin, Bronzewing Ave, Howard Springs, 15 Apr. 2012, C. Doungsa-ard, A.R. McTaggart, R. Berndt & R.G. Shivdas, BRIP 56549.

Notes — *Endoraecium auriculiforme* has foveolate urediniospores with an acute and thickened apex, and digitate paraphyses that resemble narrow teliospores. *Endoraecium violae-faustiae* and *E. peggii* also produce similar paraphyses. These three species all occur on hosts in the Juliflorae, with *E. auriculiforme* restricted to *A. auriculiformis*, *E. violae-faustiae* to *A. aulacocarpa* and *A. crassicarpa*, and *E. peggii* to *A. holosericea*. In the phylogenetic analyses, *E. auriculiforme* was recovered as sister to *E. peggii* (Fig. 1).

*Endoraecium bicinctum* (McAlpine) M. Scholler & Aime, Mycoscience 47: 163. 2006

Basionym. *Uromyces bicinctus* McAlpine, Rusts of Australia: 93. 1906.≡ *Pileolaria bicinta* (McAlpine) Dietel, Ann. Mycol. 19: 302. 1921.≡ *Atelocauda bicinta* (McAlpine) Cummins & Y. Hirats., Illust. Gen. Rust Fungi, rev. edn (St. Paul): 147. 1983.≡ *Racospermyces bicinctus* (McAlpine) J. Walker, Australas. Mycol. 20: 16. 2001.

Type. AUSTRALIA, Queensland, Rockhampton, on A. fasciculifera, 30 Nov. 1886, G.H. Robinson (holotype VPR 5751).

Notes — *Endoraecium bicinctum* is known from four collections, which were examined by Walker (2001). It is only known to occur on *A. fasciculifera* in Botrycephalae (Murphy et al., 2010, Maslin 2013).

*Endoraecium carnegiei* McTaggart & R.G. Shivdas, sp. nov. — MycoBank MB080981; Fig. 3

Etymology. Named after the Australian forest pathologist and fungal taxonomist, Dr Angus J. Carnegie, who generously assisted this study by collecting many specimens of rust on Acacia, including the type specimen on which this taxon is based.

*Endoraecium carnegiei* a. Telia on leaves (BRIP 59218); b. gall (BRIP 57924); c. urediniospores (BRIP 57924); d. e. teliospores (BRIP 57924). — Scale bars: b = 1 cm; c–e = 10 μm.

Notes — *Endoraecium carnegiei* is one of three species that forms galls on the stems of its host. The other two species, *E. digitatum* and *E. irroratum*, also infect species of *Acacia* in the Botrycephalae. *Endoraecium carnegiei* is only known to occur on *A. dealbata* in south-eastern Australia.

*Endoraecium digitatum* (G. Winter) M. Scholler & Aime, Mycoscience 47: 163. 2006.

Basionym. *Uromyces digitatus* G. Winter, Rev. Mycol. (Toulouse) 8: 209. 1886.≡ *Coemorus digitatus* (G. Winter) Kuntze (as ‘Coeomurus’), Revis. Gen. Pl. 3: 450. 1898.≡ *Atelocauda digitata* (G. Winter) Cummins & Y. Hirats., Illust. Gen. Rust Fungi, rev. edn (St. Paul): 147. 1983.≡ *Racospermyces digitatus* (G. Winter) J. Walker, Australas. Mycol. 20: 13. 2001.

Type. AUSTRALIA, South Australia, near Gawler, on A. notabilis, 1 July 1885, J.G.O. Tepper (holotype SF35352); South Australia, west of Gawler, along road to Mallala (-34.5665, 138.7184), on A. notabilis, 16 Oct. 2009, V. Faust-Berndt & R. Berndt (epitype SF35352).

Notes — Our study shows that the known host range of *E. digitatum* s.str. is restricted to *A. notabilis* in Botrycephalae. Walker (2001) adopted a broad host range for *E. digitatum*, but suspected it was a complex of closely related taxa, confined to one or a small group of hosts. Berndt (2011) divided *E. digitatum* into five species in Australia. He accepted *E. phyllocladorum* as distinct from *E. digitatum*, and further described three new taxa, *E. parvum*, *E. violae-faustiae* and *E. walkerianum*. Berndt (2011)
designated an epitype for *E. digitatum* on *A. notabilis*, and listed six species of *Acacia* as hosts. We found four of these hosts, *A. dealbata*, *A. falciformis*, *A. irrorata* and *A. podalyriifolia*, were infected by novel species of *Endoraecium*. The remaining two hosts, *A. deanei* and *A. oshanesii*, most likely represent two new hosts of *Endoraecium*. The urediniospores of *E. digitatum* were not examined in this study, however, the description of the epitype (Berndt 2011) is similar to other species of *Endoraecium* with subhyaline to golden yellow urediniospores and reticulate ornamentation on species of *Acacia* in Botrycephalae.

**Endoraecium disparrimum** McTaggart & R.G. Shivas, sp. nov.

— MycoBank MB808982; Fig. 4

*Etymology.* Name refers to the host, *Acacia disparrima*, on which it was found.

*Type.* AUSTRALIA, Queensland, Babinda (-17.3397, 145.8675), on *A. disparrima*, 3 Apr. 2012, C. Doungsa-ard, A.R. McTaggart, R. Berndt, V. Faust-Berndt, M.D.E. & R.G. Shivas (holotype BRIP 55626).

*Uredinia* on both phyllode surfaces, forming bullate swellings up to 1 cm long, or pulverulent, linear to round, up to 1 mm diam, yellowish brown. *Urediniospores* subglobose to ovoid, apex obtuse, yellowish brown, 29–41 × 20–26 µm; wall 2–4 µm thick at sides and 5.5–9.0 µm thick at apex, reticulate,
with 2–5 equatorial germ pores; pedicel 2 µm or absent. Telia formed from uredinia, yellowish brown. Teliospores cylindrical to fusiform, apex acuminate to rounded, hyaline to subhyaline, 31–50 × 20–26 µm; wall 1–2 µm thick at sides, 4–14 µm thick at apex; pedicel persistent, up to 33 µm.

On phyllodes of *A. disparrima* (Juliflorae).

Additional specimen examined, AUSTRALIA, Queensland, Herberton, Silver Valley Drive, on *A. disparrima*, 10 Apr. 2012, R. Berndt & V. Faust-Berndt, BRIP 55659; Queensland, near Yungaburra, Danbilla State Forest, at the Chimney’s Rest Area, on *A. disparrima*, 9 Apr. 2012, R. Berndt & V. Faust-Berndt, BRIP 55632.

Notes — *Endoraecium disparrimum* occurs on *A. disparrima* in Juliflorae. It was recovered as sister to *E. violae-faustiae*, which occurs on closely related species of *Acacia*. It differs from *E. violae-faustiae* in that the urediniospores have an obtuse apex with reticulate rather than foveolate ornamentation, and paraphyses are absent.

*Endoraecium falciforme* McTaggart & R.G. Shivas, sp. nov. — MycoBank MB808983; Fig. 5

Etymology. Name refers to the host, *Acacia falciformis*, on which it was found.

Type. AUSTRALIA, Queensland, Mt Tibrogargan (-26.9283, 152.9494), on *A. falciformis*, 15 Aug. 2012, C. Doungsa-ard & A.R. McTaggart (holotype BRIP 57583).

Spermogonia on fruit or phyllodes, amphiogenous, subepidermal, erumpent, c. 100 µm. *Uredinia* on fruit or on both phyllode surfaces, causing distortion, surrounding spermogonia, subepidermal, erumpent, pulverulent, linear, round to ellipsoidal, greater than 10 mm, reddish brown. *Urediniospores* ellipsoidal to ovoid, subhyaline to yellow, 34–43 × 21–25 µm; wall unevenly thickened at equator, 3.0–6.5 µm and 3–5 µm thick at apex, reticulate, with 4–9 equatorial germ pores; pedicel 2 µm. *Telia* on both phylloide surfaces, formed separately from uredinia, erumpent, c. 1 mm, orange to yellowish brown. *Teliospores* cylindrical to clavate, apex rounded, 2–5-digitate, subhyaline, 47–63 × (13–)15–23 µm; wall 1.5–2.0 µm thick at sides, 12–24 µm thick at apex; pedicel persistent, up to 64 µm long × 6–8 µm thick.

On phyllodes and fruit of *A. falciformis* (Botrycephalae).

Additional specimen examined, AUSTRALIA, Queensland, Mt Tibrogargan, 4 Sept. 2012, K.M. Thomson, BRIP 57643.

Notes — *Endoraecium falciforme* is morphologically similar to *E. walkeri*anum, which both occur on species of *Acacia* species in Botrycephalae. *Endoraecium falciforme* has distinctively thicker walls at the equator of the urediniospores (3.0–6.5 µm) than *E. walkeri*anum (3.0–4.5 µm). *Endoraecium falciforme* is recorded from south-east Queensland, whereas *E. walkeri*anum is known from southern Australia. *Urediniospores* from a para-type specimen of *E. walkeri*anum (BRIP 14205) were found to have thickened apices, whereas those of *E. falciforme* were thickened at the equator, or the wall was of uniform thickness.

*Endoraecium irroratum* McTaggart & R.G. Shivas, sp. nov. — MycoBank MB808984; Fig. 6

Etymology. Name refers to the host, *Acacia irrorata*, on which it was found.

Type. AUSTRALIA, Queensland, Main Range National Park, on *A. irrorata*, 11 June 2012, A.D.W. Geering (holotype BRIP 57286).

*Uredinia* forming galls on stems, up to 2 cm long, yellowish brown. *Urediniospores* ovoid, apex obtuse, subhyaline, yellow to yellowish brown, 32–42 × 17–24 µm; wall 2.0–3.5 µm thick at sides, apex sometimes thickened (up to 4 µm), reticulate, with 4–10 equatorial germ pores. *Telia* formed from uredinia, yellowish brown. *Teliospores* cylindrical to subfusiform, apex acuminate to rounded, 2–7-digitate, subhyaline to yellow, 47–73 × 15–22 µm; wall 1.0–1.5 µm thick at sides, 11–21 µm thick at apex; pedicel persistent, up to 46 µm.

On stems and phyllodes of *A. irrorata* (Botrycephalae).

Additional specimen examined, AUSTRALIA, New South Wales, Warrumbungle National Park, on *A. irrorata*, 20 Mar. 2012, R. Berndt & V. Faust-Berndt, BRIP 55671; Queensland, Mt Mee, Mt Mee State Forest, on *A. irrorata*, 3 June 2012, C. Doungsa-ard & R.G. Shivas, BRIP 57279; Queensland, Mt Glorious, Wivenhoe Dam lookout area (-27.3077, 152.7136), *A. irrorata*, 30 Nov. 2012, A.D.W. Geering, BRIP 58054.

Notes — *Endoraecium irroratum* occurs on *A. irrorata* in Botrycephalae. Berndt (2011) considered that the rust on *A. irrorata* was *E. digitatum* based on morphology. There are no clear morphological differences that separate *E. irroratum* from the epitype of *E. digitatum* (Berndt 2011). However, the results from the molecular phylogenetic analysis in this study indicate the rusts on Botrycephalae are each restricted to a single host species.

*Endoraecium maslinii* McTaggart & R.G. Shivas, sp. nov. — MycoBank MB808985; Fig. 7

Etymology. Named after the Australian botanist Bruce R. Maslin, an expert on *Acacia* taxonomy, who has published approximately 250 *Acacia* taxa and kindly identified many specimens in this study.

Type. AUSTRALIA, Western Australia, Midlands Rd, 10 km SE of Mingenew (-29.2847, 115.5319), on *A. daphnifolia*, 28 Sept. 2012, C. Doungsa-ard & A.R. McTaggart (holotype BRIP 57872).

![Fig 6 Endoraecium irroratum. a. Stem gall (BRIP 55671); b, c. urediniospores (BRIP 55671); d. teliospore (BRIP 57286). — Scale bars: a = 1 cm; b–d = 10 µm.](Image 57x49 to 539x211)
Uredinia forming bullate swellings on fruit and both phyllode surfaces, round, up to 1 cm, yellowish brown. *Urediniospores* elliptoidal, ovoid to fusiform, apex obtuse, subhyaline to yellowish brown, 37–46 × 20–26 µm; wall 2.5–5.0 µm thick at side, apex slightly thickened, 3.5–6.0 µm, reticulate, with 6–8 equatorial germ pores; pedicel absent or up to 2.5 µm.

On phyllodes of *A. daphnifolia* (Botrycephaleae).

Notes — *Endoraecium maslinii* occurs on *A. daphnifolia* in Botrycephaleae and is the only species of *Endoraecium* known from Western Australia. Only *Urediniospores* have been found, which are yellowish brown and reticulate, and morphologically similar to other species on *Acacia* in Botrycephaleae.

*Endoraecium parvum* Berndt, Mycol. Progr. 10: 510. 2011

(Type. AUSTRAlia, Queensland, Caloundra, on *A. leiocalyx*, 25 Aug. 1932, S.T. Blake (holotype BRIP 7543)).

*Uredinia* on both phyllode surfaces, subepidermal, erumpent, linear to round, yellow brown. *Urediniospores* globose, subglobose to ovoid, apex obtuse, yellowish brown to reddish brown, 25–38 × 16–22 µm; wall 3–4 µm thick at equator, hardly thickened at apex, reticulate, with 2–4 equatorial germ pores, pedicel 1.5–3.0 µm. *Telia* formed from *Uredinia*, erumpent, linear to dome-shaped, reddish brown. *Teliospores* oval, apex rounded, 1–3-digitate, hyaline to subhyaline, 31–60 × 13–27 µm; wall 1–2 µm thick, mostly thickened at apex (5–14 µm); pedicel persistent, up to 66 µm.

Additional specimens examined. AUSTRAlia, Queensland, Caloundra, on *A. leiocalyx*, 25 Aug. 1932, S.T. Blake, BRIP 7543; Queensland, Mt Coolum (–26.5656, 153.0942), on *A. leiocalyx*, 27 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57872. Queensland, Brisbane, Geebung (–27.3375, 152.5189), on *A. leiocalyx*, 1 Aug. 2012, C. Doungsa-ard, A.R. McTaggart, A.D.W. Geering & R.G. Shivas, BRIP 57631; Queensland, Brisbane, Mt Coot-tha Botanic Gardens (–27.477655, 152.972270), on *A. holosericea*, Nov. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 58324.

Notes — *Endoraecium peggii* is known from *A. holosericea* in Juliflorae. This species of *Acacia* is native to northern Australia (Maslin 2013). The rust was also collected in south-east Queensland on a plant in the Mt Coot-tha Botanic Gardens. The teliospores of *E. peggii* lack the apical digitations found in all other species of *Endoraecium*, although this ornamentation is present on the paraphyses.

*Endoraecium phyllodiorum* (Berk. & Broome) Berndt, Mycol. Progr. 10: 503. 2011

*Basionym. Melampsora phyllodiorum* Berk. & Broome, Trans. Linn. Soc. London 2, ser. 2: 67. 1883.

*Uromyces phyllodiorum* Berk. & Broome, *MycoBank* MB808986; Fig. 8

Etymology. Named after the Australian forest pathologist and rust specialist, Dr Geoff S. Pegg, who has discovered several new plant pathogens in Australia.

Type. AUSTRAlia, Northern Territory, Darwin, 8 km from airport, on *A. holosericea*, 7 May 2012, R.G. Shivas (holotype BRIP 55502).

*Uredinia* on both phyllode surfaces, pulvulrent, subepidermal, erumpent, linear to round, up to 2 mm, yellowish brown; paraphyses intrasoral, cylindrical, yellow, with pedicel, 37–84 × 9–10 µm, thickened at apex, digitate. *Urediniospores* ovoid, apex obtuse, yellowish brown to reddish brown, 31–45 × 20–25 µm; wall 3–5 µm thick at sides, apex 4–10 µm thick, foveolate to reticulate, with 2–3 equatorial germ pores; pedicel 3–6 µm. *Telia* rare, on both surfaces of phyllode, darker than uredinia, erumpent, linear, brown to black. *Teliospores* oval, apex rounded, no digitations, hyaline to subhyaline, 45–60 × (15–)19–27 µm; wall 1.5–2.0 µm thick at sides, sometimes thickened at apex, 7–17 µm; pedicel persistent, up to 52 µm.

On phyllodes of *A. holosericea* (Juliflorae).

Additional specimens examined. AUSTRAlia, Queensland, Dumbillah, Bourke Developmental Road, on *A. holosericea*, 6 Apr. 2012, C. Doungsa-ard, A.R. McTaggart, R. Berndt, V. Faust-Berndt, M.D.E. Shivas, BRIP 55631; Queensland, Mt Coot-tha Botanic Gardens (–27.477655, 152.972270), on *A. holosericea*, Nov. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 58324.

Notes — *Endoraecium peggii* is known from *A. holosericea* in Juliflorae. This species of *Acacia* is native to northern Australia (Maslin 2013). The rust was also collected in south-east Queensland on a plant in the Mt Coot-tha Botanic Gardens. The teliospores of *E. peggii* lack the apical digitations found in all other species of *Endoraecium*, although this ornamentation is present on the paraphyses.
Uromyces phyllodii Cooke & Massee (as 'phyllodiae'), in Cooke, Grevillea 17: 70. 1889.
≡ Coeomurus phyllodii (Cooke & Massee) Kuntze (as 'Caeomurus'), Revis. Gen. Pl. 3: 450. 1898.

Type. AUSTRALIA, Queensland, Brisbane, on Acacia sp., F.M. Bailey no. 269, K(M) 146703.

Uredinia on both phyllode surfaces, subepidermal, erumpent, pulverulent or on bullate swellings, linear, round to irregular, yellowish brown. Urediniospores subglobose to oval, apex obtuse, yellowish brown, (28–)30–52 × 17–26 µm; wall 2.5–4.0 µm thick at sides, 5–10 µm thick at apex, reticulate, with 3–7 equatorial germ pores; pedicel absent or 1.5–3.5 µm.

Telia formed from uredinia, erumpent, linear, reddish brown. Teliospores cylindrical to oval, apex rounded, 1–4-digitate, hyaline to subhyaline, 38–58 × 17–28 µm; wall 1–2 µm thick at sides, 6–17 µm thick at apex; pedicel persistent, up to 30 µm.

Additional specimens examined. AUSTRALIA, Queensland, Mount Coolum (-26.5611, 153.0839), on A. aulacocarpa, 28 July 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57310; Queensland, Mt Coolum (-26.5611, 153.0839), on A. aulacocarpa, 28 July 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57516; New South Wales, Woombah, at the beginning of Iluka Road (-29.3544, 153.2492), on A. aulacocarpa, 11 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57578; New South Wales, Woombah, at the beginning of Iluka Road (-29.3544, 153.2492), on A. aulacocarpa, 11 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57580; New South Wales, Woombah, Iluka Bluff (-29.3967, 153.3722), on A. aulacocarpa, 11 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57579; New South Wales, Shark Creek (-29.5664, 153.2003), on A. aulacocarpa, 13 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57569; New South Wales, Shark Creek (-29.5664, 153.2003), on A. aulacocarpa, 13 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57570; Queensland, Mt Tibrogargan (-26.9264, 152.9417), on A. aulacocarpa, 15 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57588; Queensland, Mt Tibrogargan (-26.9258, 152.9508), on A. aulacocarpa, 15 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57589; Queensland, Mt Tibrogargan (-26.9278, 152.9378), on A. aulacocarpa, 15 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57590.

Notes — Berndt (2011) discussed the taxonomy of E. phyllodiorum, and listed the hosts as A. aulacocarpa, A. crassicarpa, A. holosericea, A. mangium and tentatively A. auriculiformis. The type specimens of Melampsora phyllodiorum and Uromyces phyllodii were collected on unidentified species of Acacia in Brisbane, Australia. Acacia aulacocarpa is the only host species listed by Berndt (2011) that occurs naturally in or near to Brisbane. The other four species of Acacia are restricted to northern Queensland and the Northern Territory (Maslin 2013). Herbarium records and field observations by the authors show that Endoraecium spp. occur on four species, A. aulacocarpa, A. irrorata, A. leiocalyx and A. podalyriifolia, in the Brisbane region. The rust on A. aulacocarpa forms bullate swellings on phyllodes, very similar to those seen in the type specimen of E. phyllodiorum and illustrated by Berndt (2011). Consequently, we suggest that A. aulacocarpa is the host of the type of E. phyllodiorum. Berndt (2011) proposed that E. phyllodiorum had a wide host range, including A. aulacocarpa, A. auriculiformis, A. holosericea and A. mangium. The rusts on A. auriculiformis and A. holosericea are now identified as E. auriculiforme and E. peggii, respectively. The rust on A. mangium is unknown. Acacia aulacocarpa is the only species of Acacia known to host two species of Endoraecium, E. phyllodiorum and E.-violae-faustiae.

Fig. 8 Endoraecium peggii. a. Uredinia (BRIP 55631); b. teliospores (BRIP 55602); c, d. urediniospores (BRIP 55631). — Scale bars: a = 1 cm; b–d = 10 µm.
Endoraecium podalyriifolium McTaggart & R.G. Shivas, sp. nov. — MycoBank MB808987; Fig. 9

Etymology. Name refers to the host, Acacia podalyriifolia, on which it was found.

Type. AUSTRALIA, New South Wales, Maclean, Wharf Street (-29.4589, 153.2111), on A. podalyriifolia, 12 Aug. 2012, C. Doungsa-ard & A.R. McTaggart (holotype BRIP 57576).

Uredinia on both phyllode surfaces, subepidermal, erumpent, pulverulent, round, 0.5–10.0 mm, yellow to yellowish brown. Urediniospores cylindrical to ovoid, apex obtuse, subhyaline to yellow, (30–)33–44 × 23–27 μm; wall 3–4 μm thick, reticulate, with 4–6 germ pores. Telia formed from uredinia, subepidermal, erumpent, yellow. Teliospores cylindrical to fusiform, apex rounded, 2–5-digitate, subhyaline to yellow, 44–60 × 12–19 μm; wall 1 μm thick at sides, 6–12 μm thick at apex; pedicel persistent, over 60 μm.

On phyllodes of A. podalyriifolia (Botrycephalae).

Additional specimen examined. AUSTRALIA, Queensland, South Ripley, Ripley Road, on A. podalyriifolia, 17 July 2012, A.D.W. Geering, BRIP 57294.

Notes — Berndt (2011) considered the rust on A. podalyriifolia was E. digitatum based on morphology and the close relationships of host species within this group. However, the results from the molecular phylogenetic analysis in this study indicate the rusts on Botrycephalae are each restricted to a single host species.

Endoraecium tierneyi (J. Walker & R.G. Shivas) M. Scholler & Aime, Mycoscience 47: 163. 2006

Basionym. Racospermyces tierneyi J. Walker & R.G. Shivas, in Walker, Australas. Mycol. 20: 23. 2001.

Type. AUSTRALIA, Queensland, Tambo, near Castle Vale, on A. harpophylla, 6 June 2000, G.S. Pegg (holotype BRIP 27071).

Uredinia on both phyllode surfaces, subepidermal, erumpent, linear, up to 500 μm, yellowish brown. Urediniospores cylindrical, oval to broadly fusiform, apex obtuse, reddish brown, 26–36 × 13–18 μm; wall 2.0–2.5 μm thick at sides, 4.0–4.5 μm thick at apex, reticulate, with 4–8 equatorial germ pores. Telia on both phyllode surfaces, erumpent. Teliospores subglobose, ovoid to obvoid, apex rounded, reddish brown, darker at the apex, 27–41 × 20–26 μm; wall 1.0 μm thick at sides, 7–13 μm thick at apex, smooth; pedicel persistent, 50–55 μm long.

Additional specimens examined. AUSTRALIA, Queensland, Springsure, on A. harpophylla, 27 Feb. 2001, G.S. Pegg, BRIP 27887; Queensland, Caldey Vale, on A. harpophylla, 1 Mar. 2001, G.S. Pegg, BRIP 27880.

Notes — Endoraecium tierneyi occurs on A. harpophylla in Plurinerves. It was recovered in the phylogenetic analyses as sister to three species of Endoraecium in Hawaii that occur on A. koa, also in Plurinerves. The teliospores are subglobose to obvoid, while other species of Endoraecium in Australia have clavate teliospores.
**Endoraecium tropicum** McTaggart & R.G. Shivas, sp. nov. — MycoBank MB808988; Fig. 10

**Etymology.** Name refers to the host, *Acacia tropica*, on which it was found.

**Type.** AUSTRALIA, Northern Territory, Gregory, Victoria Highway (-15.6003, 131.2136), on *A. tropica*, 20 Apr. 2012, C. Doungsa-ard, A.R. McTaggart, R. Berndt, V. Faust-Berndt, M.D.E. & R.G. Shivas (holotype BRIP 56557).

**Uredinia** on both phylloide surfaces, subepidermal, pulvulent, up to 2 mm, brown. *Urediniospores* ovoid to fusiform, apex oblique, yellowish brown, not forming bulbalate sori; paraphyses cylindrical with digitate heads, subhyaline to yellow, 35–88 × 6–15 µm thick at sides, thickened at apex. *Urediniospores* globose, subglobose, obvoid to oval, apex acute, yellowish brown, 28–53 × 17–26 µm; wall 2.5–4.5 µm thick at sides, apex mostly thickened, 5.0–10.5 µm thick, foveolate, with 3–5 equatorial germ pores; pedicel 3–5 µm. *Telia* formed from uredinia, erumpent. Teliospores clavate, apex rounded, papillate rather than digitate, 40–53 × 16–23 µm; wall 1.5–2.0 µm thick at sides, 8–11 µm thick at apex; pedicel persistent, 5 µm.

Notes — *Endoraecium tropicum* was closely related to *E. parvum* in the phylogenetic analysis. Both species have urediniospores with uniformly thickened spore walls. The distribution of *A. tropica* is restricted to the Northern Territory and north-west Queensland. *Acacia leiocalyx*, the host of *E. parvum*, occurs in eastern Australia (Maslin 2013).

**Endoraecium violae-faustiae** Berndt, (as ‘violae-faustiae’) Mycol. Progr. 10: 513. 2011

**Type.** AUSTRALIA, Queensland, Cairns, Barron Gorge, MacDonald’s trail, on *A. crassicarpa* (as *Acacia sp.*), 18 Aug. 2006, V. Faust-Berndt & R. Berndt (holotype BRIP 53388).

**Uredinia** on both phylloide surfaces, subepidermal, erumpent, pulvulent, linear to round, yellowish brown, not forming bulblet sori; paraphyses digitate, subhyaline to yellow, 35–88 × 6–15 µm thick at sides, thickened at apex. *Urediniospores* globose, subglobose, obvoid to oval, apex acute, yellowish brown, 28–53 × 17–26 µm; wall 2.5–4.5 µm thick at sides, apex mostly thickened, 5.0–10.5 µm thick, foveolate, with 3–5 equatorial germ pores; pedicel 3–5 µm. *Telia* formed from uredinia, erumpent, reddish brown. Teliospores obvoid to oval, rounded, 1–4–digitate, hyaline to subhyaline, 41–53 × 20–28 µm; wall 1.5–3.0 µm thick at sides, 5–14 µm thick at apex; pedicel persistent, up to 43 µm.

Notes — Berndt (2011) described the urediniospores of *E. violae-faustiae* as foveolate, with a thickened and acute apex. The most distinctive character was the variable paraphyses, which resembled thin teliospores, similar to those found in *E. auriculiforme* and *E. peggi*. *Endoraecium violae-faustiae* was reported on *A. crassicarpa* and *A. violae-faustiae*, also in *U. foveolate*, as well as *A. flavescens* in *Plurinerves* (Berndt 2011). The host of the holotype (BRIP 53388), was re-identified as *A. crassicarpa*, which is closely related to *A. violae-faustiae* (Maslin 2013). The host plant of the specimen on *A. crassicarpa* (BRIP 25816) was re-identified as *A. crassicarpa*. The distribution of *E. violae-faustiae* is restricted to the northern parts of Australia on *A. crassicarpa*, *A. violae-faustiae* and *A. difficiilis*.

**Endoraecium walkerianum** Berndt, Mycol. Progr. 10: 509. 2011

**Type.** AUSTRALIA, New South Wales, Cavan Gap near Yass, on *A. penninervis*, 20 Nov. 1951, E. Gauba (holotype SF35354).

Additional specimen examined. AUSTRALIA, New South Wales, Bald Rock, on *A. penninervis*, 26 Feb. 1984, J.W. Tienney, paratype BRIP 14205.

Notes — *Endoraecium walkerianum* was reported from *A. penninervis* and *A. obliquinervia* (Berndt 2011) in Botrycephalae (Maslin 2013).
A KEY TO THE KNOWN SPECIES OF ENDORAECIUM IN AUSTRALIA

1. Urediniospores hyaline to pale yellow (on Botrycephalae) .................................................. 2
2. Urediniospores golden or reddish brown ................................................................. 7
3. Urediniospore wall up to 5 µm or thicker at sides .................................................. 3
4. Urediniospore wall 2.0–4.5 µm thick at sides .................................................. 4

3. Forming galls on stems of A. notabilis ..................................... E. digitatum
4. Forming hypertrophied lesions on A. falciformis .................................................. 13
5. Forming hypertrophied lesions on A. daphnifolia .................................................. E. maslinii
6. Forming hypertrophied lesions on phyllodes .................................................. 5
7. Teliospores globose to ellipsoid on life cycle and morphology, but are identical in the LSU region of
   Acacia.............................................................................................................................. 6
8. Urediniospore with thickened apex ................................................................. 10
9. Teliospores digitate, on ................................................................. E. parvum
10. Urediniospores reticulate, paraphyses absent .................................................. 13
11. Urediniospores not acute, on ................................................................. E. parrimum
12. On ................................................................. E. auriculiforme
13. On ................................................................. E. parvum

DISCUSSION

Phylogenetic analyses of loci from nuclear rDNA and mitochondrial DNA showed that species of Endoraecium in Australia have narrow host ranges. Savile (1971) hypothesised that rusts speciated either by divergence with their hosts or by host jumps. The close relationship between Endoraecium and species/subspecies of Acacia observed in this study indicates that Endoraecium diversified by co-evolution with its hosts. For example, the five species of Endoraecium on Botrycephalae, namely, E. camegiei, E. falciforme, E. irroratum, E. maslinii and E. podalyriformis, were closely related with few differences in the studied genes and short branch lengths between species in the recovered phylogenetic trees. Species of Acacia in Botrycephalae diversified c. 3.4–3.8 million years ago (Miller et al. 2013), which would represent the maximum age of the corresponding Endoraecium species.

Endoraecium tierneyi on A. harpophylla in Australia was recovered as sister to the Hawaiian species, E. acaciae, E. hawaiiense and E. koae, on A. koae. These Australian and Hawaiian rusts all occur on species of Acacia in Plurinerves. Hodges & Gardner (1984) and Walker (2001) proposed that the Australian species of Endoraecium were the ancestor of the Hawaiian rusts. Our study supports this view by showing the rusts on Plurinerves had an Australian ancestor (pleiomorphic state). Further, the three rusts on Acacia in Hawaii have differences in life cycle and morphology, but are identical in the LSU region of rDNA. These rusts have diversified on A. koae after its relatively recent split from Australian species of Acacia (Brown et al. 2012). Endocyclic species occur in Hawaii but not in Australia, which shows that a reduced life cycle is a derived character in Endoraecium.

Endoraecium hyalosporum from South-East Asia infects A. confusa, which is the only example of a species of Endoraecium on a host outside of the p.u.b. clade of Acacia (Brown et al. 2012). This may represent an example of a host jump. However the systematic position of E. hyalosporum is unknown, and it is possible that it does not have a close phylogenetic relationship to other species of Endoraecium. It is noteworthy that E. hyalosporum has been assigned to other genera at various times, namely, Maravalia (Dietel 1924), Poliotelium (Main 1939) and Atlolocauda (Oro 1984).

The morphology of urediniospores may be synapomorphic for the three clades of Endoraecium. For example, the rusts on Juliflorae have reticulate to foliate ornamentation on golden-brown urediniospores. The rusts on Botrycephalae have a raised reticulate ornamentation on subhyaline to pale yellow urediniospores. Endoraecium tierneyi was the only rust examined on Plurinerves, and it had reticulate, reddish brown urediniospores. Berndt (2011) noted the urediniospores of species of Endoraecium on A. koa have similar morphology to the rusts on Juliflorae, such as E. phylloidiorm. We cannot propose any apomorphies for the rusts on Plurinerves at this stage. The rusts on Juliflorae, namely, E. auriculiforme, E. parvum, E. parrimum, E. phylloidiorm and E. violae-faustiae, have urediniospores with thickened apices, whereas their sister rusts E. parvum and E. tropicum, also in Juliflorae, have uniformly thickened spore walls.

Other morphological characters were less useful for species delimitation in Endoraecium. In general, the teliospores of rusts on species of Acacia in Botrycephalae had a raised, reticulate teliospore on subhyaline to pale yellow urediniospores. Berndt (2011) noted the urediniospores of species of Endoraecium on A. koa have similar morphology to the rusts on Juliflorae, such as E. phylloidiorm. We cannot propose any apomorphies for the rusts on Plurinerves at this stage. The rusts on Juliflorae, namely, E. auriculiforme, E. parvum, E. parrimum, E. phylloidiorm and E. violae-faustiae, have urediniospores with thickened apices, whereas their sister rusts E. parvum and E. tropicum, also in Juliflorae, have uniformly thickened spore walls.

REFERENCES

Aime MC. 2006. Toward resolving family-level relationships in rust fungi (Uredinales). Mycoscience 47: 112–122.
Berkeley MJ, Broome CE. 1983. List of fungi from Brisbane, Queensland; with descriptions of new species (part ii). Transactions of the Linnean Society of London 2: 53–73.
Berndt R. 2011. Taxonomic revision of Endoraecium digitatum (rust fungi). Urediniales with description of four new species from Australia and Hawaii. Mycological Progress 10: 497–517.
Brown GK, Murphy DJ, Kidman J, et al. 2012. Phylogenetic connections of phyllodinous species of Acacia outside Australia are explained by geological history and human-mediated dispersal. Australian Systematic Botany 25: 390–403.

Castracana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17: 540–552.

Cummins GB, Hiratsuka Y. 1983. Illustrated genera of rust fungi. APS, St. Paul, MN.

Dietet P. 1921. Zur Umgrenzung der Gattung Pileolaria Cast. Annales Mycologici 19: 300–303.

Dietet P. 1924. Kleine Beiträge zur Systematik der Uredineen. IV. Annales Mycologici 22: 269–273.

Doungsa-ard C, McTaggart AR, Geering ADW, et al. 2014. Uromycladium falcatarium sp. nov., the cause of gall rust on Paraserianthes falcataria in South-East Asia. Australasian Plant Pathology: doi 10.1007/s13313-014-0301-z.

Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118.

Gardner DE. 1991. Atelocauda angustiphylloda n. sp., a microcyclic rust on Acacia koa in Hawaii. Mycologia 83: 650–653.

Hodges Jr CS, Gardner DE. 1984. Hawaiian forest fungi. IV. Rusts on endemic Acacia species. Mycologia 76: 332–349.

Kato K, Asimenos G, Toh H. 2009. Multiple alignment of DNA sequences with MAFFT. In: Posada D (ed), Bioinformatics for DNA sequence analysis. Humana Press, New York, USA: 39–64.

Laundon GF. 1939. Studies in the Uredinales, the genus Maravalia. Bulletin of the Torrey Botanical Club 66: 173–179.

Maslin BR. 2013. World Wide Wattle. Available: http://www.worldwidewattle.com/ Accessed: January 2014.

McAlpine D. 1906. The rusts of Australia: Their structure, nature and classification. Government Printer, Melbourne.

McTaggart AR, Geering ADW, Shivas RG. 2014. The rusts on Goodeniaceae and Stylidiaceae. Mycological Progress 13: 1017–1025.

Miller JT, Murphy DJ, Ho SYW, et al. 2013. Comparative dating of Acacia: combining fossils and multiple phylogenies to infer ages of clades with poor fossil records. Australian Journal of Botany 61: 436–445.

Murphy DJ, Brown GK, Miller JT, et al. 2010. Molecular phylogeny of Acacia Mill. (Mimosoideae: Leguminosae): evidence for major clades and informal classification. Taxon 59: 7–19.

Nylander JAA, Wilgenbusch JC, Warren DL, et al. 2008. AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24: 581–583.

Ono Y. 1984. A monograph of Maravalia (Uredinales). Mycologia 76: 892–911.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Savile DBO. 1971. Coevolution of the rust fungi and their hosts. The Quarterly Review of Biology 46: 211–218.

Sawada K. 1913. Uromyces hyalosporus Sawada. sp. nov. causing the disease to the shoots of Acacia confusa Merrill. The Botanical Magazine 27: 16–20.

Scholler M, Aime MC. 2006. On some rust fungi (Uredinales) collected in an Acacia koa – Metrosideros polymorpha woodland, Mauna Loa Road, Big Island, Hawaii. Mycology Science 47: 159–166.

Stamatakis A. 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics: doi 10.1093/bioinformatics/btu033.

Stevens FL. 1925. Hawaiian fungi. Bernice P. Bishop Museum, Honolulu, USA.

Tamura K, Peterson D, Peterson N, et al. 2011. MEGAS: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28: 2731–2739.

Vialle A, Feau N, Allaire M, et al. 2009. Evaluation of mitochondrial genes as DNA barcode for basidiomycota. Molecular Ecology Resources 9: 99–113.

Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172: 4238–4246.

Walker J. 2001. A revision of the genus Atelocauda (Uredinales) and description of Racospermyces gen. nov. for some rusts of Acacia. Australasian Mycologist 20: 3–28.

White TJ, Bruns TD, Lee S, et al. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, et al. (eds), PCR protocols: a guide to methods and applications: 315–322. Academic Press Inc., San Diego, USA.

Winter G. 1886. Fungi Australiensis. Revue Mycologique 8: 207–213.